Chapter 1

Lotka-Volterra (Predator prey)

We consider time-dependent growth of a species whose population size will be represented by a function $x(t)$ (say greenflies!). If we assume the food supply of this species is unlimited it seems reasonable that the rate of growth of this population would be proportional to the current population size, as there are more potential couplings, *i.e.*

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax \Rightarrow x(t) = A\mathrm{e}^{at}. \tag{1.1}$$

with $a > 0$ the growth (birth ratio per person) and $A = x(0)$ the initial population size. The clear problem with this model is that the population grows without bound over time. One method to correct this problem one might specify that the the growth rate a becomes a function of the population size, decreasing as x increases. Alternatively we could model a second population $y(t)$ which represents a second species, ladybirds, which prey on the greenflies. In this case the greenfly population x will decrease proportionally to the number of ladybirds y multiplied by the number of greenflies x, *i.e.* the number of interactions of the two species which may lead to a sad little greenfly funeral. This law will be in the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax - bxy. \tag{1.2}$$

with b the rate at which fatal interactions occur. But we must then also model the changing Ladybird population $y(t)$. We assume in the absence of greenflies it will decrease as its food supply has vanished.

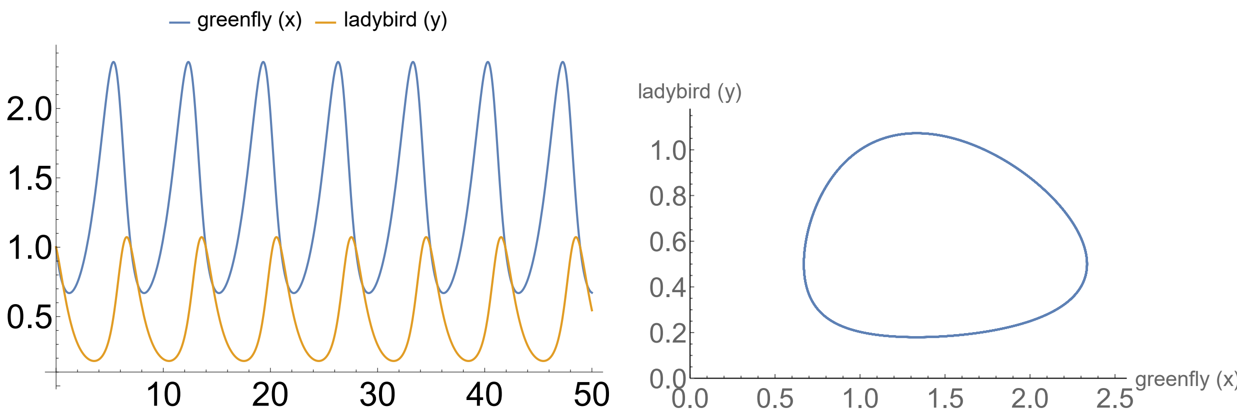
$$\frac{\mathrm{d}y}{\mathrm{d}t} = -c\,y. \tag{1.3}$$

However it will also grow proportionally to the interactions of the two species (at some rate d), so

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -c\,y + dxy \tag{1.4}$$

So we have a coupled set of ordinary differential equations

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= ax - bxy, \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -c\,y + dxy \end{aligned} \tag{1.5}$$



(a) (b)

Figure 1.1: (a) A plot of the solutions $x(t)$ and $y(t)$ for $t \in [0, 50]$, for the set $(a, b, c, d) = (2/3, 4/3, 1, 1)$, $x(0) = 1$, $y(0) = 1$. (b) the phase plot of (a).

This system represents both the individual growth/decay of the species (self interactions) as well as their mutual interaction. This is the so-called Lotka-Volterra (predator-prey) system discovered separately by Alfred J. Lotka (1910) and Vito Volterra (1926). In more modern theories there will be multiple species each with their own interactions but we will limit ourselves to this simpler but highly instructive classical system. An example solution is shown for the parameters $(a, b, c, d) = (2/3, 4/3, 1, 1)$, $x(0) = 1$, $y(0) = 1$ in Figure 1.1(a). We see the peaks in the greenfly population which then naturally increase the ladybird food supply, its population then increases. In turn this leads to the greenfly population dropping as they get eaten, then this decrease in food supply leads to the ladybird population to drop as food becomes competitive. This periodic behavior is made clear using a **Phase Plot**, as shown in Figure 1.1(b), in this case a parameterised plot $(x(t), y(t))$, a geometric plot of the variables of the system (2-D here as there are two variables). Closed curves in phase space indicate a periodic relationship between the two parameters.

1.0.1 Analysis and solutions

Parameter reduction

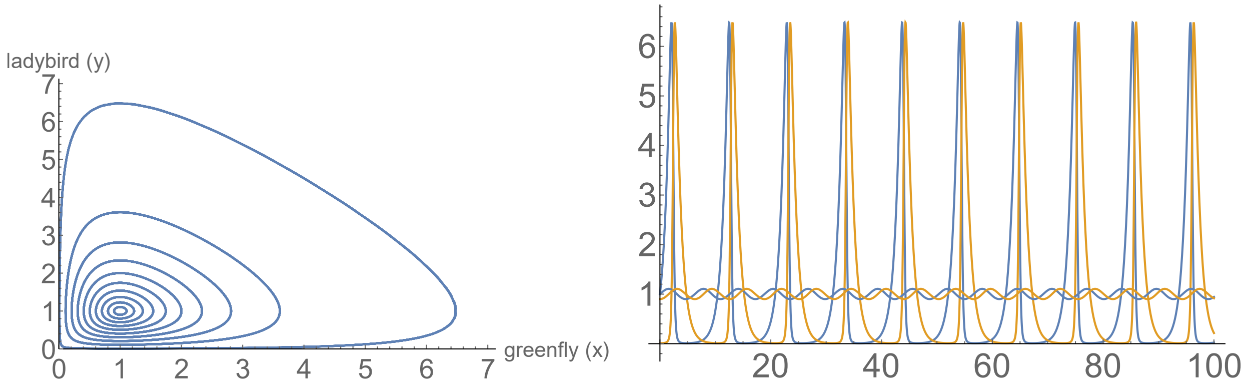
The parameters (a, b, c, d) play a key role in determining the system's behaviour. However, they are not all independent. If we make the transformations $x \to \hat{x}(c/d)$ and $y \to \hat{y}(a/b)$ and $t \to \hat{t}/a$ then the system can be written as

$$\frac{\mathrm{d}\hat{x}}{\mathrm{d}\hat{t}} = \hat{x} - \hat{x}\,\hat{y}, \tag{1.6}$$

$$\frac{\mathrm{d}\hat{y}}{\mathrm{d}\hat{t}} = \gamma(-\hat{y} + \hat{x}\,\hat{y}). \tag{1.7}$$

where

$$\gamma = c/a \tag{1.8}$$



(a) (b)

Figure 1.2: Phase and parametric solutions to the scaled Lotka-Volterra equation (1.6). (a) show phase curves for $\gamma = 1$, $\beta = 1$, $x(0) = 1$ and $y(0)$ a set of values from 0.01, the outer curve, to 0.9 the inner curve, all of which circle the equilibrium $x = y = 1$ with decreasing radius. (b) the parametric solutions for $y(0) = 0.01$, the sharp curves which peak ¿6, and $y(0) = 0.9$ the low amplitude sinusoidal curves.

Dynamic Solutions

We can solve this system using separation of variables, dividing the two equations (and dropping hats) we obtain

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\gamma y}{x}\left(\frac{-1+x}{1-y}\right). \Rightarrow \mathrm{d}y\frac{1-y}{y} = -\gamma \mathrm{d}x\frac{1-x}{x}. \tag{1.9}$$

Intergating both sides of (1.9) we obtain

$$\log(y) - y = -\gamma(\log(x) - x) + C. \tag{1.10}$$

Where the constant C can be set by some initial condition $(x(0), y(0))$. Unfortunately it is not possible to write this relationship in explicit form. This gives us the phase curves determined by the value of the constant C Parameterising this curve then gives the solutions $x(t)$ and $y(t)$, i.e. we could choose some behaviour for $x(t)$, (1.10) will then determine the behaviour of y. We will find this kind of solution is common to such systems.

In a homework sheet we will use this relationship to show that the phase curves must be closed curves.

Equlibria

Looking at the R.H.S of (1.6) we can see there are two possible equilibria $\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{\mathrm{d}y}{\mathrm{d}t} = 0, \forall t$

$$(x = 0, y = 0), \text{ and } (x = 1, y = 1) \tag{1.11}$$

(in dynamical systems you will call these fixed points or steady state solutions). The $x = y = 0$ solution corresponds to both populations being extinct! The second corresponds to the non-zero population densities at which the population sizes will remain fixed. In Figure 1.2(a) we see the varying behaviour of the closed curves phase curves of the system. All curves encircle the equilibrium at $(1, 1)$ and as the initial conditions get closer to the equilibrium value the radius of the curve decreases. In Figure 1.2(b) we see the dramatic variety of morphology the parametric curves can exhibit. When the pair $(x(0), y(0))$ are initially close to the equilibrium the curves have low amplitude sinusoidal shape, whilst if $y(0)$ is initially small the curves have extremely sharp gradients and dramatic rates of change at the maxima.

Stability ?

We have our dynamic solutions (1.10) and the fixed point equlibria (1.11). A number of questions begged to be asked at this point.

1. Can one or both of the species die out if they are both non-zero at some time t?

2. Can an oscillating pair of populations relax to their non-zero fixed values, *i.e.* do the populations ever settle?

An immediate observation in regards to (i) is that (1.10) only allows $x = 0$ when $y = 0$ and vice versa, so they would have to become extinct simultaneously. The existence of periodic solutions as shown in Figure 1.2 seems to suggest neither (i) or (ii) can occur, because the system repeats itself cyclically. A solution which decayed into equilibrium would have to have a phase space diagram which spiraled inwards. In fact we have a precise means of determining the answear to such questions which we discuss in the second chapter.

1.1 Summary

1. We have derived a simple model for a predator-pray relationship between two species based on simple interaction and growth models.

2. We have covered various standard tools for analysing such systems, dynamic solutions, equilibrium solutions, phase curves.

3. In addition we have raised the notion of stability and reachability of the equilibrium solutions. The phase curve behaviour we have observed appears to forbid reaching the equilibria form out-of-equilibrium states.

Chapter 2

Stability and the pendulum equation

In the previous lecture we asked if the Lotka-Volterra solutions could relax so the populations had fixed values, given they vary at some initial time. In order to answear this question we look at the behaviour of the system in the neighborhood of the fixed point equilibria. This is called a linear stability analysis. To give a clear picture of this technique, which we shall utilise continually in this course, we take a side step to look at a simpler system.

We consider a rigid pendulum, i.e. a bead if mass m attached to a rigid rod of length l Figure 2.1(a). The force under gravity g, given the rod makes an angle θ to the vertical is has two components $-mg\sin(\theta)$ along the (instantaneous) direction of swing $\frac{\mathrm{d}\theta}{\mathrm{d}t}$ and the component along the axis of the rod which is balanced by the rod's tension T balances the weight along its length. Finally there is a frictional force which we model as $\nu\frac{\mathrm{d}\theta}{\mathrm{d}t}$, with ν the coefficient of friction between the pendulum bead an the surrounding medium (*i.e.* air). The velocity is the change in arclength $l\theta$, $l\frac{\mathrm{d}\theta}{\mathrm{d}t}$ and hence the acceleration $a = l\frac{\mathrm{d}^2\theta}{\mathrm{d}t^2}$. Using Newton's law we have

$$F = ma \Rightarrow \frac{\mathrm{d}^2\theta}{\mathrm{d}t^2} + \frac{\nu}{m}\frac{\mathrm{d}\theta}{\mathrm{d}t} + \frac{g}{l}\sin(\theta) = 0. \tag{2.1}$$

This is a non linear O.D.E, our physical intuition tells us the systems basic behaviour the pendulum will swing with a decreasing amplitude until it relaxes to $\theta = 0$.

2.0.1 Analaysis

Dynamic solutions:

The damped pendulum system is not an integrable system, there are no general closed form solutions, this is generally the case for mechanical systems with friction. On the other hand numerical solutions are very simple to obtain. An example is shown in Figure (2.2)(a) the solution is indeed oscillatory with a decreasing amplitude. In (b) we see a Long pendulum with very high coefficient of friction (pendulum in fluid say) the damping is so strong that the angle never becomes negative, that is to say its motion is killed off on the first swing.

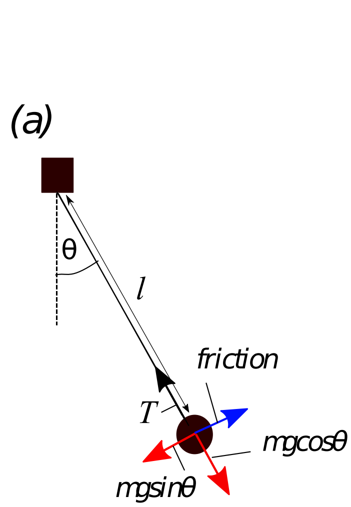


Figure 2.1: Schematic figures of the rigid pendulum model. (a) the geometry and forces are discplayed. (b) the unstable up-vertical $\theta = \pi$ solution.

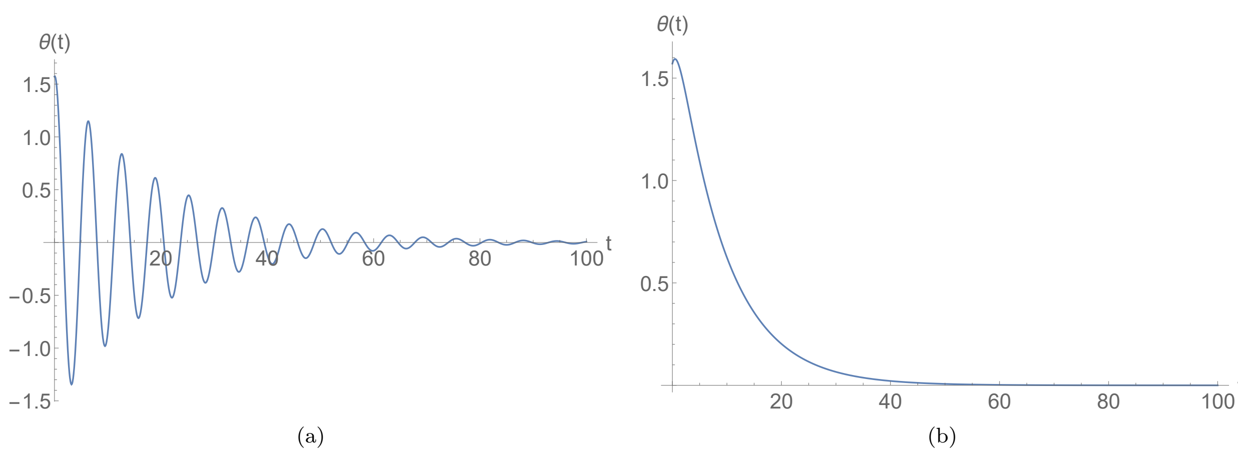


Figure 2.2: Solutions to the damped pendulum equation (2.1). (a) a solution which shows the swing cycles of the pendulum gradually decreasing in amplitude. (b) a heavily damped case where the swing is killed off on the first cycle.

Equilibria

Accounting for periodicity there are two equilibria. $\theta(t) = 0\,\forall t$ and $\theta(t) = \pi$ for all t, corresponding to the vanishing of the $\sin(\theta)$ term. The first $\theta = 0$ solution corresponds to a pendulum starting at the bottom of its cycle and not moving. The second solution is far more interesting, this is when the pendulum rod is vertically upwards as in Figure 2.1(b). The forces in the system are balanced as the rod tension balances gravity and the rotating moments are equal in either direction balance. But anyone ever trying to achieve such a balance would find, no matter how hard they try, it eventually fails and the pendulum starts to rotate back to its $\theta = 0$ equilibrium. Why? Any small variation in the pendulum, *i.e.* breeze or vibration in the rod, not matter how small, always grows over time. In practice no system is perfect and such variations always exist. Mathematically we represent small variations by a **linear stability analysis**.

2.1 Linear stability analysis

The basic steps of a linear stability analysis are as follows

1. Find the system's equlibria θ_0 (we have already done this).
2. Assume a value which is changed from this equilibrium value by a very small amount, $\theta = \theta_0 + \epsilon\theta_1$, with $\epsilon \ll 1$. This is supposed to mimic the small vibration in the system. Put this in the equation and retain only terms of order $\mathcal{O}(\epsilon)$, this the behaviour of the system equation where only small vibrations matter.
3. Solve this system to find out if θ_1, the small vibration, grows (like it would for $\theta_0 = \pi$) or decays (as it would for $\theta_0 = 0$).
4. Conclude that the equilibrium is stable if we have decay (small vibrations would dissiapear) and unstable if they grow.

2.1.1 The order notation $\mathcal{O}$ and its use in stability analysis.

A function $g(x)$ is $\mathcal{O}(f(x))$ if

$$\lim_{\epsilon\to 0} \frac{g(x)}{f(x)} = C. \tag{2.2}$$

with C some **bounded constant**. So, for example $f(x) = \epsilon$ and $g(x) = C\epsilon$

$$\lim_{\epsilon\to 0} \frac{g(x)}{f(x)} = C, \tag{2.3}$$

so $C\epsilon$ is $\mathcal{O}(\epsilon)$. But if $f(x) = \epsilon$ and $g(x) = C\epsilon^2$

$$\lim_{\epsilon\to 0} \frac{g(x)}{f(x)} = 0. \tag{2.4}$$

So $C\epsilon^2$ is $\mathcal{O}(\epsilon)$. The fact that the constant is zero basically says when ϵ is very small, $C\epsilon^2$ is much smaller. On the other hand if $f(x) = \epsilon$ and $g(x) = C$

$$\lim_{\epsilon\to 0} \frac{g(x)}{f(x)} = \infty. \tag{2.5}$$

So C is in some way much bigger than ϵ when $\epsilon \to 0$, we would say C is $\mathcal{O}(1)$ but not $\mathcal{O}(\epsilon)$.

Long story short: in what follow if something $\mathcal{O}(\epsilon^n)$ it is the same size or significantly smaller than ϵ^n when $\epsilon \to 0$.

[NEM The usual definition of $\mathcal{O}$ has $C > 0$ not C bounded. I used the above definition so I could say something like

$$1 + \epsilon + \frac{\epsilon^2}{2} + \frac{\epsilon^4}{24}. \tag{2.6}$$

is $1 + \epsilon + \frac{\epsilon^2}{2}$ to $\mathcal{O}(\epsilon^3)$, *i.e.* any difference between the two is **no bigger** than ϵ^3 (even though the ϵ^3 term might be zero). If I had chosen the $C > 0$ definition the difference would have been $\mathcal{O}(\epsilon^4)$. You should have no reason in this course to ever really have to worry about this distinction though.
]

We can apply this idea to functions, for example

$$g(x) = (x_0 + \epsilon x_1)^2 - (x_0^2 + 2\epsilon x_0 x_1), \quad f(x) = \epsilon \tag{2.7}$$

so

$$\lim_{\epsilon \to 0} \frac{g(x)}{f(x)} = 0. \tag{2.8}$$

So if ϵ is very small the effect of ignoring the $\mathcal{O}(\epsilon^2)$ term is negligible. The same holds for derivatives *i.e.*

$$g(x) = \left(\frac{\mathrm{d}x_0}{\mathrm{d}t} + \epsilon \frac{\mathrm{d}x_1}{\mathrm{d}t}\right)^2 - \left(\frac{\mathrm{d}x_0}{\mathrm{d}t}^2 + 2\epsilon \frac{\mathrm{d}x_0}{\mathrm{d}t}\frac{\mathrm{d}x_1}{\mathrm{d}t}\right), \quad f(x) = \epsilon, \tag{2.9}$$

so

$$\lim_{\epsilon \to 0} \frac{g(x)}{f(x)} = 0. \tag{2.10}$$

We can now apply this procedure to our pendulum equation, this is part (ii) of our linear stability analysis.

(ii) Linearisation

We assume the equilibrium solution θ_0 is changed to

$$\theta(t) = \theta_0 + \epsilon\theta_1(t). \tag{2.11}$$

with θ_1 the changing behaviour and $\epsilon \ll 1$ such that this is a vanishingly small change. Ignoring all $\mathcal{O}(\epsilon^2)$ terms we substitute (2.11) into (2.1) and expand to obtain

$$\frac{\mathrm{d}^2\theta_0}{\mathrm{d}t^2} + \frac{\nu}{m}\frac{\mathrm{d}\theta_0}{\mathrm{d}t} + \frac{g}{l}\sin(\theta_0) + \epsilon\left(\frac{\mathrm{d}^2\theta_1}{\mathrm{d}t^2} + \frac{\nu}{m}\frac{\mathrm{d}\theta_1}{\mathrm{d}t} + \frac{g}{l}\cos(\theta_0)\theta_1\right) + \mathcal{O}(\epsilon^2) = 0 \tag{2.12}$$

Note, to get the linear order of the $\sin(\theta)$ term we use a Taylor expansion. Say we have some function $f(\epsilon) = \sin(\theta_0 + \epsilon\theta_1)$, we expand

$$f(\epsilon) = f(\epsilon = 0) + \left.\frac{\partial f}{\partial \epsilon}\right|_{\epsilon=0} \epsilon + \mathcal{O}(\epsilon^2). \tag{2.13}$$

So for the function at hand this gives

$$\sin(\theta_0 + \epsilon\theta_1) = \sin(\theta_0) + \cos(\theta_0)\epsilon + \mathcal{O}(\epsilon^2). \tag{2.14}$$

The idea is that if $\epsilon \ll 1$ then (2.12) will basically give us the solution to the full system (if θ is very close to θ_0).

[NEM: This notion of "basically the same" can be made precise using a combination inverse function theorem and the contraction mapping theorem (this is for any non-linear O.D.E not just the pendulum equation), but this proof is beyond the scope of this course. Suffice to say we can show that we can choose a suitable ϵ is very small then the difference between the approximate solution and the actual solution is less than some value δ for any $\delta > 0, \forall t$.]

For what we need to know, we have chosen θ_0 to be an equilibrium value ($\frac{\mathrm{d}\theta}{\mathrm{d}t} = 0$, so the $\mathcal{O}(1)$ term vanishes), this gives $\cos(\theta_0) = \pm 1$, depending on whether we are looking at the $\theta = 0$ or π solutions. So to make (2.12) true we must solve

$$\frac{\mathrm{d}^2\theta_1}{\mathrm{d}t^2} + \frac{\nu}{m}\frac{\mathrm{d}\theta_1}{\mathrm{d}t} \pm \frac{g}{l}\theta_1 = 0 \tag{2.15}$$

(iii) Solve

The linear equation (2.15) is a constant coefficient linear ordinary differential equation. We thus seek solutions in the form $\mathrm{e}^{\lambda t}$. The general solutions are

$$\theta(t) = A\mathrm{e}^{-\frac{\lambda_1}{2}t} + B\mathrm{e}^{\frac{\lambda_2}{2}t}, \tag{2.16}$$

$$\lambda_1 = \sqrt{\left(\frac{\nu}{m}\right)^2 \mp 4\frac{g}{l}} + \frac{\nu}{m}, \quad \lambda_2 = \sqrt{\left(\frac{\nu}{m}\right)^2 \mp 4\frac{g}{l}} - \frac{\nu}{m}. \tag{2.17}$$

This will be subject to the boundary conditions $\theta_1 = \Delta(\theta)$, $\frac{\mathrm{d}\theta_1}{\mathrm{d}t} = 0$, some small change in angle and no initial velocity, so that this solution will only begin to change in time if the system allows so. The solution is then

$$\theta_1 = \frac{\Delta\theta}{\left(1 + \frac{\lambda_1}{\lambda_2}\right)}\left[\mathrm{e}^{-\frac{\lambda_1}{2}t} + \frac{\lambda_1}{\lambda_2}\mathrm{e}^{\frac{\lambda_2}{2}t}\right] \tag{2.18}$$

(iv) Asses stability

$\theta = 0$

For this case we have

$$Re\left(\sqrt{\left(\frac{\nu}{m}\right)^2 - 4\frac{g}{l}}\right) < \frac{\nu}{m} \tag{2.19}$$

so the real part of $\lambda_1 > 0$ and the real part of λ_2 is negative. Thus we see the solutions (2.18) must always decay exponentially. The physical interpretation of this is what we expected, around the bottom of the pendulum cycle $\theta = 0$ all small oscillations will decay to relaxation at $\theta_0 = 0$.

$\theta = \pi$

For this case

$$Re\left(\sqrt{\left(\frac{\nu}{m}\right)^2 + 4\frac{g}{l}}\right) > \frac{\nu}{m} \tag{2.20}$$

also λ_1 and λ_2 are both guaranteed to be real. Thus the term $\exp(\lambda_2 t/2)$ will grow exponentially. Again this matches our physical intuition and small oscillations about $\theta = 0$ will grow such that the pendulum moves away from the top of its arc.

2.1.2 The frictionless pendulum

If there is no friction $\nu = 0$ then our linearised solution would be

$$\theta_1(t) = A\mathrm{e}^{-\frac{\lambda}{2}t} + B\mathrm{e}^{\frac{\lambda}{2}t}, \tag{2.21}$$

$$\lambda = \sqrt{\mp 4\frac{g}{l}}, \tag{2.22}$$

$$\theta_1 = \frac{\Delta\theta}{2}\left[\mathrm{e}^{-\frac{\lambda_1}{2}t} + \mathrm{e}^{\frac{\lambda_2}{2}t}\right] \tag{2.23}$$

If $\theta = 0$ λ is pure imaginary and the solutions are just sinusoidal oscillations which do not decay in time. If $\theta = \pi$ then λ_1 and λ_2 are real and the second exponential will grow exponentially.

The $\theta = 0$ case is interesting in that it tells us that any small oscillation will be maintained, this is neither stable or unstable. In fact in the case $\lambda = 0$ the equation (2.1) is integrable (its solutions can be written in terms of Elliptic integrals) and the solutions are oscillatory with constant amplitude, that is to say if there is no friction there is no reason for the swings of the pendulum to decay.

The growth instability of the $\theta = \pi$ solution and the periodic nature of the system's solutions (it is possible to prove the periodicity) highlights a second issue. The linearised solutions (exponential growth) often tell us little about the full non linear behaviour of the system (periodic), it just so happens in this case the divergence between the full and linear solutions is rapid. We will not pursue this issue much further here as it is not important in what follows.

2.2 Summary

1. To test the feasibility (stability) of equilibrium solutions we linearise the equation about the equilibrium state

2. We analyse the solutions for exponential decay or growth, if there is only decay then the solution is stable in that it is resistant to small changes, if there is any growth it is unstable as small changes destroy the solution.

3. Some special systems will have neither growth nor decay, in this case we know form the non-linear behaviour of the frictionless $\lambda = 0$ pendulum equation, that this is because neighbouring solutions are periodic.

We can make these conclusions far more general.....

Chapter 3

General linear stability analysis for O.D.E's

3.1 n^{th} order O.D.E's to matrix of first order O.D.E's

We note that the expansion of (2.1) transformed a non-linear equation into a linear equation with constant coefficients. This will always be the case as any n product of functions $\{f_i\}_i^n$ will expand to linear order to give a linear term

$$(f_1^0 + \epsilon f_1^1 + \dots)(f_2^0 + \epsilon f_2^1 + \dots)\dots\left(f_n^0 + \epsilon f_n^1 + \dots\right) \tag{3.1}$$
$$= f_1^0 f_2^0 \dots f_n^0 + n\epsilon\left(f_1^1(f_2^0 \dots f_n^0) + \dots + \dots f_n^1(f_1^0 \dots f_{n-1}^0)\right) + \mathcal{O}(\epsilon^2).$$

from the binomial theorem. Also as we use the Taylor expansion the coefficients of this expansion would be evaluated at a fixed point (the equilibrium point in our application). Thus any sufficiently differentiable non-linear O.D.E can be expanded to linear order to yield a linear O.D.E equation.

In what follows we use the notation $x^{'n} = \frac{\mathrm{d}^n x}{\mathrm{d}t^n}$. Consider an non-linear n^{th} dimensional O.D.E. whose general form is

$$F(x(t), x', \dots, x^{'n}) = 0. \tag{3.2}$$

When expanded about the equilibrium solution x_0, $x = x_0 + \epsilon x_1 + \epsilon^2 x_2 + \dots$

$$F^0(x^0) + \epsilon\left(\frac{\partial F}{\partial x}x_1 + \frac{\partial F}{\partial x'}x_1' + \dots \frac{\partial F}{\partial x^{'n}}x_1^{'n}\right) = 0 \text{ to } \mathcal{O}(\epsilon^2). \tag{3.3}$$

If the ground state is in equilibrium ($F^0(x^0) = 0$) this reduces to a linear O.D.E with constant coefficients. We drop the subscript $x \equiv x_1$ for clarity in what follows. To find the general solution we write this as a series of first order O.D.E's as follows. First define $y_1 = x$, $y_2 = x', \dots, y_n = x^{(n-1)'}$, so that

$$y_1' = y_2,\, y_2' = y_3 \dots, y_{n-1}' = y_n, \quad y_n' = -\frac{1}{\frac{\partial F}{\partial x^{'n}}}\left(\frac{\partial F}{\partial x}y_1 + \frac{\partial F}{\partial x'}y_2 + \dots \frac{\partial F}{\partial x^{'(n-1)}}y_n\right). \tag{3.4}$$

The final equation is well defined as the coefficients $\frac{\partial F}{\partial x'^n}$ are constants. This can be written as a matrix equation in the form

$$\left(\begin{array}{c} y_1' \\ y_2' \\ . \\ . \\ y_n' \end{array}\right) = \left(\begin{array}{ccccc} 0 & 1 & . & . & 0 \\ 0 & 0 & 1 & . & . \\ 0 & 0 & 0 & . & . \\ 0 & 0 & 0 & . & . \\ -\frac{1}{\frac{\partial F}{\partial x'^n}}\frac{\partial F}{\partial x} & -\frac{1}{\frac{\partial F}{\partial x'^n}}\frac{\partial F}{\partial x'} & -\frac{1}{\frac{\partial F}{\partial x'^n}}\frac{\partial F}{\partial x'^2} & . & . \end{array}\right) \left(\begin{array}{c} y_1 \\ y_2 \\ . \\ . \\ y_n \end{array}\right) \tag{3.5}$$

as we will discuss the solution to the system is fairly straightforward.

3.1.1 General systems of O.D.E'S

Some systems such as the Lotka-Volterra (1.5) are already in matrix form . In general we will consider systems of the form

$$\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}t} = A\,\mathbf{y}. \tag{3.6}$$

With $\mathbf{y} = (y_1, y_2, \dots y_n)$ and A an $n \times n$ matrix. Generically the matrix A could have functional dependence on the vector $\mathbf{y}$, but we will consider the linearised system, that is writing $\mathbf{y} = \mathbf{y}_0 + \epsilon\mathbf{y}_1 + \dots$ and expanding (3.6) to $\mathcal{O}(\epsilon)$ we obtain

$$\frac{\mathrm{d}\mathbf{y}_0}{\mathrm{d}t} - A_0\,\mathbf{y}_0 + \epsilon\left(\frac{\mathrm{d}\mathbf{y_1}}{\mathrm{d}t} - A_1\mathbf{y_1}\right) = 0,\ \text{to } \mathcal{O}(\epsilon^2) \tag{3.7}$$

where A_0 is A evaluated at the equilibrium point and y_1 has entries $A_{1ij} = \sum_{i=1}^{n}\frac{\partial A y_i}{\partial y_j}$ (where $A\mathbf{y}$ is a vector given by the matrix product A acting on $\mathbf{y}$, this is easy to see with a little algebra, try the 2X2 case first). For example we can write the Lotka-Volterra system (1.6) as

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(\begin{array}{c} x \\ y \end{array}\right) = \left(\begin{array}{cc} 1 & -x \\ \gamma y & -\gamma \end{array}\right)\left(\begin{array}{c} x \\ y \end{array}\right) \tag{3.8}$$

In this case A_1 would be

$$A_1 = \left(\begin{array}{cc} 1-y & -x \\ \gamma y & \gamma(-1+x) \end{array}\right). \tag{3.9}$$

In general we might have some system of equations of various orders. In the previous section we have shown how n^{th} order (linearised) systems can be written as an n by n system of matrix equations. So we will always end up with a matrix equation in the form (3.6). In what follows A_1 will always represent the matrix of the linearised O.D.E.

3.2 Solving the system

Since it is not the primary focus of the course we will only skim over the details. The basic idea is that the solution to the linearised system

$$\frac{\mathrm{d}\mathbf{y}_1}{\mathrm{d}t} = A_1\mathbf{y_1}. \tag{3.10}$$

where, as discussed above A_1 is a matrix of constant terms, is

$$\mathbf{y}(t) = \mathrm{e}^{A_1 t}\mathbf{y}(0), \text{ where, } \mathrm{e}^{A_1 t} = \sum_{k=0}^{\infty} \frac{1}{k!} A_1^k t^k. \tag{3.11}$$

where A_1^k implies $A_1.A_1.A_1.A_1 \dots A$, the matrix product applied $k-1$ times. This is the matrix equivalent of the exponential. It then transpires one can always write the matrix exponential in the form

$$\mathrm{e}^{At} = \begin{pmatrix} e^{\lambda_1 t} & 0 & \dots & 0 \\ 0 & e^{\lambda_2 t} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & e^{\lambda_n t} \end{pmatrix} \tag{3.12}$$

Where the $\lambda_1, \lambda_2, \dots, \lambda_n$ are the eigenvalues of the matrix A. For the case in which our matrix A was obtained from an n^{th} order O.D.E (as shown above) this is is equivalent to saying the solution to the original single O.D.E was

$$x(t) = \sum_{i=1}^{n} C_i \mathrm{e}^{\lambda_i t}. \tag{3.13}$$

3.2.1 Growth modes

In order to find our solutions we need to find the eigenvalues of the matrix A_1, that is to say we need to solve

$$\det\left(A_1 - \lambda I\right) \tag{3.14}$$

with I the identity matrix. This of course leads us to solve a n^{th} order polynomial. The fundamental theorem of algebra guarantees n complex solutions. If just one of them has a real part which is positive then the solution will grow without bound. If $\mathrm{Re}(\lambda_i) < 0\,\forall i$ then the solution is stable (the technical term is asymptotically stable). If all of the solutions are purely imaginary then the system is stable but not asymptomatically stable (its doesn't decay). If you are taking the Dynamical systems course you will cover this topic in more depth. For what is required in this course however we really only really require the knowledge that there is growth or not. If there is growth then it is assumed the equilibrium solution will not exist as any small imperfection will be instantaneously magnified. Sometimes changing one parameter of the system will lead to a change from stability to instability and a system will suddenly change. It is this change which we will be interested in in later Chapters.

3.2.2 Example 1: the pendulum

The matrix of the pendulum equation would be

$$A_1 = \begin{pmatrix} 0 & 1 \\ \mp\frac{g}{l} & -\frac{\nu}{m} \end{pmatrix} \tag{3.15}$$

and the polynomial $\det\left(A_1 - \lambda I\right) = 0$

$$\lambda\left(\frac{\nu}{m} + \lambda\right) \pm \frac{g}{l} = 0. \tag{3.16}$$

The solutions for which are

$$\lambda_1 = \frac{1}{2}\left[-\frac{\nu}{m} + \sqrt{\left(\frac{\nu}{m}\right)^2 \mp 4\frac{g}{l}}\right]. \tag{3.17}$$

$$\lambda_2 = \frac{1}{2}\left[-\frac{\nu}{m} - \sqrt{\left(\frac{\nu}{m}\right)^2 \mp 4\frac{g}{l}}\right] \tag{3.18}$$

hence (2.18). The stability analysis detailed in the previous chapter then follows.

3.2.3 Example 2: Lotka-Volterra

In (3.9) we found the linear matrix A_1 for the Lotka-Volterra system. When evaluated at the equilibrium $x_0 = 0$ and $y_0 = 0$ the eigen-value polynomial (3.14) becomes

$$(1-\lambda)(\lambda+\gamma) = 0. \tag{3.19}$$

So one of the eigenvalues is positive and hence the system is unstable at this point. This tells us that neither population of the Lotka-Volterra system ever die! We should not be happy with this conclusion as real life populations can be made extinct.

The second equilibrium at $x_0 = 1$ and $y_0 = 1$ leads to an eigen-equation

$$\lambda^2 + \gamma = 0 \tag{3.20}$$

so $\lambda = \pm\sqrt{\gamma}\mathrm{i}$ and the solutions are pure imaginary. This tells us that system is neither asymptotically stable or unstable. But we knew this already as the solutions to (3.14) are periodic.

3.3 Summary

1. We have shown that the linearisation of non-linear n^{th} order O.D.E's can be written as an n-dimensional system of first order O.D.E's.

2. Further we have detailed the linearised version of more general systems of non-linear O.D.E's

3. The matrix exponential solution to these linear systems can be written as a diagonal matrix whose entries are in the form $\mathrm{e}^{\lambda_i t}$ where λ_i is an eigenvalue of A_1, the matrix of this linear system.

4. The stability can be assessed by solving $\det(A_1 - \lambda I) = 0$ and looking at the real part of all eigenvalues. If $\mathrm{Re}(\lambda_i) > 0$ for any i then the system is unstable, if $\mathrm{Re}(\lambda_i) < 0, \forall$ then it is stable, else if $\mathrm{Re}(\lambda_i) = 0$ the system does not decay (local periodic orbits), this is classed as instability in the sense that any small vibrations in the system will not dissapear.

Chapter 4

The competitive Lotka-Volterra equations

The absence of extinction in the classic Lotka-Volterra results from the fact that if population y drops close to zero, then x is subject to unconstrained growth which eventually leads to an increase in y stopping it from dropping to zero. A better model would be to include a notion of self-competition in the individual populations, *i.e.* we need a term which is small for small x allowing the population to grow, but dominates the growth term when x gets larger, thus restricting its growth. This should mimic some fixed constraint which limits a population through self-competition alone, for example a fixed food supply for species x. The simplest example of such a model (for a single population first) is the *Logistic equation*, originally introduced by Pierre-Francois Verhulst in 1838, the equation is non-linear and takes the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax\left(1 - \frac{x}{K}\right). \tag{4.1}$$

where $a > 0$ is the usual growth term and, as we shall see K is the limiting population. We see there is a non trivial equilibrium $x = K$. The term $1 - x/K$ is negative if $x > K$ and positive if $x < K$ so we might expect it to either decay towards K from above and up towards K if from below.

4.1 Dynamic solutions

We can separate (4.1)

$$\int \frac{\mathrm{d}x}{x(1 - x/K)} = at + C. \tag{4.2}$$

We can integrate the first integral using partial fractions, *i.e.*

$$\frac{1}{x(1 - x/K)} = \frac{1}{x} + \frac{1}{K\left(1 - \frac{x}{K}\right)}. \tag{4.3}$$

so that

$$\ln(x) - \ln(1 - x/K) = t + C. \Rightarrow \frac{x}{1 - x/K} = A\mathrm{e}^{at} \tag{4.4}$$

finally

$$x(t) = \frac{A\mathrm{e}^{at}}{1 + \frac{A}{K}\mathrm{e}^{at}} \tag{4.5}$$

so that in the limit $t \to \infty$, $x(t) \to K$, this is independent of the initial condition.

4.1.1 Stability analysis

This is unnecessary as we have seen all positive initial conditions decay to $x = K$. Thus the equilibrium $x = K$ will be stable as all small changes just relax back to $x = K$. In turn the equilibrium $x = 0$ will be unstable as any small positive changes from zero will end up at $x = K$. For you own sake I would test your understanding of the linearisation process by doing the linear analysis here.

4.2 The competitive Lotka-Volterra equations

The first change we might make is to assume the greenflies have some finite size food supply which replenishes. In this case we add a logistic term to the greenfly(x) equation of (1.5)

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= ax(1 - \frac{x}{k}) - bxy, \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -c\,y + dxy\end{aligned} \tag{4.6}$$

at this stage there is no need to do the same to the ladybird (y) equation, as its food supply is the greenflies.

4.2.1 Dynamic solutions

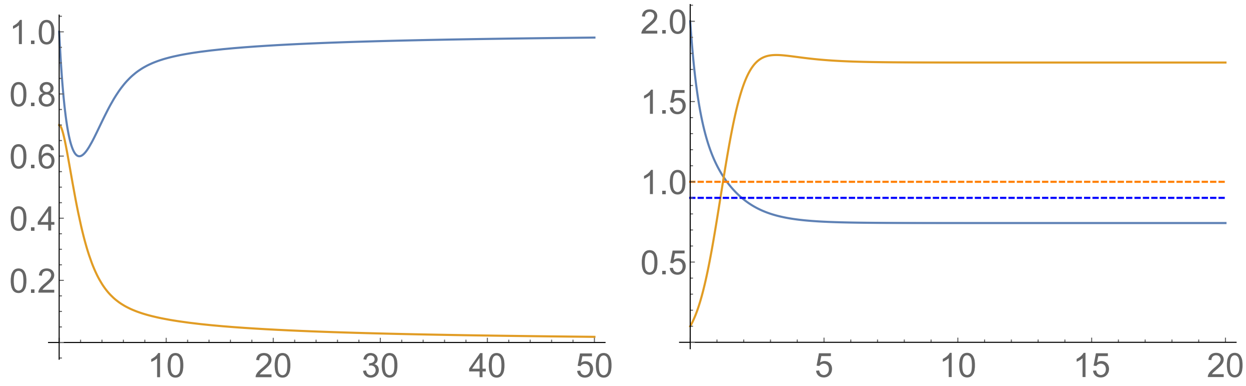
The system is not generally integrable but numerical solutions immediately indicate a problem with the system. We see in Figure 4.1(a) that the ladybird population decays to zero whilst its food supply is still active, this is typical of the system (4.6) and results from the fact that the decay of $y(t)$ is exponential whilst the logistic behaviour of $x(t)$, which limits its growth, cannot counter-balance as it does in the classical Lotka-Volterra (1.6).

4.2.2 A better model

Instead we impose logistic growth on both populations, and rely on the interaction to alter the behaviour of the system.

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= ax\left(1 - \frac{x}{\eta_1}\right) - bxy, \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= cy\left(1 - \frac{y}{\eta_2}\right) + dxy\end{aligned} \tag{4.7}$$

This has self-interaction for both species x and y, through the logistic terms, as well as mutual interaction through the xy terms. We non-dimensionalise by setting $x = \hat{x}\eta_1$, $y = \hat{y}\eta_2$, $t = \hat{t}/a$,



(a) (b)

Figure 4.1: Solutions to variants of the competitive Lotka-Volterra system. (a) only logistic behaviour for x, equations (4.6) , the ladybird population $y(t)$ decays to extinction. (b) both species have logistic behaviour, the dotted lines are the values the population would take in the absence of the interaction term.

$\gamma = b\eta_2/a$ and $\beta = d\eta_1/a$ and $\delta = c/a$. On substituting and dropping hats we obtain.

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x\,(1-x) - \gamma xy, \qquad (4.8)$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \delta y\,(1-y) + \beta xy$$

An example solution is shown in Figure 4.1(b), we see both populations eventually settle on fixed values, though the competition through the mutual competition terms γxy and βxy ensures these fixed values are not those of the logistic behaviour alone.

Species extinction

In Figure (4.2) we see a particular case for which the greenfly population becomes extinct, whilst the ladybird population settles at its Logistic level, *i.e.* the predator species dominates.

Equlibria

Equation (4.8) allows for the trivial null population solutions, but interestingly it also allows for solutions where one or the other populations is extinct.

$$x = 0 \quad y = 1, \text{ and } x = 1, \quad y = 0 \qquad (4.9)$$

so in both cases the non extinct population takes on its logistic value. The final equilibrium takes the form

$$x = \frac{\delta - \delta\gamma}{\delta + \gamma\beta}, \quad y = \frac{\beta + \delta}{\beta\gamma + \delta} \qquad (4.10)$$

Stability analysis

The Jacobian matrix A_1 takes the form

$$A_1 = \begin{pmatrix} 1 - 2x_0 - \gamma y_0 & -\gamma x_0 \\ \beta y_0 & \delta(1 - 2y_0) + \beta x_0 \end{pmatrix}. \tag{4.11}$$

The $x_0 = 0, y_0 = 0$ case leads to a polynomial

$$(1 - \lambda)(\delta - \lambda) = 0 \tag{4.12}$$

so the equilibrium is unstable as $\mathrm{Re}(\lambda_1 > 0)$. That is to say the two populations cannot die out simultaneously.

For the case $x_0 = 0, y_0 = 1$ the eigen-polynomial is

$$(1 - \gamma - \lambda)(-\delta - \lambda) = 0 \tag{4.13}$$

So $\lambda_1 = 1 - \gamma$ and $\lambda_2 = -\delta$. This is stable if $\gamma > 1$ (we assume $\delta > 0$), the requisite condition for the the predator to kill off the prey. The plots in 4.2(a) and (b) show the dynamic relaxation to the stable case (a) and the unstable case (b), for which both populations are non zero. The analysis of the $x_0 = 1, y_0 = 0$ case is left to the assignment.

The final equlibrium (4.10) leads to a somewhat more complex quadratic. In one of your problem sheets we shall show, that, under some reasonable physical assumptions, all initial conditions converge to a stable constant solution equilibrium, that is to say there are no periodic solutions, as is the case of the classical Lotka-Volterra system.

4.3 Reflections

We have introduced the notion of independent growth limitation on the individual populations to our system. We have done this through the Logistic model. The advantages of this are that we now have a model which allows one species to "win", in addition to cases where both populations settle on fixed values. But there are limitations to this model. The first is that we have lost the periodic/cyclic nature of the original Lotka-Volterra model (1.6), one famous well studied example is the relationship between snowshoe rabbits and the Canadian lynx (see Figure 4.2(b)). In the original model (1.6) the control of the greenfly and ladybird populations was mediated entirely by the xy interaction term. In our competitive model the populations are also self controlled by the logistic part of (4.8), which is independent of the interacting population, *i.e.* η_1 has no dependence on the size of y. A popular variation of the competition model is to make η_1 and η_2 depend on y and x respectively. This re-introduces the periodicity to the model, but still allows for extinction. In Chapter 12 we will encounter and example of a model which can do both.

[NEM There has been a significant body of work regarding extensions to the predator-pray model, including the above behaviour as well as extensions to n populations. For example 3 or more populations the system can show chaotic behvaiour. Well regarded mathematicians such as Stephen Smale and Morris Hirsch have proved some deep results regarding the asymptotic (limiting) behaviour of more general systems, however, these results are somewhat out of the scope of this course.]

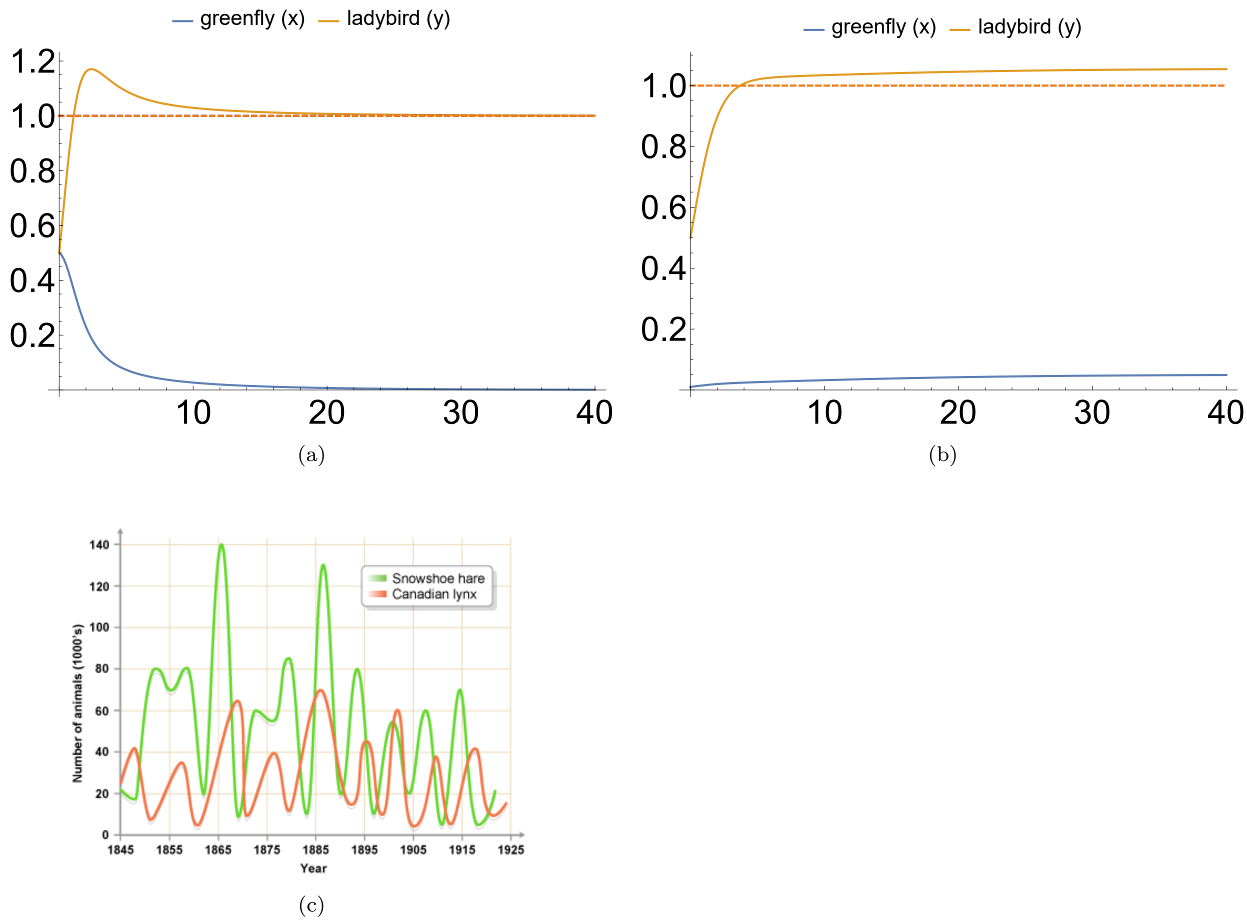


Figure 4.2: (a) Solutions to (4.8) for which the predator kills off the prey. (b) solutions for which the the equilibrium of (a) is unstable. (c) variations in the snowshoe hare/lynx populations, taken from here

4.3.1 Spatial behaviour

The main ingredient missing from these models is the absence of spatial dependence in the model. For example if the ladybirds and geenflies are originally in different parts of their ecosystem they cannot interact. But the interaction constants γ and β have no dependence on the position of the species, it just assumes they interact at a given frequency regardless. Our next aim must be to model the movement in space of the populations x and y. With this we turn to the notion of diffusion.

Chapter 5

Diffusion of populations

Modelling the behaviour of individual members of a species of a population is a significantly difficult task. How do we represent the motivation of each individual to move? The answer is intensive computational power, but even this is limited. Rather we concentrate on the bulk statistical behaviour of a large population. As a concrete example let us consider an "individual" on a line initially at a position zero and moving left or right in integer steps with a probability of moving left p and hence right of $(1-p)$, after n steps a path can be encoded as $LRLLRRR\ldots$. If we repeat this process a large number of times we get a set of paths, random walks. In Figure (5.1) we show five random walks of length 100 for $p = 0.5, 0.6$ and 0.9 respectively, here you see the individual paths, in (5.2) we see the same expect for 200 walks. For $p = 0.5$ the end positions are reasonably evenly spread about 0, for $p = 0.6$ the story is similar except that the spread is about the mean positions $n - 2np$ and the spread is not equal either side of this mean. This non-zero mean can be interpreted as a natural drift of the set of individuals all starting a the same point due to the probability bias.

[NEM In Figure (5.3) we see bar charts of the final displacement, where k L steps and $n-k$ R steps give a length of $k-(n-k)$, as a function of the total number of steps n for $p = 0.8$, a reasonably biased walk. As n increase the distribution becomes gradually more symmetric. Indeed since this is essentially a binomial distribution (with specific weighting) we should have expected this as we know that a Binomial distribution $B\tilde{(}n,p)$ approximates a normal distribution with mean np and variance $np(1-p)$ as n gets large. We shall shortly see the importance of this example.]

5.1 Continuum limit-Not examinable

In our course we will focus on the continuum limit of such a model. If rather than make the steps of size 1 we specify them to be $\mathrm{d}x$ which will be vanishingly small, and each step is taken in a time dt. We let $c(x,t)$ be the continous probability that, at a time t a particle (population member) reaches a displacement x at a time t. This implies that a a time $t - \delta t$ the particle must have been at either $x - \mathrm{d}x$ or $x + \mathrm{d}x$, so that

$$c(x,t) = pc(x - \mathrm{d}x, t - \mathrm{d}t) + (1-p)c(x + \mathrm{d}x, t - \mathrm{d}t) \tag{5.1}$$

If we expand this to $(O)(\epsilon^2)$, where $\epsilon = \max(\mathrm{d}t, \mathrm{d}x)$, we obtain

$$c(x,t) \approx c(x,t) - \frac{\partial c}{\partial t}\mathrm{d}t - (1-2p)\frac{\partial c}{\partial x}\mathrm{d}x + \frac{\partial^2 c}{\partial x^2}\frac{(\mathrm{d}x)^2}{2} + \frac{\partial^2 c}{\partial t^2}\frac{\mathrm{d}t^2}{2} + (1-2p)\frac{\partial c}{\partial t}\frac{\partial c}{\partial x}\mathrm{d}x\mathrm{d}t. \tag{5.2}$$

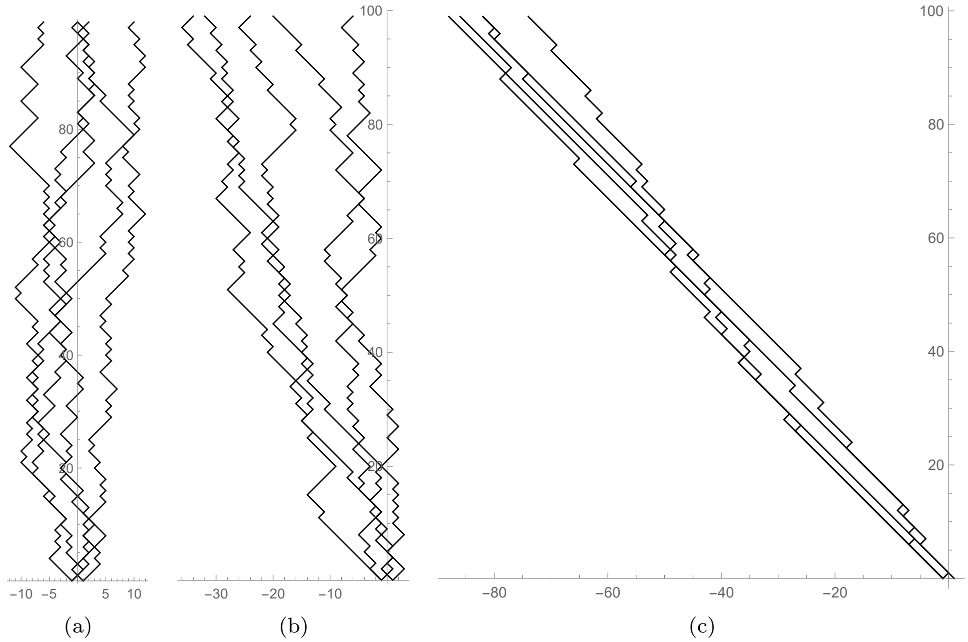


Figure 5.1: Five random walks with respectively (a) p=0.5, (b) p=0.6 and (c) p= 0.9. Position is on the horizontal axis and time the vertical axis.

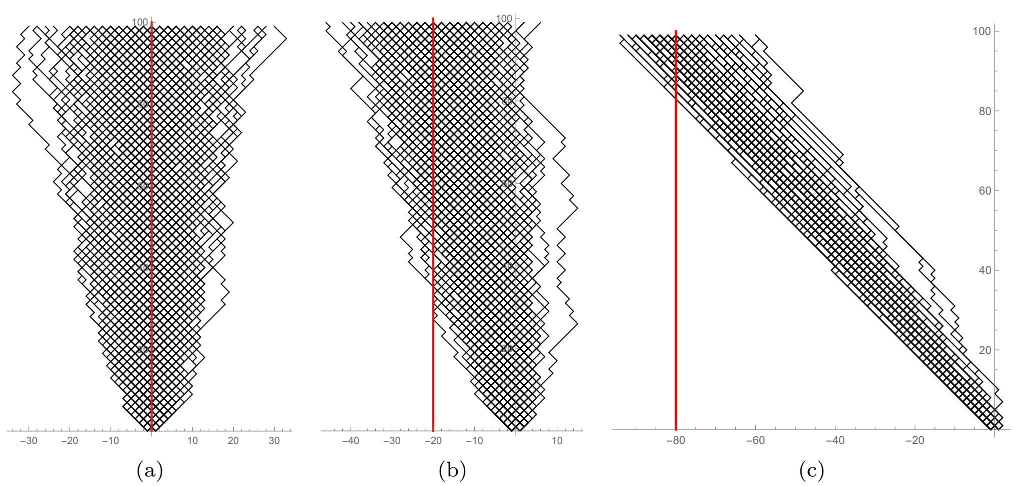


Figure 5.2: 200 random walks with respectively (a) p=0.5, (b) p=0.6 and (c) p= 0.9. Position is on the horizontal axis and time the vertical axis.

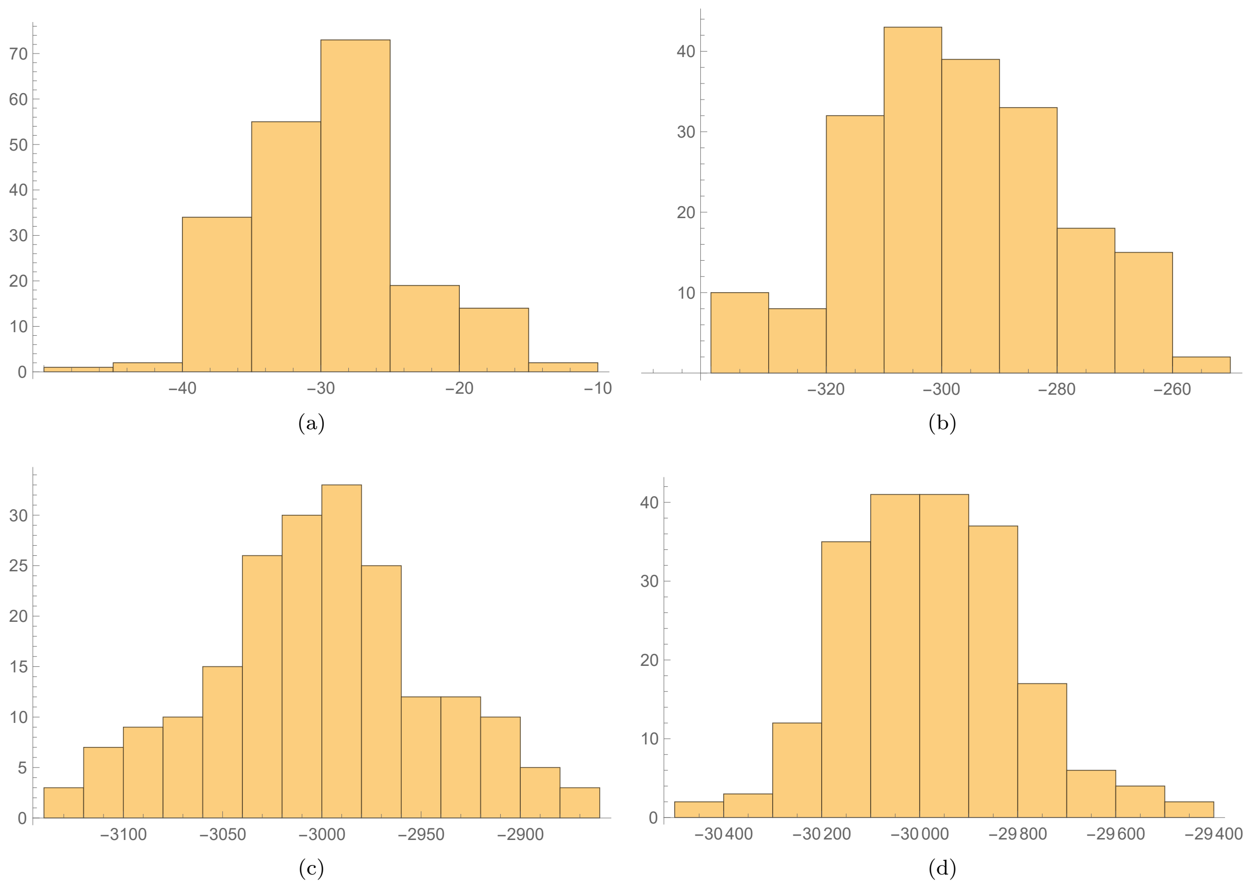


Figure 5.3: Histograms of final displacement (on the x-axis) for 200 random walks for p=0.8 for a walklength (a)50, (b)500, (c)5000 (d) 50000

so that to order $(O)(\epsilon^2)$ where $\epsilon = \max(\mathrm{d}t, \mathrm{d}x)$

$$\frac{\partial c}{\partial t} = (2p-1)\frac{\partial c}{\partial x}\frac{\mathrm{d}x}{\mathrm{d}t} + \frac{\partial^2 c}{\partial x^2}\frac{(\mathrm{d}x)^2}{2\mathrm{d}t} + \frac{\partial^2 c}{\partial t^2}\frac{\mathrm{d}t}{2} + (1-2p)\frac{\partial c}{\partial t}\frac{\partial c}{\partial x}\mathrm{d}x. \tag{5.3}$$

Taking the limit $dx \to 0$ and $dt \to 0$ the terms involving $\frac{\partial^2 c}{\partial t^2}$ and $\frac{\partial c}{\partial t}\frac{\partial c}{\partial x}$ will vanish. The coefficient $(1-2p)\frac{\mathrm{d}x}{\mathrm{d}t}$ has the dimensions of a velocity, so we set $\lim_{\substack{\mathrm{d}x\to 0\\ \mathrm{d}t\to 0}}(1-2p)\frac{\mathrm{d}x}{\mathrm{d}t} = v$ and we define a constant D

$$\lim_{\substack{\mathrm{d}x\to 0\\ \mathrm{d}t\to 0}} \frac{(\mathrm{d}x)^2}{2\mathrm{d}t} = D. \tag{5.4}$$

which we call *the diffusion constant* for reasons which will follow. Then we have

$$\frac{\partial c}{\partial t} = -v\frac{\partial c}{\partial x} + D\frac{\partial^2 c}{\partial x^2} \tag{5.5}$$

a partial differential equation determining the behaviour of $c(x,t)$. Note if $p = 1/2$ then there is no velocity, we shall come to associate this term with a drift. The physical description of the term D can be seen by deriving (5.5) in a continuum setting.

5.2 Advection diffusion equation, Examinable

Let S be a surface, surrounding a volume V containing a density $c(\mathbf{x},t)$, this could be a population density or maybe a chemical density. Basic conservation of mass has

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_V c(\mathbf{x},t)\mathrm{d}v = -\int_S \mathbf{J}\cdot\mathrm{d}\mathbf{S} + \int_V f\mathrm{d}V. \tag{5.6}$$

where $\mathbf{J}$ is the flow of $c(x,t)$ through a surface element $\mathrm{d}\mathbf{S}$ and f some source of $c(x,t)$ in the body V (ants coming up through the ground or a chemical reaction!). Applying the Liebniz rule to the time derivative on the left hand side we obtain

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_V c(\mathbf{x},t)\mathrm{d}V = \int_V \frac{\partial c}{\partial t}\mathrm{d}V + \int_S c(x,t)\mathbf{v}\cdot\mathrm{d}\mathbf{S} \tag{5.7}$$

Where $\mathbf{v}$ is the local velocity field of the changing shape of the surface S . Using the divergence theorem on the surface integrals we have

$$\int_V \left[\frac{\partial c}{\partial t} + \nabla\cdot(c\mathbf{v}) + \nabla\cdot J - f\right]\mathrm{d}V = 0. \tag{5.8}$$

If we assume $c(\mathbf{x},t)$ is sufficiently differentiable we can shrink V infinitesimally to obtain the general **Advection-Diffusion** law

$$\frac{\partial c}{\partial t} = -\nabla\cdot(c\mathbf{v}) - \nabla\cdot J + f. \tag{5.9}$$

In this case $\mathbf{v}$ is the velocity of motion of the concentration $c(\mathbf{x},t)$ at the point $\mathbf{x}$ and time t. The term $-\nabla\cdot(c\mathbf{v})$ is the Advection term, it is associated with motion of the concentration, and the term $\nabla\cdot J$ the diffusion (or diffusive flux), which is associated with the spreading out of the density.

In this form the equation is not complete (too many unknowns $f, \mathbf{v}, c, \mathbf{J}$ for one equation). So we have to make some further assumptions, these are called *constitutive laws.* For example lets say f is zero (no concentration creation or annihilation) $\mathbf{v}$ is constant, that is to say the concentration's centre of mass is moving with a constant velocity, and we assume *Fick's law*

$$\mathbf{J} = -D\nabla c \tag{5.10}$$

with D a constant so that

$$\frac{\partial c}{\partial t} = -\mathbf{v} \cdot \nabla c + D\nabla^2 c. \tag{5.11}$$

where $\nabla^2 c = \nabla \cdot \nabla c$ is the Laplacian operator. The one dimensional version of this equation is just (5.5), so we come to relate the velocity $\mathbf{v}$ with the probability drift. Now we have an equation for c alone which is complete.

Fick's law

Fick's law assumes that the density c moves from a region of high concentration to low. For example if we have a small (continuous) source of heat at the centre of a cold room this heat will gradually diffuse radially outwards to fill the room, until the room is at a constant temperature and the gradient vanishes. The constant, D, which has units of area per unit time is a measure of this expansion rate. The law was originally proposed by Adolf Fick whose experiments concerned the diffusion of salt through tubes of water. A more modern application is the diffusion of drugs in the vitreous body of the human eye. In all cases the diffusive material, a gas, salt chemical or population is composed of microscopic bodies which are in randomised motion, often colliding. Thus when confined to a small space the bodies will tend to move apart. We must stress that whilst diffusion does lead to motion, in the spreading of the body, it is different from the advection. Advection alone is movement of the concentration whilst the concentration area is held fixed. When $\mathbf{v} = 0$ (5.5) becomes the *Diffusion equation* (sometimes called Fick's second law).

The relationship between the probabilistic interpretation of random motion and Diffusion is further highlighted through the fundamental solution.

Chapter 6

The fundamental solution

In our thought experiment at the start of the previous chapter, represented by the random walks in Figure (5.2), we started with a large number of "particles" at a single point. Over time their random motion lead them to spread out, this is the diffusive element of the system. In the cases (b) and (c) the probability bias meant there was a net motion of the paths, in addition to the diffusive spreading. This is the equivalent of advective motion with the probability bias dictating its "velocity".

We try to replicate this as a continuous system by considering a point density at $x = 0, t = 0$. In a continuous setting we would represent this as a delta function

$$c(x, 0) = Q\delta(x) \tag{6.1}$$

where Q is the particle density and $\delta(x)$ is a function which is 1 if $x = 0$ and 0 otherwise. Such a function only exists as an integral but this is not critical in what follows. What you need to know is its definition is such that, for any function $f(\mathbf{x})$,

$$\int_V \delta(\mathbf{x} - \mathbf{s}) f(\mathbf{s}) \mathrm{d}\mathbf{s} = \begin{cases} f(\mathbf{x}) & \text{if } \mathbf{x} \in V, \\ 0 & \text{if } \mathbf{x} \text{ is not contained in } V. \end{cases} \tag{6.2}$$

We now seek to solve the problem

$$\frac{\partial c}{\partial t} = D\nabla^2 c, \quad c(x, 0) = Q\delta(x), \quad c(\pm\infty, t) = 0. \tag{6.3}$$

One way to solve this equation is to transform it using the Fourier transform.

6.1 The Fourier transform

The Fourier transform of a function $f(x)$, denoted $\mathcal{F}(k)[f(x)]$ is given by

$$\mathcal{F}(k)[f(x)] = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \mathrm{e}^{-\mathrm{i}kx} f(x) \mathrm{d}x. \tag{6.4}$$

its inverse $\mathcal{F}^{-1}(x)[g(k)]$, which is

$$\mathcal{F}^{-1}(x)[g(k)] = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \mathrm{e}^{\mathrm{i}kx} g(k) \mathrm{d}k. \tag{6.5}$$

Crucially it can be shown that

$$\mathcal{F}^{-1}[\mathcal{F}[f(x))]] = f(x). \tag{6.6}$$

I do not expect you to derive this result, merely be aware of it. The critical property of Fourier transforms which make them of use in solving P.D.E's is its effect on derivatives. The following result can be fairly easily demonstrated

$$\mathcal{F}(k)\left[\frac{\partial^n c}{\partial x^n}\right] = (\mathrm{i}k)^n \mathcal{F}(k)[f(x)] \tag{6.7}$$

Again I am not worried about you deriving this result, I just want you to know how to apply it.

6.2 Solving the problem

Applying (6.7) to the first of (6.3) we obtain

$$\frac{\partial \mathcal{F}(k)[c]}{\partial t} = -Dk^2 \mathcal{F}(k)[c] \tag{6.8}$$

So we have trasnformed a second order P.D.E into a first order O.D.E, its solution is clearly an exponential

$$\mathcal{F}(k)[c(x,t)] = \mathcal{F}(k)[c(x,0)]\mathrm{e}^{-Dk^2 t}. \tag{6.9}$$

With $\mathcal{F}(k)[c(x,0)]$ the To get the real space solution, we must apply the inverse operator, this is the price we pay for using the transform to simplify the system. This is not always straightforward, but in this case this is not so problematic. First we must find the initial condition $\mathcal{F}(k)[c(x,0)]$, which, from (6.2), is the Fourier transform of the Delta function,

$$\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} Q\delta(x)\mathrm{e}^{-ikx}\mathrm{d}x = \frac{Q}{\sqrt{2\pi}}. \tag{6.10}$$

Thus our final solution is

$$c(x,t) = \mathcal{F}^{-1}[\mathcal{F}(k)[c(x,t)]] = \frac{Q}{2\pi}\int_{-\infty}^{\infty} \mathrm{e}^{ikx}\mathrm{e}^{-Dk^2 t}\mathrm{d}k \tag{6.11}$$

In order to perform this integral we note the following known result

$$F(k)[\mathrm{e}^{-\alpha x^2}] = \frac{1}{\sqrt{2\alpha}}\mathrm{e}^{-k^2/4\alpha}, \tag{6.12}$$

(I will ask you to derive this in a homework problem), so that

$$c(x,t) = \frac{Q}{2\sqrt{\pi D t}}\mathrm{e}^{-x^2/4Dt}. \tag{6.13}$$

Ask yourself why I was able to use a forward transform $\mathcal{F}$ result for an inverse $\mathcal{F}^{-1}$ operation ?

So the density spreads out over time following a Gaussian distribution, as depicted in Figure 6.1.

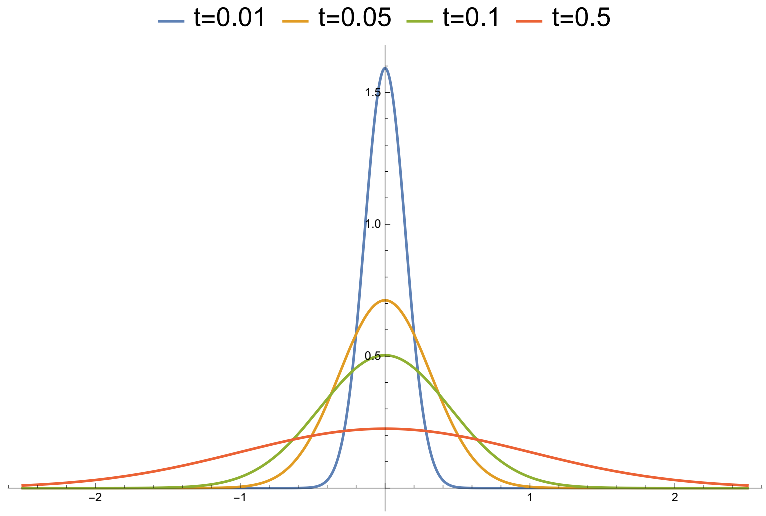


Figure 6.1: Plots of (6.13) for $D = Q = 1$, $x \in [-2.5, 2.5]$ for various values of t, we see the fairly rapid spreading of the distribution

6.2.1 Back to probability

As I remarked back in the last chapter, the limit of the random walk as the step size was reduced to zero was a Gaussian distribution. We then showed, using a slightly hand-wavy argument, that a limit of this distribution was the advection-diffusion equation. We have now squared the circle so to speak, in the sense that we have shown the diffusion equation gives Gaussian like spreading of a point source. In fact it was Einstein (and Marian Smoluchowski) who first made this link precise at the turn of the previous century.

6.2.2 Reflections on the model

There is one critical problem with the fundamental solution, the Gaussian distribution is always positive, so in theory the prediction is that there is always some small concentration infinitely far away form the source, for all t. This cannot be physically realistic (think of this as a population). On the other hand the density drops away exponentially so the actual density large distances away from the source will be negligible.

Chapter 7

Finite diffusion and spherically symmetric denstities

In order to solve the problem of infinitely fast travelling waves encountered in the previous chapter one proposition would be that the diffusion constant should be made dependent on the density, for example a popular assumption is that

$$D(c) = D_0 \left(\frac{c}{c_0} \right)^m . \tag{7.1}$$

for some $D_0 > 0$, $m > 0$. Thus as the density expands and its value drops (compared to its initial value) the diffusion rate also decreases, as we shall see this leads to a diffusive distribution with finite width. Rather than carrying on with the standard one dimensional case we instead turn to a radially symmetric two dimensional case. We will again ignore source terms $f \equiv 0$ and we shall assume no velocity $\mathbf{v}$ so only diffusive behaviour is present. We seek a fundamental solution, that is to say we are seeking a solution to the problem

$$\frac{\partial c}{\partial t} = D_0 \nabla \cdot \left[\left(\frac{c}{c_0} \right)^m \nabla c \right], \quad c(\mathbf{x}, 0) = Q\delta(\mathbf{x}), \quad c(\mathbf{x} \to \infty, t) = 0. \tag{7.2}$$

With $c(\mathbf{x} \to \infty, t)$ implying the distribution must eventually go to zero in all directions. In polar coordinates (r, θ)

$$\nabla c = \frac{\partial c}{\partial r} \hat{\mathbf{r}} + \frac{1}{r} \frac{\partial c}{\partial \theta} \hat{\theta}. \tag{7.3}$$

and for some vector $\mathbf{A} = A_r \hat{\mathbf{r}} + A_\theta \hat{\theta}$,

$$\nabla \cdot \mathbf{A} = \frac{1}{r} \left(\frac{\partial r A_r}{\partial r} + \frac{\partial A_\theta}{\partial \theta} \right). \tag{7.4}$$

If we assume $c(r, \theta, t) \equiv c(r, t)$, radial symmetry, then the right hand-side yields

$$D_0 \nabla \cdot \left[\left(\frac{c}{c_0} \right)^m \frac{\partial c}{\partial r} \hat{\mathbf{r}} \right] = \frac{D_0}{r} \frac{\partial}{\partial r} \left(r \left(\frac{c}{c_0} \right)^m \frac{\partial c}{\partial r} \right). \tag{7.5}$$

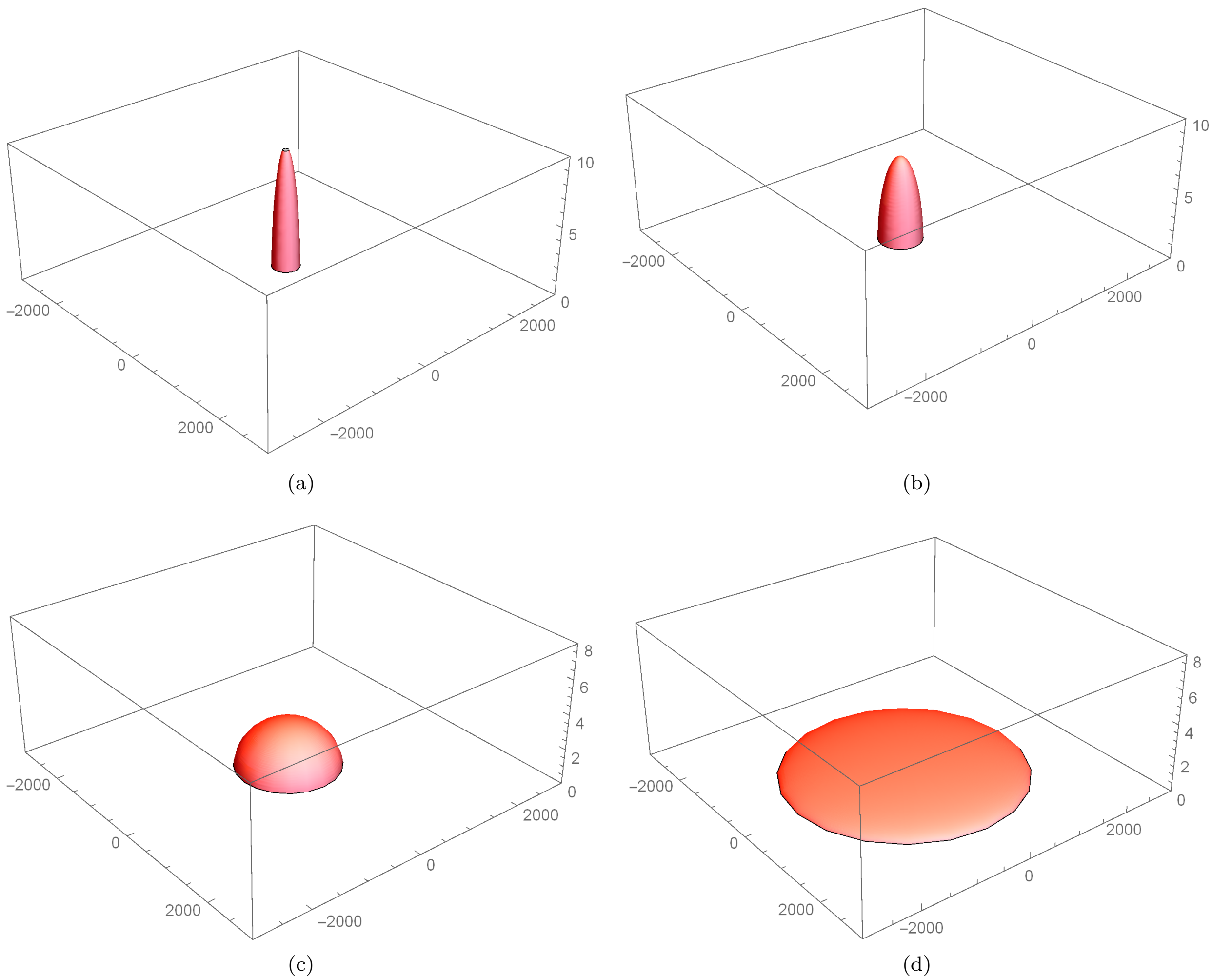


Figure 7.1: Examples solutions given by (7.6).

This is an example of the so called *Porus media equation.* You will be deriving the solution to (7.5) in your problem sheet. The solution is

$$c(x,t) = \begin{cases} \frac{c_0}{\lambda(t)} \left[1 - \left(\frac{r}{r_0 \lambda(t)} \right)^2 \right]^{1/m} & r \leq r_0 \lambda(t), \\ 0 & r \leq r_0 \lambda(t). \end{cases} \tag{7.6}$$

where

$$\lambda(t) = \left(\frac{t}{t_0} \right)^{1/(2+m)}, \quad t_0 = \frac{r_0^2 m}{2D_0(m+2)}, \quad r_0 = \frac{Q\Gamma(1/m + 3/2)}{\pi^{1/2} c_0 \Gamma(1/m+1)}. \tag{7.7}$$

Where $\Gamma(z)$ is the Gamma function. The solution has compact support (it is zero outside of a finite radius), this is a common property of hyperbolic P.D.E's. The volume Q is conserved and we see in Figure (7.1) the solution spreading out over time.

Chapter 8

Green's method

I'm sure the interested reader has wondered why we keep talking about the "fundamental solution", i.e. a Delta function which spreads out over time? In general we might have some **Linear** differential operator L. When acting on a function $u(\mathbf{x})$ we want to solve the following initial value problem on a domain V with boundary ∂V,

$$Lu(\mathbf{x}) = 0, \quad u(\mathbf{x}, 0) = g(\mathbf{x}), \quad u_f(\partial V, t) = 0. \tag{8.1}$$

e.g., the diffusion equation operator is $L = \frac{\partial}{\partial t} - D\nabla^2$, so that

$$Lu(\mathbf{x}) = \frac{\partial u}{\partial t} - D\nabla^2 u = 0. \tag{8.2}$$

The fundamental solution of L is defined as the solution to the following problem

$$Lu_f(\mathbf{x}) = 0, \quad u_f(\mathbf{x}, 0) = \delta(\mathbf{x}), \quad u_f(\partial V, t) = 0. \tag{8.3}$$

We can relate the two initial conditions by the delta-function identity

$$\int_V \delta(\mathbf{x} - \mathbf{s}) g(\mathbf{s}) \mathrm{d}\mathbf{s} = g(\mathbf{x}). \tag{8.4}$$

We now propose that the following relationship holds

$$\int_V u_f(\mathbf{x} - \mathbf{s}) g(\mathbf{s}) \mathrm{d}\mathbf{s} = u(\mathbf{x}). \tag{8.5}$$

To see this we note that, as the domain of integration is fixed we can take the operator inside

$$\int_V Lu_f(\mathbf{x} - \mathbf{s}) g(\mathbf{s}) \mathrm{d}\mathbf{s} = Lu(\mathbf{x}). \tag{8.6}$$

Remembering that all derivatives in L will be with respect to $\mathbf{x}$ (8.1) and (8.3) ensure see both sides vanish. In addition, as $\lim_{t\to 0} u_f = \delta(\mathbf{x})$, we will obtain the right initial condition through (8.4) . Thus, solving 8.1 can be reduced to solving the fundamental problem (8.3), generally an easier task, then integrating (8.5) leaves us with the full solution. This can often be of benefit for analytic solutions and asymptotic approximations.

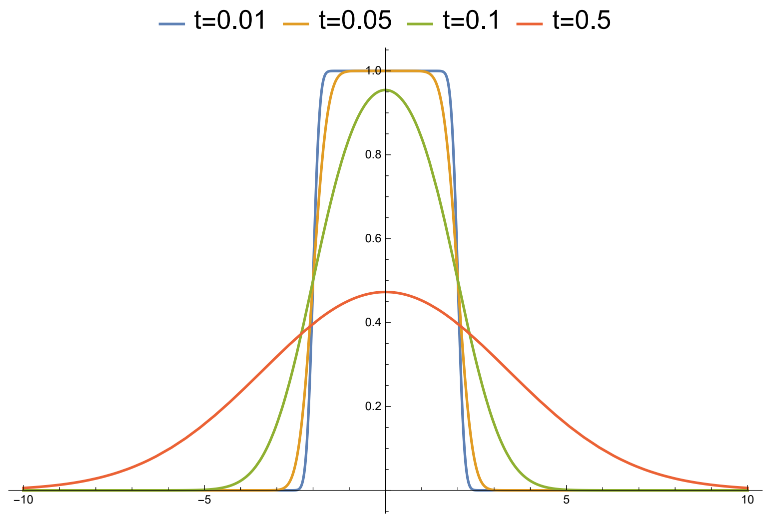


Figure 8.1: Solutions to the problem (8.7) with $D = Q = 1$ and $a = 2.5$ for various values of t

8.0.1 Example: The heat equation

Let us say we wish to solve the following problem.

$$\frac{\partial c}{\partial t} = D\nabla^2 c, \quad c(x,0) = \begin{cases} 0 & x < -a \\ 1 & a \leq x \leq a \\ 0 & x > a \end{cases}, \quad c(\pm\infty, t) = 0. \tag{8.7}$$

The initial condition is a "population" spread evenly over a domain $x \in [-a, a]$. Using the fundamental solution (6.13) and (8.5), the solution to the problem (8.7) is

$$c(x) = \frac{Q}{2\sqrt{\pi D t}} \int_{-a}^{a} \mathrm{e}^{-(x-s)^2/4Dt} \mathrm{d}s. = \frac{Q}{2}\left[\mathrm{erf}\left(\frac{a-x}{\sqrt{4Dt}}\right) + \mathrm{erf}\left(\frac{a+x}{\sqrt{4Dt}}\right)\right] \tag{8.8}$$

where

$$\mathrm{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x \mathrm{e}^{-s^2} \mathrm{d}s. \tag{8.9}$$

is the Error-Function, a function with well known properties. The solution is shown to vary with t in Figure 8.1.

8.0.2 This is only for linear systems

Step (8.6) does not generally work if the operator is non linear, e.g.

$$L[u] = \left(\frac{\mathrm{d}^2 u}{\mathrm{d}x^2}\right)^2 + u. \tag{8.10}$$

so

$$L\left[\int_{-\infty}^{\infty} u_f(x-s)g(s)\mathrm{d}s\right] = \left(\int_{-\infty}^{\infty} \frac{\mathrm{d}^2 u_f(x-s)}{\mathrm{d}x^2} g(s)\mathrm{d}s\right)^2 + \int_{-\infty}^{\infty} u_f(x-s)g(s)\mathrm{d}s. \tag{8.11}$$

Which is not necessarily zero. This unfortunately means the porous media fundamental solution cannot be used to solve general diffusion problems.

Chapter 9

Pursuit and Evasion in Predator-Prey

We are now in place to consider a predator-prey system with spatial dependence. This brings in the interesting possibility of pursuit of the two populations. We consider the following model

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_1\nabla^2 u + a_1 u(1 - b_1 u - c_1 v), \\ \frac{\partial v}{\partial t} &= D_2\nabla^2 v + a_2 v(1 - b_2 v - c_2 u).\end{aligned} \tag{9.1}$$

where the functions $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ have both spatial and temporal dependence. This is essentially the predator prey model used in Chapter 4, with the addition of diffusion (and hence spatial dependence). One can view this as two linked Advection-Diffusion equations

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_1\nabla^2 u + f_1(u, v), \\ \frac{\partial v}{\partial t} &= D_2\nabla^2 v + f_2(u, v).\end{aligned} \tag{9.2}$$

With neither having an advective term and the logistic growth/interaction terms acting as sources (they indicate growth and death). The system (9.2) is generally known as the reaction-diffusion system. We will be studying it exclusively hereafter. It is capable of a frankly staggering variety of behavior!

9.0.1 Non-Dimensionalise

We non dimensionalise by setting $\mathbf{x} = (D_1/a_1)^{1/2}\hat{\mathbf{x}}$, $t = \hat{t}/a_1$, $\kappa = D_2/D_1$, $\beta = a_2/a_1$, $\gamma_1 = c_1/b_2$, $\gamma_2 = c_2/b_1$, $u = \hat{u}/b_1$, $v = \hat{v}/b_2$ (and dropping hats) to get

$$\frac{\partial u}{\partial t} = \nabla^2 u + u(1 - u - \gamma_1 v), \tag{9.3}$$

$$\frac{\partial v}{\partial t} = \kappa\nabla^2 v + \beta v(1 - v - \gamma_2 u). \tag{9.4}$$

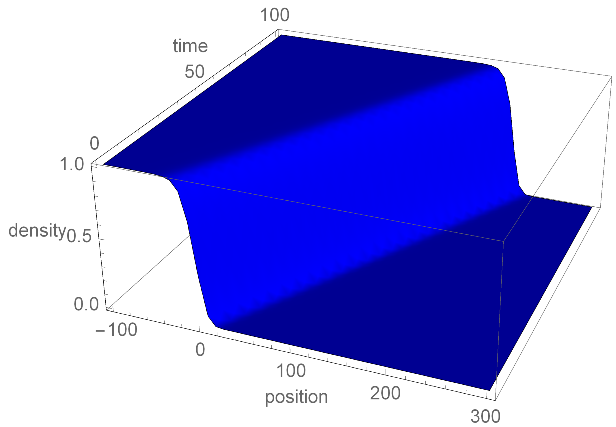


Figure 9.1: Travelling wave solutions to (9.3). (a) solutions to $w = u + v$ for position x and time t, the travelling wave nature of the solution is clear.

where $\gamma_1 < 1$ and $\gamma_2 > 1$ (this ensures) population u is the predator. Generally the system is not integrable and has to be treated numerically, though this is not necessarily a particularly arduous task as the system is quite well behaved. However, there are some special solutions which help to highlight certain aspects of the system's behaviour.

9.1 Dynamics : Pursuit solutions-Travelling waves

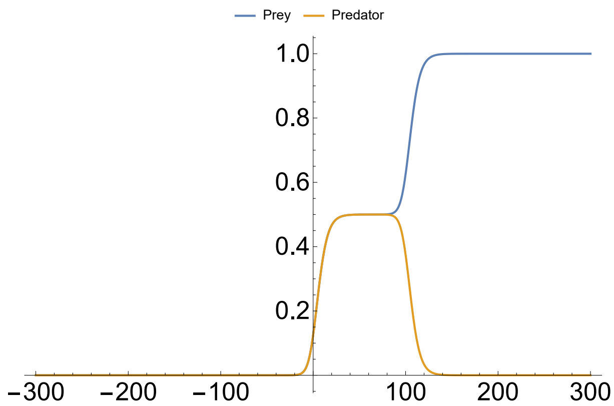
We focus on the one (spatial) dimensional case. We are going to seek a solution whose (x, t) dependence is in the form $x - ct$, *i.e.* a travelling wave solution, i.e. we look for functions $(u(z), v(z))$, $z = x - ct$. With this assumption (9.3) takes the form

$$\frac{\mathrm{d}^2 u}{\mathrm{d}z^2} + c\frac{\mathrm{d}u}{\mathrm{d}z} + u(1 - u - \gamma_1 v) = 0, \tag{9.5}$$

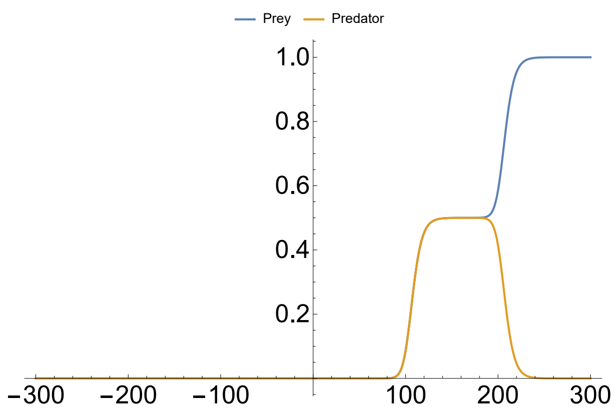
$$\kappa\frac{\mathrm{d}^2 v}{\mathrm{d}z^2} + c\frac{\mathrm{d}v}{\mathrm{d}z} + \beta v(1 - v - \gamma_2 u) = 0 \tag{9.6}$$

So now we have a system of O.D.E'S which give us the fixed shape of the system, the relationship $z = x - ct$ just means this behaviour moves at a constant velocity c in the x direction. We seek a solution with the boundary conditions $u = 0, v = 0$ as $z \to -\infty$ (total annihilation!), and $u + v = 1$ as $z \to \infty$, assuming $t \in [0, \infty)$ this implies that initially the populations are balanced at one end of the domain. In general it can be shown this system is not integrable, however, in the case $\beta = 1$ $\kappa = 1$ we can add the two equations to get

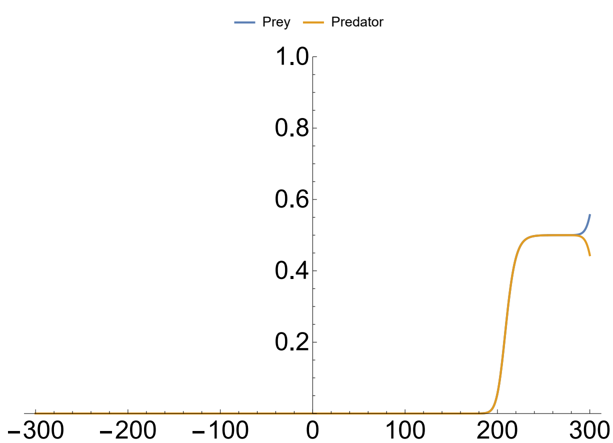
$$\frac{\mathrm{d}^2 u + v}{\mathrm{d}z^2} + c\frac{\mathrm{d}u + v}{\mathrm{d}z} + (u + v) - (u^2 + v^2) - (\gamma_1 uv + \gamma_2 uv) = \tag{9.7}$$



(a)



(b)



(c)

Figure 9.2:

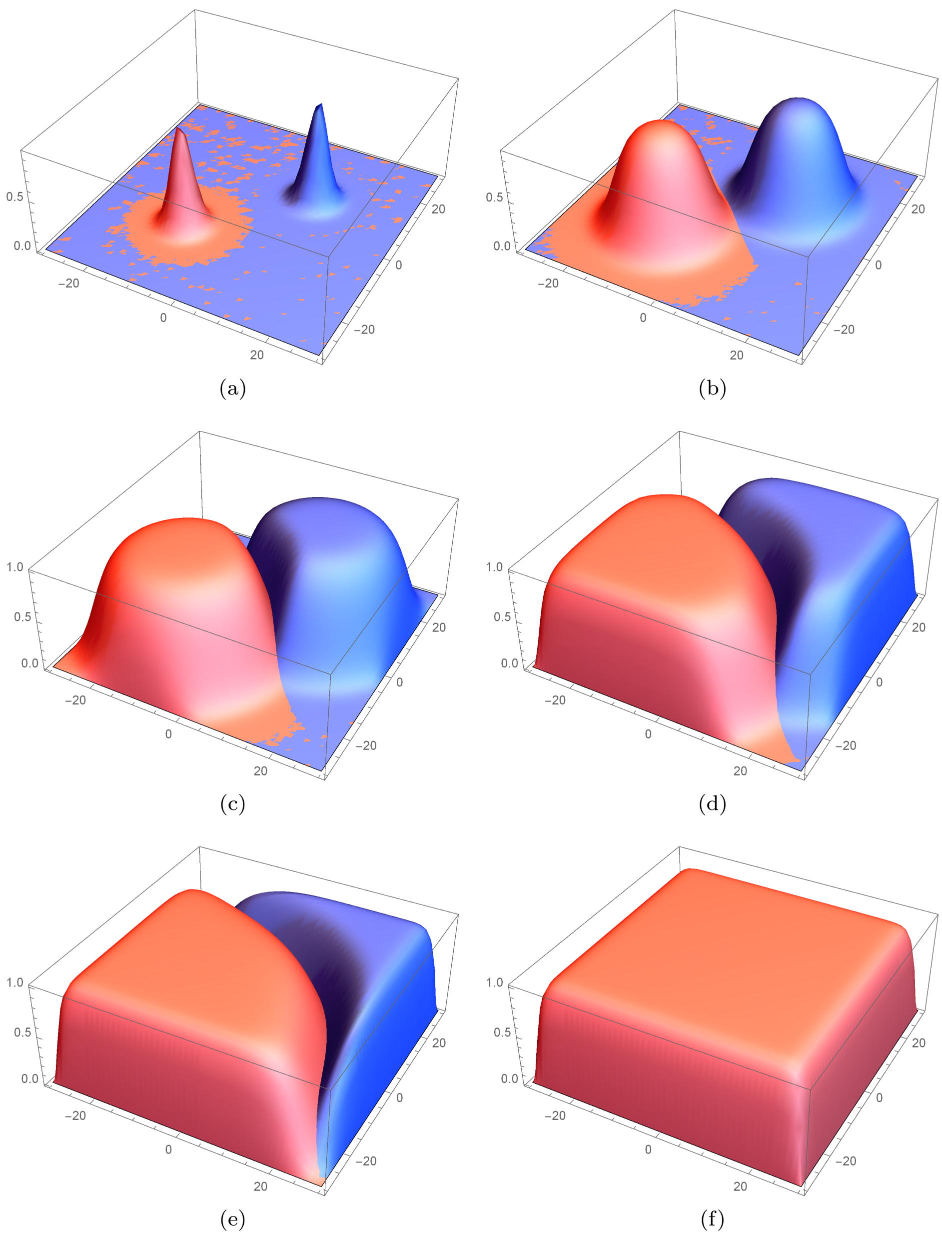


Figure 9.3: Snapshots of numerical simulations of solutions to 9.3 with a pair of Gaussian population peaks as initial conditions, the parameters are $\gamma_1 = 1.5$, $\gamma_2 = 0.5$ $\kappa = 1$ and (a) $t = 0$, (b) t=5, (c) t=10, (d) t=15, (e) t=20, (f) t=50.

so if $\gamma_1 + \gamma_2 = 2$ we have

$$\frac{\mathrm{d}^2 w}{\mathrm{d}z^2} + c\frac{\mathrm{d}w}{\mathrm{d}z} + w(1-w) = 0. \tag{9.8}$$

where $w = u + v$ subject to $w = 0$ at $z = -\infty$ and $w = 1$ at $z = \infty$. Even then it is difficult to find closed form solutions, it took 50 years after the equation was first proposed! Unfortunately the solution method is probably too far out of scope for the course (it uses complex analysis), we wish only to cover general techniques here so rather we just analyse the solution. If we make the assumption that $c = \pm 5/\sqrt{6}$, then the solution can be shown to be

$$w(z) = (1 + C\mathrm{e}^{-z/\sqrt{6}})^{-2}. \tag{9.9}$$

Where C is some constant value. An example solution for the positive root in (x,t) space is shown in Figure 9.1(a). The positional behaviour shows a sharp drop in density from 1 to 0, the centre of this drop is seen to move with a velocity $c = \pm 5/\sqrt{6}$ in time. To make this solution concrete we set

$$u(x,t) = \begin{cases} \frac{w(x+100+ct)}{2} + \frac{1}{2} & \text{if } x > 50 + ct \\ \frac{w(x+ct)}{2} & \text{if } x \leq 50 + ct. \end{cases} \tag{9.10}$$

(using the negative branch) At $t = 0$ the prey u is dominant until $x = 100$ where a "bump"-like predator population exists (the sum must be one). there is s brief domain where the populations are equal and then the populations drop off. This balanced region then moves with the wavefront speed $c = \pm 5/\sqrt{6}$ (b) and (c), effectively the predator bump is moving in the positive x direction and killing of the prey as it goes. This is sometimes referred to a a pursuit solution, but I am not quite sure this is the correct term, its more like the predator moving through a prey population devouring it as it goes. Note, that this solution does not reach any form of equilibrium in a finite time.

In Figure 9.3 we see snapshots of a numerical simulation of the system (9.3), whose initial conditions are two Gaussian populations which diffuse and interact.The boundary conditions are that both populations are zero on the boundary. From (a)-(b) the populations diffuse and begin to interact. In (c)-(e) we see the predator gradually out-competing its pray. This ends with the prey becoming extinct (f). This case **does** lead to a finite-time equilibrium.

9.2 Equilibrium

Equilibrium solutions require we solve the following system.

$$\begin{aligned} \nabla^2 u &= -u(1 - u - \gamma_1 v), \\ \nabla^2 v &= -\frac{\beta}{\kappa} v(1 + v - \gamma_2 u) \end{aligned} \tag{9.11}$$

This is a more complicated matter than in the non-spatially dependent (O.D.E) system as the choice of boundary conditions drastically affect what kind of solutions are permissible. As such we cannot be exhaustive here and I will instead present some interesting cases which highlight aspects of the system.

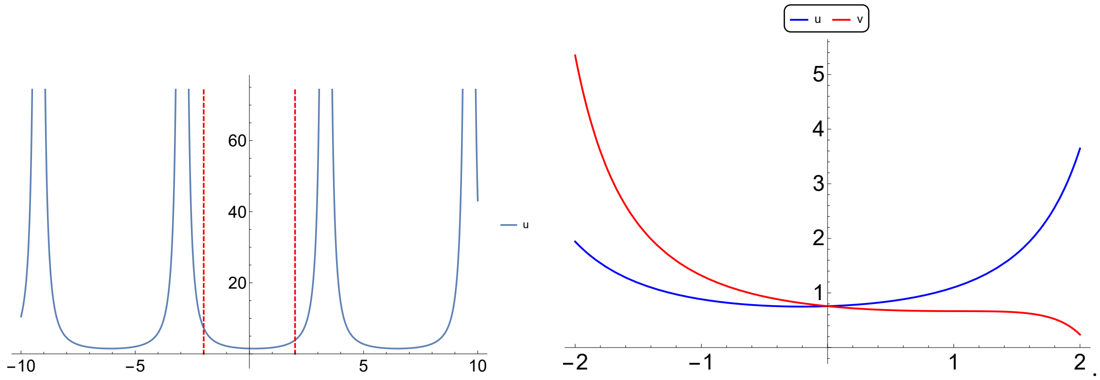


Figure 9.4: Solutions to the equilibrium equations (9.11). (a) is a single extinction solution to (9.12) with $C_2 = -0.1$. The dotted lines represent some imagined boundary. (b) is a solution to 9.20 where $u = \mathrm{e}^{-x^2}$ and $A = 1$.

9.2.1 Single extinction

We can have solutions which have the total extinction of one population *i.e.* $u = 0$, and

$$\nabla^2 v = -v(1 - v). \tag{9.12}$$

(for simplicity we assume $\beta/\kappa = 1$ (which is true up to a scaling in x). We should be clear that this is only true for boundary conditions on u where u and all its derivatives vanish at the boundaries of the system (be they finite or infinite). Any non zero boundary conditions for u clearly don't permit this. The simulation shown in Figure 9.3 satisfies such conditions and we see that the prey u indeed vanishes.

As for v, equation (9.12) allows for sets of equilibria which include the trivial solution and logistic solution $v(x) = 0, 1\,\forall x$, the same boundary as for u would apply then apply. But there are other non trivial solutions also. In one dimension we can make some progress. Multiplying 9.12 by $\frac{\mathrm{d}v}{\mathrm{d}x}$ we obtain

$$\frac{\mathrm{d}v}{\mathrm{d}x}\frac{\mathrm{d}^2v}{\mathrm{d}x^2} = \frac{\mathrm{d}v}{\mathrm{d}x}v(v-1) \Rightarrow \left(\frac{\mathrm{d}v}{\mathrm{d}x}\right)^2 = v^2\left(\frac{2}{3}v - 1\right) + C_1 \tag{9.13}$$

with C_1 a constant of integration. Thus we have a first order $O.D.E$

$$\frac{\mathrm{d}v}{\mathrm{d}x} = \pm\sqrt{C_1 + v^2\left(\frac{2}{3}v - 1\right)}. \tag{9.14}$$

and

$$\int \frac{\mathrm{d}v}{\sqrt{C_1 + v^2\left(\frac{2}{3}v - 1\right)}} = \pm x + C_2 \tag{9.15}$$

A special case, which has a fairly presentable solution is the case $C_1 = 0$, (requires $\frac{\mathrm{d}v}{\mathrm{d}x} = 0$ when

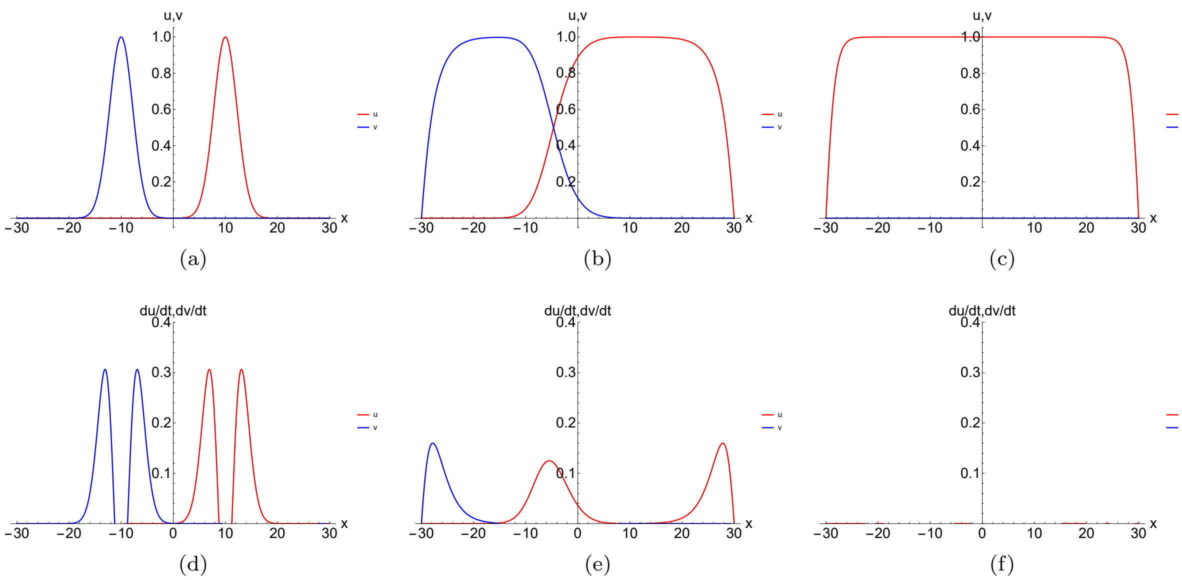


Figure 9.5: Plots of a simulation of (9.3) with Gaussian initial conditions (see panel (a) $t = 0$) for both the predator (v) and prey (u),the boundary conditions are for both populations to be 0. In (b) $t = 10$ and (c) $t = 100$ we see the predator gradually wins out. In (d)-(f) we see the velocities *derivut* and $\frac{\mathrm{d}v}{\mathrm{d}t}$ for the same times, in (f) the velocities have vanished, indicating the curves in (c) are in equilibrium.

$v = 0$ or $v = 3/2$).

$$\int \frac{\mathrm{d}v}{v\sqrt{\frac{2}{3}v - 1}} = \pm x + C_2 \tag{9.16}$$

Making the substitution $w^2 = \frac{2}{3}v - 1$, $\mathrm{d}v = 3w\,\mathrm{d}w$ we obtain

$$\int \frac{\mathrm{d}v}{v\sqrt{\frac{2}{3}v - 1}} = 2\int \frac{\mathrm{d}w}{1 + w^2} = 2\arctan(w) = 2\arctan\left(\sqrt{\frac{2}{3}v - 1}\right). \tag{9.17}$$

so

$$v = \frac{3}{2}\left[\tan^2\left(\pm x/2 + C_2\right) + 1\right]. \tag{9.18}$$

So we have one further boundary condition to impose. A plot of the function for $C_1 = -0.1$ is shown in Figure 9.4(a) along with some fictitious boundaries (the vertical red-dotted lines), i.e. we imagine this domain to be $x \in [-2, 2]$. We note that the constant C_2 only shifts the function along the x, axis it cannot scale the solution. So we cannot have this choice of C_1 and have bounded solutions for domains of larger size than 2π. Also (9.18) does not permit solutions which are anywhere zero. This is not a general conclusion. For example in Figure (9.3) we show the relaxation (solution to the full system 9.3) of two initial Gaussian populations u and v (panel (a)), subject to the boundary conditions $u(-30) = u(30) = v(-30) = v(30) = 0$. We see in(c) it has relaxed to a state where the prey is wiped out, $u = 0\forall x$, and the predator v has its spatially constant logistic value on most of the domain, except near the boundary. In (d)-(f) we plot the time derivatives $\frac{\mathrm{d}u}{\mathrm{d}t}$ and $\frac{\mathrm{d}v}{\mathrm{d}t}$ for same times as shown in the plots (a)-(c). By (c) the derivatives have vanished, indicating an equilibrium has been reached (it is also almost certainly stable). This solution satisfies the same boundary conditions as the $u = v = 0$ total extinction solutions, **this highlights possibility of multiple equilibria with the same boundary conditions**.

9.2.2 Co-existing Equilibria

Once again, we can have constant u and v solutions (requires zero derivative boundary conditions). These are simply the non-zero solutions to the Lotka-Volterra system as we have killed the diffusion terms, so

$$u(1 - u - \gamma_1 v) = 0, \text{and } v(1 - v - \gamma_2 u) = 0 \tag{9.19}$$

But there are also spatially varying equlibria. For example if we set $\gamma_1 + \gamma_2 = 2$ and $\beta/\kappa = 1$ then we can combine (9.11) to have

$$\frac{\mathrm{d}^2 w}{\mathrm{d}x^2} + w(1 - w) = 0, \quad w = u + v. \tag{9.20}$$

Which is the equation we solved above, of course in this case (9.18) would represent the sum $u + v$ and then fixing some function u, say, will fix v. We have to be careful in this scenario as we also want u and v to be positive and some choices of u might lead to non physical v. As an example we choose

$$w(x) = \frac{3}{2}\left[\tan^2\left(\pm x/2 - 0.1\right) + 1\right], \quad u(x) = w(x + 0.4). \tag{9.21}$$

The plots are shown in Figure (9.6). There are regions where the predator dominates and the prey dominates as well as in the central region where they are roughly equal.

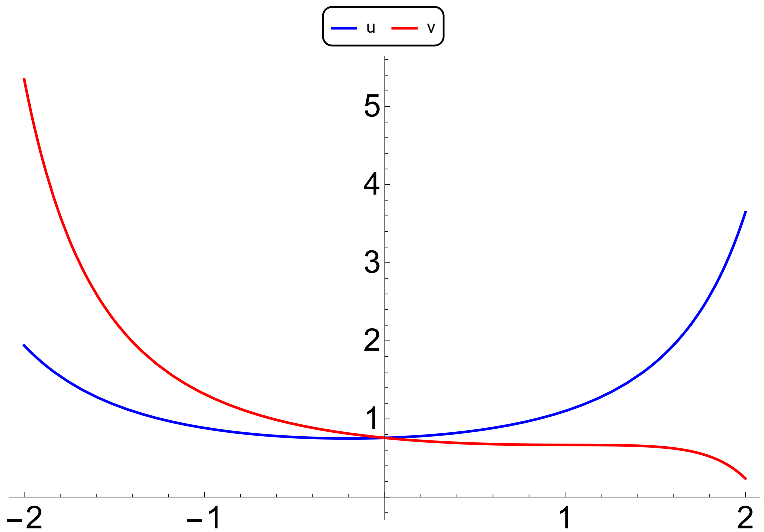


Figure 9.6: A spatially varing co-existingequlibrium of the system 9.3

Whilst by no means extensive, we have found a number of equilibrium solutions for our spatial-temporal predator-prey system (9.3). The question remains to ask, which if any of them are stable. In order to answer this question we are going to have to extend our notion of linear stability to Partial differential equations.

Chapter 10

Linear stability for P.D.E's - Euler Buckling and scale limited cows.

10.1 P.D.E stability is harder than O.D.E stability.

The question of stability for equilibrium solutions to partial differential equations is far more complex than for ordinary differential equation systems. This is primarily for two reasons

1. We have boundary conditions not just initial conditions as is the case for O.D.E's
2. The equlibria can be spatially dependent, as we shall see later in the year this generally means linearised sets of equations for which the coefficients aren't constant, this means we can't always assume a general form for the solutions. This was possible with the exponential form of the O.D.E case.

10.1.1 Homogenous equilibria

We introduce some terminology,

- **Equilibrium**: A function u is in equilibrium when all temporal derivatives $\frac{\partial^n u}{\partial t^n}$ vanish.
- **Homogeneity**: A function is homogeneous when all its spatial derivatives $\frac{\partial^n u}{\partial x_i^n}$ vanish.

Equilibria can have non-trivial spatial derivatives, as we saw in the last chapter. Also we can have homogeneous solutions which can grow in time out of equilibrium (if the boundary conditions allow). There exists a special class of equilibria, homogeneous equilibria which represent non-changing uniform densities/populations. Of course this is only permissible for a specific set of boundary conditions, namely that all derivatives vanish on the boundary of the domain. But there are very good number of scenarios where this is relevant, physically this really just says populations are required to stay within the given domain, such boundary conditions are commonly referred to as **no-flux**. For these types of equlibria the stability analysis is relatively straight forward. We start with a (relatively) simple example which has an interesting biological relevance.

The Euler Buckling Problem

We consider an thin tubular elastic body which is initially lined up along the $\hat{z}$ axis. It is subjected to a load N at one end and clamped at the other end. We assume its ends stay lined up along z as it is (possibly) deformed under the force and we monitor the deflection d from the $\hat{z}$ axis (see Figure 10.1). The equations of motion of this system can be shown to be

$$\frac{\partial^4 d}{\partial s^4} + \frac{N}{EI}\frac{\partial^2 d}{\partial s^2} + \rho A \frac{\partial^2 d}{\partial t^2} = 0. \tag{10.1}$$

with s the (arc)length along the tube, ρ the tube density A its cross-sectional area, E its Young's modulus (resistance to stretching) and I a moment of inertia (I don't expect you to derive this equation). The boundary conditions will be

$$d(0) = 0, \quad d(L) = 0, \quad \frac{\mathrm{d}d}{\mathrm{d}s}(0) = 0 \quad \frac{\mathrm{d}d}{\mathrm{d}s}(L) = 0\,\forall t. \tag{10.2}$$

So no deflection at either end and the derivative condition basically means it straightens out to wards the end of the beam (these are so-called "clamped conditions"). There is a trivial equilibrium solution $d_0(s) = 0\,\forall s$, which corresponds to the body remaining straight. Note this is true whatever the applied load N. However, our experience tells us the tube would give way under enough force. To ascertain when this would happen we perform a linear stability analysis using the same steps as in the O.D.E case

Find the equilibria

In this case we are only interested in the homogeneous equilibrium $d(0)$. I know from my own experience there are whole classes of inhomogeneous equilibria but we will not pursue them here.

Linearise the system

We expand out solution as $d(s,t) \approx d_0 + \epsilon d_1(s,t)$. This equation 10.1 is already linear with constant coefficients so the linearised equation is simply

$$\frac{\partial^4 d_1}{\partial s^4} + \frac{N}{EI}\frac{\partial^2 d_1}{\partial s^2} + \rho A \frac{\partial^2 d_1}{\partial t^2} = 0. \tag{10.3}$$

(it will not always be this easy !).

Solve the linearised system

We seek solutions which will either grow or decay in time, i.e. solutions in the form

$$d_1(s,t) = f(s)\mathrm{e}^{\lambda t}. \tag{10.4}$$

with λ the critical growth constant, then (10.3) reduces to

$$\frac{\partial^4 f}{\partial s^4} + \frac{N}{EI}\frac{\partial^2 f}{\partial s^2} + \rho A f(s)\lambda^2 = 0. \tag{10.5}$$

In essence this is an eigen-value problem for the operator

$$\frac{\partial^4 f}{\partial s^4} + \frac{N}{EI}\frac{\partial^2 f}{\partial s^2}. \tag{10.6}$$

Since the equation has constant coefficients we seek sinusoidally varying solutions in the form

$$f(k) = A\mathrm{e}^{iks}. \tag{10.7}$$

with k to be determined by out boundary conditions. This solution is assumed to satisfy the $d_1(0) = d_1(L) = 0$ (no further end deflection), this can only be satisfied for the sin part of $f(s)$ so we set $A = -\mathrm{i}$ and require

$$kL = n\pi \tag{10.8}$$

The derivatives are not required to be zero for these small perturbations and the change in value of the derivatives wouldl set the magnitude of A, the size of the mode of vibration (solutions of the form 10.7 are "vibrations" of the system, see Figure 10.1), but this will not be important to us here.

It might seem odd to use the complex wave function rather than say in this case cos or sin (it has even derivatives), but this is a more general solution and A can just be made imaginary to choose the sin solution. It is also handy where there are odd derivatives and a growth/decaying exponential is required for the solution (k cab have an imaginary part). It is standard practice to use this complex waveform, and since we never actually need to set the value of A (we are just interested in λ) it is easier to do so.

With this assumption for $f(s)$ we have

$$k^4 - \frac{N}{EI}k^2 + \rho A\lambda^2 = 0 \Rightarrow \lambda^2 = \frac{1}{\rho}k^2\left(\frac{N}{EI} - k^2\right). \tag{10.9}$$

10.1.2 Analyse stability

To obtain real λ we require

$$k^2 \leq \frac{N}{EI}. \tag{10.10}$$

and there are possible positive eigenvalues, thus system will be unstable as it grows in time. It would also appear that if $k^2 < \frac{N}{EI}$, that the solutions are imaginary, and hence the system is not asymptotically stable or unstable. But actually it is not possible for the solutions to satify the boundary conditions in this case. The solutions would be in the form

$$A\mathrm{e}^{i(ks+\nu t)}, \quad \text{where } \nu = \pm\frac{k}{\sqrt{\rho}}\sqrt{\left(k^2 - \frac{N}{EI}\right)}. \tag{10.11}$$

But $A\sin(ks + \nu t)$ cannot continually satisfy the boundary conditions; by having only imaginary λ we have killed the solution's ability to satisfy our constraints. Physically this is equivalent to saying the vibrations could not exist. Here we see the first example of the complexity of P.D.E stability by comparison to O.D.E stability.

So, using (10.10) and (10.8) we see that if the force N satisfies the following inequality

$$N \geq \frac{n^2\pi^2 EI}{L^2}. \tag{10.12}$$

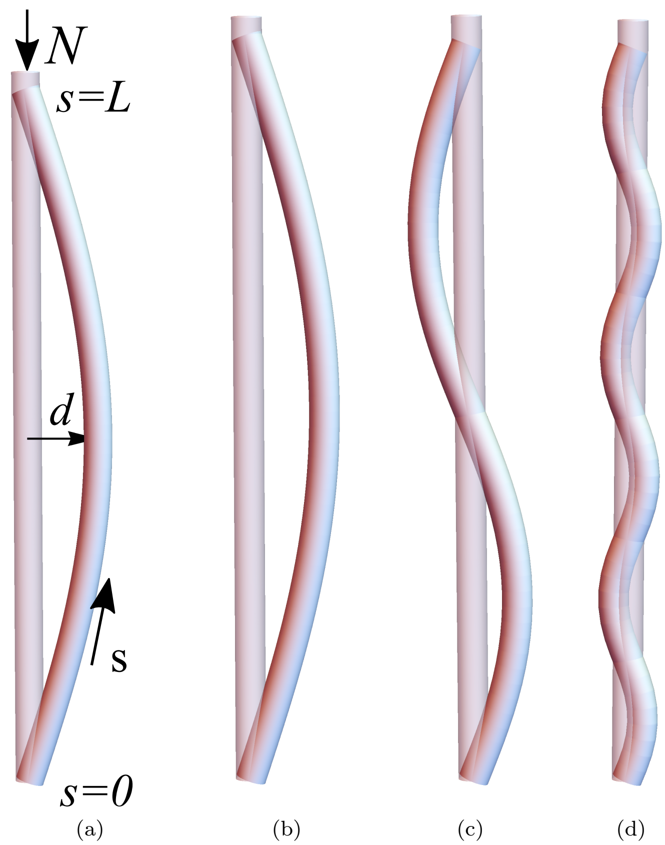


Figure 10.1: The tube model schematic (a) and various buckling modes of our elastic tube, (b) n=1, (c) n=2, (d) n=6.

then the initial $d = 0, \forall s$ solution is unstable and the beam will give way under the applied force N. The lowest force N for which this will be true is the $n = 1$ mode. So the minimum critical force N_c at which the loses stability is

$$N_c = \frac{\pi^2 EI}{L^2}. \tag{10.13}$$

this is a famous result due to Euler (though the way he derived it is a little different). It has actually been shown to have some biological relevance...

10.2 Cow buckling

Mammals tend to use their legs to support the force of their bodies. Let us imagine a cow with four cylindrical legs, for a cylinder I is $\pi R^4/4$; its main body (the meaty bit!) has a volume V and density ρ_c so that its weight is $\rho_c V g$. If we assume this weight (a load) is split equally amongst the four legs then

$$N = \rho_c V g/4 \tag{10.14}$$

Now, lets say we increased the dimensions of the animal by a factor a, we have

$$V_{new} = a^3 V \tag{10.15}$$

so the load on each leg grows cubically in the scaling a. Next we look at the critical force equation (10.13), the left hand side grows as

$$\frac{R_{new}^4}{L_{new}^2} = a^2 \frac{R^2}{L^2}. \tag{10.16}$$

under this scaling. The E is a material constant so N_c, the critical load under which the legs(beams) will give way scales as the square of a. So under this change in dimensions the size of the imposed force grows faster than the critical load N_c ; that is to say scaling up the animal increases the possibility that the animal's weight would cause its legs to give way, providing a possible explanation for why land mammals are limited in size, unlike sea mammals like whales. It has also been used as an explanation for the length to width scaling of animals as a function of their size, smaller animals (by mass) tend to be more slender tall and thin, whilst larger animals like elephants tend to be relatively wide with thick legs.

Chapter 11

Stability of the constant solutions to Lotka-Volterra

In this chapter we begin to generalise the P.D.E stability technique developed in the previous chapter by conducting a stability analysis of the Lotka-Volterra system given by (9.3).

Find the equilibria

Again we concentrate on homogenous equilibria, these are solutions to the equations

$$u(1-u-\gamma_1 v)=0, \text{ and } v(1-v-\gamma_2 u)=0. \tag{11.1}$$

We found all these solutions in Section 4.2.2.

Linearise the system

We linearise the Lotka-Volterra system by expanding the variables u and v about their equilibrium values u_0 and v_0, i.e. $u \approx u_0 + \epsilon u_1$ and $v \approx v_0 + \epsilon v_1$. To keep matters simple and consider a one-dimensional domain $[0, L]$. We impose the boundary conditions $u_1(0) = u_1(L) = v_1(0) = v_1(L) = 0$, the variations vanish at the boundary, so u and v keep their original boundary conditions. To $\mathcal{O}(\epsilon)$ we have

$$\begin{aligned}\frac{\mathrm{d}u_1}{\mathrm{d}t} &= \frac{\partial^2 u_1}{\partial x^2} + u_1 - 2u_0u_1 - \gamma_1(u_0v_1 + v_0u_1), \\ \frac{\mathrm{d}v_1}{\mathrm{d}t} &= \kappa\frac{\partial^2 v_1}{\partial x^2} + \beta\left(v_1 - 2v_0v_1 - \gamma_2(u_0v_1 + v_0u_1)\right).\end{aligned} \tag{11.2}$$

Solve the linearised system

Since the linear order equations are constant coefficient we seek solutions in the form $u_1 = A_u\mathrm{e}^{ikx+\lambda t}$ and $v_1 = A_v\mathrm{e}^{ikx+\lambda t}$. The boundary conditions require $kL = n\pi$ for $n = 1, 2, 3\ldots$. We cannot have non-zero u_1 and v_1 for the $n = 0$ case and satisfy the boundary conditions unless $A_1 = 0$ and the

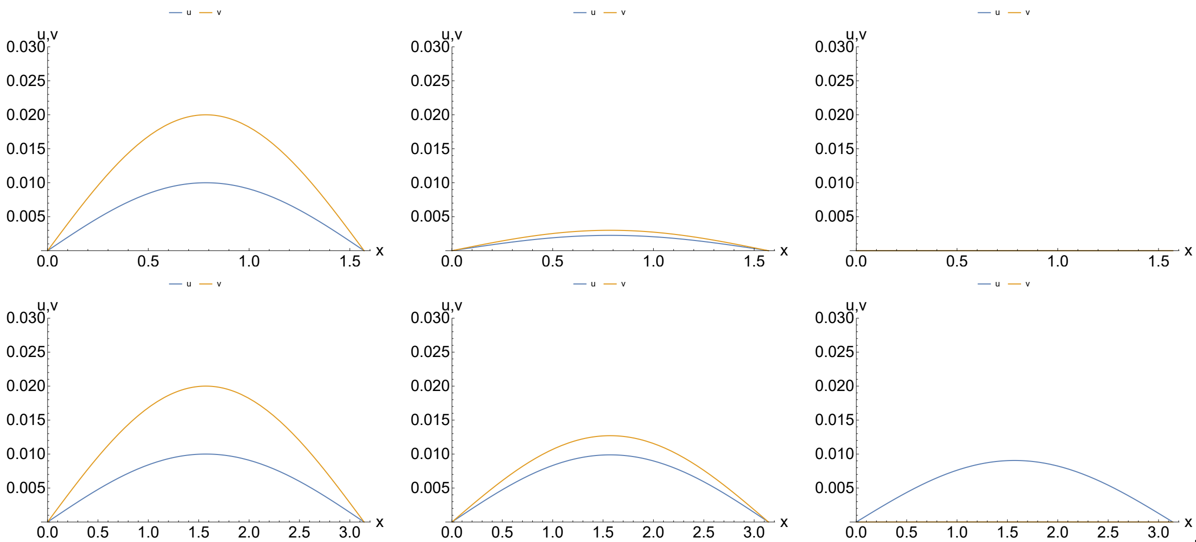


Figure 11.1: Two mode 1 perturbations of the system around $(u_0 = 0, v_0 = 0)$, the first (a)-(c) $t = 0, 0.5, 10$ respectively, is asymptoptically stable, the second (d)-(f) at the same times is not stable. The domain is doubled in size for the second case.

solutions are trivial. Substituting these forms into (11.2) we find

$$\begin{aligned} \lambda u_1 &= -k^2 u_1 + u_1 - 2u_0 u_1 - \gamma_1(u_0 v_1 + v_0 u_1), \\ \lambda v_1 &= -\kappa k^2 v_1 + \beta\left(v_1 - 2v_0 v_1 - \gamma_2(u_0 v_1 + v_0 u_1)\right). \end{aligned} \tag{11.3}$$

Note, that we could not have solutions in the form $u_1 = A_u \mathrm{e}^{ik_1 x + \lambda t}$ and $v_1 = A_v \mathrm{e}^{ik_2 x + \lambda t}$, with differing wave-numbers k_1, k_2, as the solutions would then be linearly independent and we could not achieve the required equality. We can write (11.3) as a matrix equation in the form

$$A_1 \mathbf{u} = \mathbf{0} \tag{11.4}$$

where $\mathbf{u} = (u_1, v_1)$, $\mathbf{0} = (0, 0)$ and

$$A_1 = \begin{pmatrix} -(\lambda + k^2) + 1 - 2u_0 - \gamma_1 v_0 & -\gamma_1 u_0 \\ -\beta\gamma_2 v_0 & -(\lambda + \kappa k^2) + \beta(1 - 2v_0 - \gamma_2 u_0) \end{pmatrix} \tag{11.5}$$

The fundamental theorem of linear algebra tells us that there are only non-trivial solutions $\mathbf{u}$ if $\det(A_1) = 0$, in essence we have the same problem as the O.D.E case, except that we must consider the domain of admissible k values.

11.0.1 Analyse stability

If we first look at the $(0,0)$ solution then we have a quadratic polynomial for λ in the form

$$a\lambda^2 + b\lambda + c = 0 \tag{11.6}$$

$$a = 1, \quad b = -1 - \beta + k^2(1+\kappa), \quad c = \kappa(k^2 - 1)(-\frac{\beta}{\kappa} + k^2), \tag{11.7}$$

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}. \tag{11.8}$$

The system **can** only be stable if $ac > 0$ (a necessary but not sufficient condition), which would require (taking the lowest mode)

$$(\pi/L) - 1 > 0 \text{ and } (\pi/L) - \sqrt{\frac{\beta}{\kappa}} > 0. \tag{11.9}$$

placing constraints on the possible length of the domain L for stable systems, to be

$$L < \pi \text{ or } L < \pi\sqrt{\frac{\kappa}{\beta}} \tag{11.10}$$

whichever is the smallest. If this is the then case we further require

$$-b = (\beta + 1) - k^2(1+\kappa) < 0 \tag{11.11}$$

to guarantee stability The $k^2(1+\kappa)$ term is positive definite as κ, the ratio of the diffusion constants, is positive (physically this must be the case for realistic diffusion), thus if

$$k^2(1+\kappa) > (\beta+1) \Rightarrow \frac{\pi^2}{L^2}(1+\kappa) > (\beta+1). \tag{11.12}$$

the system is asymptopically stable. We used the $n = 1$ mode as all other modes would give a condition which is satisfied of the $n = 1$ case is satisfied. A word of warning; **the n=1 case will not always give the critical equality, you must always check if it does or not**.

In Figure (11.1)(a)-(c) I show a numerical simulation of the full system (9.3) with the mode one perturbation given as an initial configuration for u. The parameters are $L = \pi/2$ and $\kappa = \beta = 1$, parameters which satisfy the stability criteria we derived above. It is shown to relax to the zero equlibrium as expected. I also simulated a case not asymptopically stable is shown in Figure (11.1)(d)-(f), I chose the domain size to be $L = \pi + 0.1$ just outside the required range for stability.

The effect of spatial behaviour and boundary condtions

This study shows clearly the difference brought about by the spatial behaviour of the system. For the system with no spatial dependence (4.8) the equlibrium $(0,0)$ was **always** unstable, whatever the parameters used, in this case we have some limited window of parameter stability, linked intrinsically to the domain size.

Next we consider the (0,1) prey extinction solution we have

$$a\lambda^2 + b\lambda + c = 0 \tag{11.13}$$

$$a = 1, \quad b = -1 + \beta + \gamma_1 + k^2(1+\kappa), \quad c = (\beta + \kappa k^2)\left(\gamma_1 + k^2 - 1\right), \tag{11.14}$$

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}. \tag{11.15}$$

First we can only have stable equilibria if $ac > 0$, fo which we require

$$\gamma_1 + (\pi/L)^2 > 1 \Rightarrow L < \frac{\pi}{\sqrt{1-\gamma_1}} \tag{11.16}$$

Again this places constaints on L, if $\gamma_1 \to 1$ there is no bound on the domain size, if $\gamma_1 > 1$ then the domain cannot be a real domain (we can never satisfy $ac > 0$). If this domain constraint is satisfied it is the sign of b which determines stability of the system. Here we require

$$\beta + \gamma_1 + k^2(1+\kappa) > 1 \Rightarrow \beta + \gamma_1 + \frac{\pi^2}{L^2}(1+\kappa) > 1 \tag{11.17}$$

For example if $\gamma_1 \to 1$ and $L \to \infty$ then β can take on any positive value.

11.1 A more complex system (linearisation practice)

In general we might consider an n-dimensional system of partial differential equations for functions u_j, whose dimension is $m+1$ (1 dimension for time t and m dimensional phase space) and which have non-spatially varying equalibria on the domain $\mathbf{x} \in [0, L_1] \times [0, L_2] \times [0, L_3] \cdots \times [0, L_m]$. The steps for a P.D.E stability analysis of **homogeneous** equilibria are:

1. Find the homogenous equilibria by setting all $\frac{\partial^n u_i}{\partial t^n}$ and $\frac{\partial^n u_i}{\partial x_k^n}$ to zero, then solving the equations.
2. Linearise the system bu expanding $u_j = u_j^0 + \epsilon u_j^1$.
3. Assume solutions to the $\mathcal{O}(\epsilon)$ variation in the form
$$u_j(\mathbf{x}, t) = A_j \mathrm{e}^{\mathbf{i}\mathbf{k}\cdot\mathbf{x}+\lambda t}. \tag{11.18}$$
and substitute into the linearised system to obtain the matrix A_1.
4. Solve $\det(A_1) = 0$ to obtain the growth constants λ and asses stability for the λ as a function of k.

For example consider the following non-linear 3-dimensional system on the 2+1 dimensional domain (x_1, x_2, t)

$$\frac{\partial^2 u_1}{\partial t^2} + \gamma\frac{\partial u_1}{\partial t} = \nabla^2 u_1 + \tan(u_1 + u_2 + u_3) = 0, \tag{11.19}$$

$$\frac{\partial u_2}{\partial t} = u_1 u_2, \tag{11.20}$$

$$\frac{\partial u_3}{\partial t} = \frac{\partial u_1}{\partial x_1} + \beta\frac{\partial u_2}{\partial x_2} + (u_1 - 1)^2 = 0. \tag{11.21}$$

Subject to the boundary conditions that $u_j = 0$ on the boundaries for $j = 1, 2, 3$. We now perform the steps of the linear stability analysis.

Find the equilibria

We find a family of spatially constant equilibria by setting $u_1 + u_2 + u_3 = n\pi$, $u_2 = 0$ and $u_1 = 1$, thus $u_3 = n\pi - 1$.

Linearise the system

Set $u_j \approx u_j^0 + \epsilon u_j^1$, we have

$$\begin{aligned}
&\frac{\partial^n u_j}{\partial t^n} = \frac{\partial^n u_j^0}{\partial t^n} + \epsilon \frac{\partial^n u_j^1}{\partial t^n}. \quad \frac{\partial^n u_j}{\partial x_k^n} = \frac{\partial^n u_j^0}{\partial x_k^n} + \epsilon \frac{\partial^n u_j^1}{\partial x_k^n},\\
&\tan(u_1 + u_2 + u_3) = \tan(u_1^0 + u_2^0 + u_3^0) + \epsilon \left[\sec^2(u_1^0 + u_2^0 + u_3^0)\left(u_1^1 + u_2^1 + u_3^1\right)\right] + \mathcal{O}(\epsilon^2),\\
&u_1 u_2 = u_1^0 u_2^0 + \epsilon\left(u_1^0 u_2^1 + u_2^0 u_1^1\right) + \mathcal{O}(\epsilon^2),\\
&(u_1 - 1)^2 = (u_1^0 - 1)^2 + \epsilon 2u_1^1(u_1^0 - 1) + \mathcal{O}(\epsilon^2).
\end{aligned}$$

Also $\sec^2(u_1^0 + u_2^0 + u_3^0) = \sec^2(n\pi) = 1$, $u_2^0 = 0$ and $(u_1^0 - 1) = 0$. So to order ϵ our equations read

$$\frac{\partial^2 u_1^1}{\partial t^2} + \gamma \frac{\partial u_1^1}{\partial t} = \nabla^2 u_1^1 + u_1^1 + u_2^1 + u_3^1 = 0 \tag{11.22}$$

$$\frac{\partial u_2^1}{\partial t} = u_2^1, \tag{11.23}$$

$$\frac{\partial u_3^1}{\partial t} = \frac{\partial u_1^1}{\partial x_1} + \beta \frac{\partial u_2^1}{\partial x_2}. \tag{11.24}$$

11.1.1 Solve the linearised system

Substituting in $u_j^1 = A_j e^{\mathrm{i}\mathbf{k}\cdot\mathbf{x} + \lambda t}$

$$\lambda^2 u_1^1 + \gamma \lambda u_1^1 = -(k_1^2 + k_2^2)u_1^1 + u_1^1 + u_2^1 + u_3^1, \tag{11.25}$$

$$\lambda u_2^1 = u_2^1, \tag{11.26}$$

$$\lambda u_3^1 = \mathrm{i}k_1 u_1^1 + \mathrm{i}\beta k_2 u_1^1. \tag{11.27}$$

Our matrix A_1 then takes the form

$$A_1 = \begin{pmatrix} -(\lambda^2 + \gamma\lambda + k_1^2 + k_2^2) + 1 & 1 & 1 \\ 0 & 1 - \lambda & 0 \\ \mathrm{i}(k_1 + \beta k_2) & 0 & -\lambda \end{pmatrix}. \tag{11.28}$$

11.1.2 Analyse stability

Step (iii) will then be to solve $\det(A_1) = 0$. As with a number of previous examples and the assignment, rather than jump straight in to calculate the quartic polynomial which would ensue, we simply note it would have a factor $(1 - \lambda)$ from the middle term of the equation. This implies a positve eigenvalue so the equilbria are unstable. This is from the exponential growth of (11.23).

11.1.3 Inhomogeneous equilibira?

Stability for spatially varying equlibria is a much harder problem, and beyond the scope of this course, so we will leave it here for now.

Chapter 12

Oscilliatory switching

So far we have looked two variants of the Lotka-Volterra system. One, in the first chapter, which had periodic solutions. The second in chapters 4 and 8 which had no cyclic solutions but allowed for the possibility of species extinction/relaxation to a fixed value. In this chapter we consider a model which has both periodic behaviour as well as decay and relaxation. We start by returning to solely temporal (O.D.E) systems. We consider the system of equations

$$\frac{\mathrm{d}u}{\mathrm{d}t} = a - u + u^2 v, \tag{12.1}$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = b - u^2 v. \tag{12.2}$$

This system is cited by Murray Ch7.4 (the course textbook) as the simplest example of an enzyme reaction system. In Figure 12.1 we see solutions to this system which show exponential non-oscillatory relaxation, this is for parameters $a = 1, b = 2$, decaying oscillatory behaviour $a = 0.19, b = 0.5$ and fixed oscillatory $a = 0.1, b = 0.5$. The question we seek to answear here is how could we identify which parameters (a, b) lead to the differing behaviour and hence critically where does the behviour switch?

The answear can be found once again by turning to the linear stability analysis of the system. In particular we are going to start to pay attention to the imaginary part of our eigenvalues. If $\lambda = a + \mathrm{i}b$ then at least part of the solution to some linearised system will look like this

$$u(t) = \mathrm{e}^{at}\cos(bt). \tag{12.3}$$

So that the linearised solution varies sinusoidally in time and the amplitude of this variation either decays or grows exponentially at a rate a (examples are shown in Figure 12.2). The point of linearising our system is that we capture accurately the behaviour of our system in the neighbourhood of the equilibrium so the existence of oscillatory behavour in the neigbourhood of the equilibrium is a good indicator of oscillatory behaviour in the general system (unless it has some very complex behaviour). Searching for oscillatory behaviour, and the transition between non-oscillatory and oscillatory behaviour can be boiled down to a search for imaginary parts of the eigen-values of our linearised system.

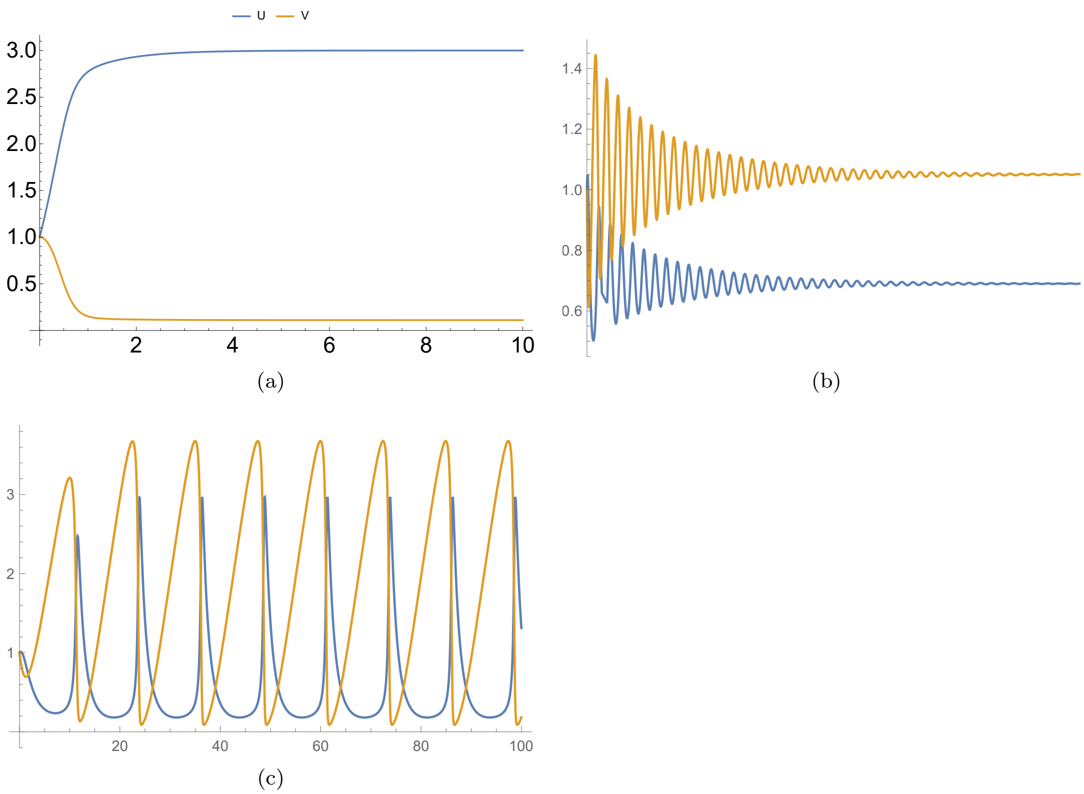
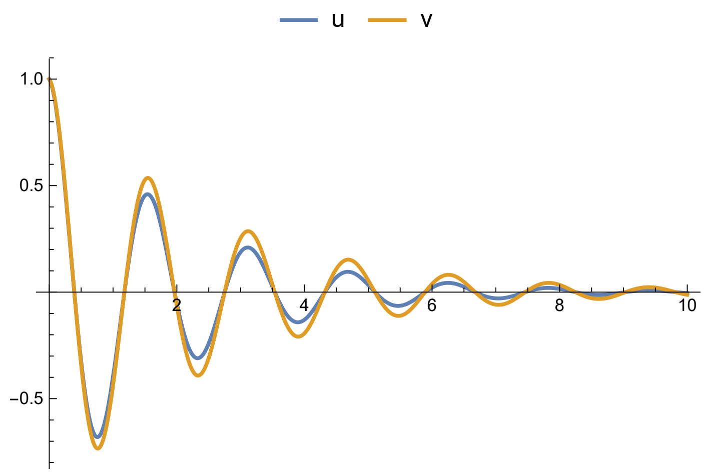
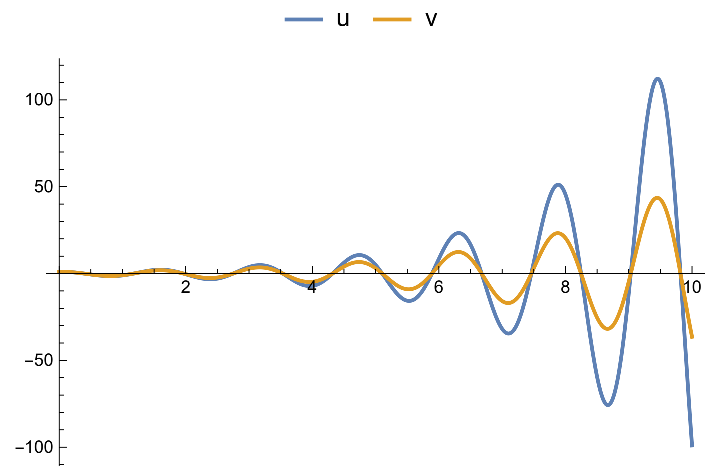


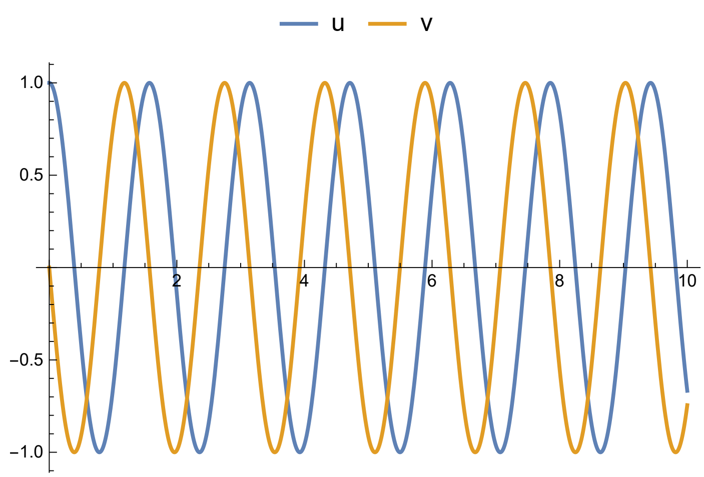
Figure 12.1: Solutions to the system (12.1) (a) with $a = 1, b = 2$, exponential relaxation to fixed non-zero values. (b) $a = 0.19, b = 0.5$, slowly decaying periodic behaviour. (c) $a = 0.1, b = 0.5$. The system transitions into a cycle of fixed period.



(a)



(b)



(c)

Figure 12.2: Linearised sinusoidal variations resulting from a linear stability analysis with complex λ. (a) A cosine variation for which λ has a negative real part, the variation decays. (b) A cosine variation for which lambda has a positive real part, the variation grows. A sine variation for which λ is purely imaginary.

12.0.1 General stability criteria and complex eigenvalues

In the last the subsequent chapters we have looked at the stability of 2-D systems which yield a polynomial $\det(A_1 - \lambda I)$ in the form

$$a\lambda^2 + b\lambda + c = 0, \quad \lambda = \frac{a}{2}\left[-b \pm \sqrt{b^2 - 4ac}\right] \tag{12.4}$$

In fact we often shouldn't have to even write out this quadratic in order to develop stability criteria. Consider 2-D system whose stability matrix A_1 is

$$A_1 = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad \det(A_1 - \lambda I) = \lambda^2 - (a+d)\lambda + ad - bc = \lambda^2 - \mathrm{Tr}(A_1)\lambda + \det(A_1) = 0. \tag{12.5}$$

$$\lambda = \frac{1}{2}\left[\mathrm{Tr}(A_1) \pm \sqrt{\mathrm{Tr}(A_1)^2 - \det(A_1)}\right]. \tag{12.6}$$

thus for stability we require.

$$\det(A_1) > 0, \text{ and } \mathrm{T_r}(A_1) < 0. \tag{12.7}$$

but we can also use this observation to search for complex behaviour (and hence oscillations)...

12.0.2 Finding complex oscillations

For an O.D.E system the only way the λ can be complex is if

$$\mathrm{Tr}(A_1)^2 - 4\det(A_1) < 0 \tag{12.8}$$

Which in turn requires

$$\det(A_1) > 0, \text{ and } 4\det(A_1) > \mathrm{Tr}(A_1)^2. \tag{12.9}$$

The oscillations will then decay if

$$\mathrm{Tr}(A_1) < 0. \tag{12.10}$$

(see Figure 12.2(a)), grow if

$$\mathrm{Tr}(A_1) > 0. \tag{12.11}$$

Figure 12.2(b), and maintain a fixed amplitude if

$$\mathrm{Tr}(A_1) = 0. \tag{12.12}$$

Figure 12.2(c).

12.0.3 Examples

The original Lotka-Volterra

For the $x_0 = y_0 = 1$ equilibrium the lotka-volterra A_1 is

$$A_1 = \begin{pmatrix} 0 & -1 \\ \gamma & 0 \end{pmatrix} \tag{12.13}$$

So $\mathrm{Tr}(A_1) = 0$ and $\det A_1 = \gamma$, so, as we found previously the perturbations have no real part and an imaginary phase γ indicating the non-decaying oscillations of the system.

Competitive Lotka-Volterra

For the $x_0 = 0, y_0 = 1$ equilibrium the Lotka-Volterra A_1 is

$$A_1 = \begin{pmatrix} 1-\gamma & 0 \\ \beta & -\delta \end{pmatrix} \tag{12.14}$$

So $\det A_1 = -\delta(1-\gamma)$ and $\mathrm{Tr} = (1-\gamma) - \delta$. So

$$\mathrm{Tr}^2 = (1-\gamma)^2 + \delta^2 - 2(1-\gamma)\delta, \quad 4\det A_1 = -4\delta(1-\gamma) \tag{12.15}$$

If $\gamma < 1$ then $\det A_1 < 0$ and there can be no imaginary solutions (we also know one of the eigenvalues is real). If $\gamma > 1$, $\det(A_1) < 0$ and, as we found earlier the system is stable, but does it ever decay in an oscillatory fashion ? The function

$$f(\gamma,\delta) = \mathrm{Tr}(A_1)^2 - 4\det A_1 = (-\gamma-\delta+1)^2 + 4(1-\gamma)\delta. \tag{12.16}$$

has positive quadratic coefficients for δ and γ it is plotted as a function of δ and γ and appears to be positive definite, perhaps we can find its minimum then we can establish if it can be negative and hence lead to complex λ. Taking partial derivatives we have

$$\frac{\partial f}{\partial\gamma} = 2(\gamma-1-\delta), \quad \frac{\partial f}{\partial\delta} = -2(\gamma-1-\delta), \quad \frac{\partial^2 f}{\partial\gamma^2} = 2, \quad \frac{\partial^2 f}{\partial\delta^2} = 2, \quad \frac{\partial^2 f}{\partial\delta\partial\gamma} = -2 \tag{12.17}$$

So the minimum requires $\frac{\partial f}{\partial\lambda} = 0$ and $\frac{\partial f}{\partial\delta} = 0$ so $\delta = \gamma - 1$ For this we would have $f = 0$. The condition for it to be a minimum is

$$\frac{\partial f}{\partial\lambda}\frac{\partial f}{\partial\delta} - \left(\frac{\partial^2 f}{\partial\delta\partial\gamma}\right)^2 > 0 \tag{12.18}$$

which is not satisfied here, this classes as indeterminate, the indeterminacy results from the fact that $\frac{\partial f}{\partial\lambda}$ and $\frac{\partial f}{\partial\delta}$ are not linearly independent. Specifically if $\delta = \gamma + a$ then the function is constant $f = (1+a)^2$, so there are lines of $\delta = \gamma + a$ for $a \in [-\infty,\infty]$ which cover the whole phase space and are of constant value. The minimum of the function is then definitely 0.

So the Competitive Lotka Volterra system does not have any long-run oscillatory behavior.

The enzyme reaction system

Let us perform a linear stability analysis on the full system.

Find the equilibria

It is straightforward to see that the equilibria take the form

$$u_0 = a + b, \quad v_0 = \frac{b}{(a+b)^2}. \tag{12.19}$$

linearise

Linearising $u \approx u_0 + \epsilon u_1$ and $v \approx v_0 + \epsilon v_1$ we have, to order ϵ

$$\frac{\mathrm{d}u_1}{\mathrm{d}t} = -u_1 + 2u_0v_0u_1 + u_0^2 v_1, \tag{12.20}$$

$$\frac{\mathrm{d}v_1}{\mathrm{d}t} = -2u_0v_0u_1 - u_0^2 v_1 \tag{12.21}$$

Solve

Assuming solutions in the form $e^{\lambda t}$ we can write our linearised system as

$$\lambda \begin{pmatrix} u \\ v \end{pmatrix} = A_1 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix}, \tag{12.22}$$

where the matrix A_1 takes the from

$$\begin{pmatrix} -1 + 2u_0v_0 & u_0^2 \\ -2u_0v_0 & -u_0^2 \end{pmatrix} \tag{12.23}$$

Analyse stability/find cyclic behaviour

On substituting in our equilibrium we have

$$\mathrm{Tr}(A_1) = \frac{b-a}{a+b} - (a+b)^2, \quad \det(A_1) = (a+b)^2 > 0 \tag{12.24}$$

So the determinant satisfies the first required condition. Let us seek solutions which are purely cyclic (purely imaginary), for this we require that $\mathrm{Tr}(A_1) = 0$ or

$$b - a = (a+b)^3 \tag{12.25}$$

We know also that the determinant is positive definite so if $\mathrm{Tr}(A_1) = 0$

$$\mathrm{Tr}(A_1)^2 - 4\det(A_1) = -4\det(A_1) < 0, \tag{12.26}$$

and the solutions will be cyclic.

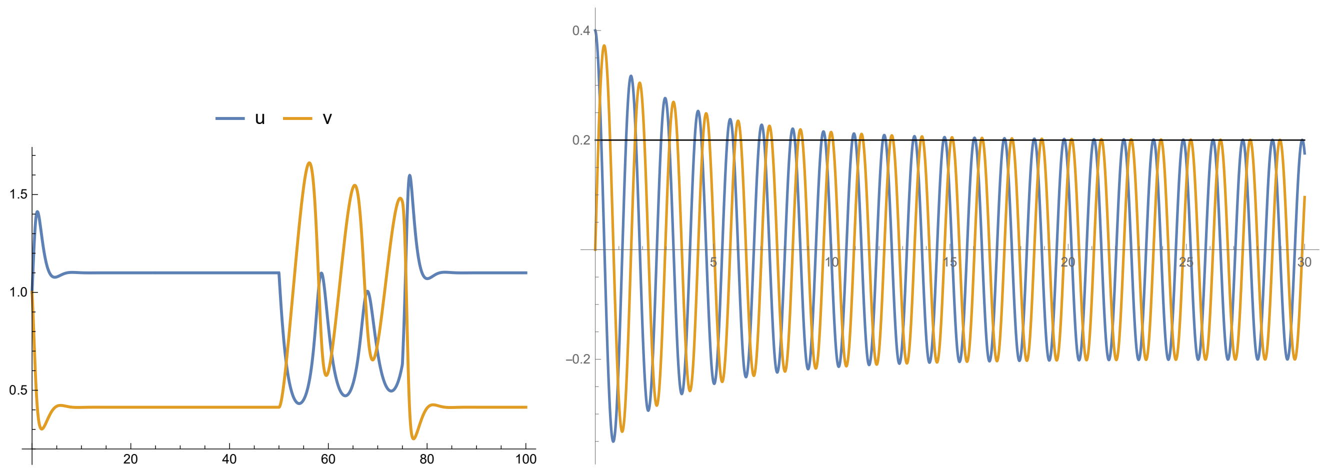
Switching

We have seen our system (12.1) can either have oscillatory behaviour or exponential/growth depending on the values of the parameters a and b. This suggests the possibility of switching. Say we have a system where we vary say a as

$$a(t) = \begin{cases} a_c & \text{if } n\Delta t < t < (n+1)\Delta t, \quad n \text{ even} \\ a_e & \text{if } n\Delta t < t < (n+1)\Delta t, \quad n \text{ odd} \end{cases} \tag{12.27}$$

This is essentially a digital signal of period Δt. We choose the value of a_c such that, for the given b, the solutions u and v are locally periodic (purely imaginary) with neither growth or decay. We choose a_e such that the system is non periodic (λ real) and asymptotically stable. The system as shown in Figure 12.3(a) will then switch between stable oscillatory behaviour and having a fixed value.

Switching type behaviour and models are popular in the modelling of nerve, where periodic excitement causes signals to be produced followed by a period of relaxation. In one of your problem sheets we will construct a switch system for which the mean of the periodic cycle and the relaxed value are the same, a "perfect switch".



(a) (b)

Figure 12.3: (a) An example of a "switch "system which switches periodically between decay and oscillatory behaviour. (b) a particular solution to the system (12.28) which is shown to decay to its limit cycle.

12.1 Limit cycles

We have seen that the enzyme-reaction system has a parameter set in which the solutions settle down to a periodic cycle (sometimes called a limit-cycle in the dynamical system terminology). **This is not an equilibrium** but it is somehow a limiting behaviour. Limit cycles are closed curves in phase space, for example the periodic behaviour of the Lotka-Volterra solutions shown in Figure 1.2.

12.1.1 Hopf Bifurcations

In the previous section we found a technique for finding limit cycles (purely imaginary eigen-values) in the linearised system in the neighborhood of the equilibrium. But we should be clear the linear system is only an approximation. A rather deep thoerem called the Poincare-Bendixson theorem actually tells us that if an equilibrium has purely imaginary eigenvalues then nearby solutions to the full equation **will** relax to a limit cycle. So we can use this technique (finding purely complex eigenvalues) as a means of finding areas of parameter space (the space of a and b values in the enzyme model) which can exhibit limit cycle behaviour. The parameter set at which the eigenvalues of our linear matrix $\det A_1 - \lambda I$ become purely imaginary is known as a **Hopf bifurcation** set.

12.1.2 Exact limit cycle solutions

Typically, however, it is hard to find systems with exact analytic solutions for the particular form of this cycle. There is one system where it is possible to find such solutions and we introduce it briefly here as a tool for the next chapter where we add spatial variance to obtain spiral wave patterns.

The system takes the form

$$\frac{\partial}{\partial t}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} f(a) & -g(a) \\ g(a) & f(a) \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix}, \quad a = \sqrt{u^2+v^2}. \tag{12.28}$$

The parameter a represents a set of circles $u(t)^2 + v(t)^2$ in phase space u-v and the functions f and g are constant on these circles. It is assumed that

$$\begin{cases} f(a) < 0 & \text{if } a > a_0 \\ f(a) > 0 & \text{if } a < a_0 \\ f(a) = 0 & \text{if } a = a_0 \end{cases} \tag{12.29}$$

and $g(a) > 0, a > 0$. The reasons for these conditions will become clear soon. The idea is that the system settles on the "cycle" $a = a_0$. It should be said that this model does not fit any known system but as we will see in the next chapter it is an excellent approximation to the limit cycle of a huge class of realistic model systems. To find solutions to this system we convert it into complex form by writing $w = u + iv$, so that

$$\frac{\mathrm{d}w}{\mathrm{d}t} = \left[f(|w|) + \mathrm{i}g(|w|)\right] w \tag{12.30}$$

So that the real and imaginary parts form the two rows of the matrix equation (12.28). We then write $w = ae^{i\theta}$ to split the system into amplitude and frequency components, *i.e.* we will have

$$u(t) = a(t)\cos(\theta(t)), \quad v(t) = a(t)\sin(\theta(t)). \tag{12.31}$$

Substituting this into (12.30) we find

$$\frac{\mathrm{d}a}{\mathrm{d}t} = af(a), \quad \frac{\mathrm{d}\theta}{\mathrm{d}t} = g(a). \tag{12.32}$$

The point of the conditions on f now become clear. If $a > a_0$ then a will decrease (the magnitude of the cycle w will decrease), if $a < a_0$ it will increase, and hence a will take a fixed value at a_0. The choice $g > 0$ just forces θ to increase with t.

The limit cycle solutions are solutions with fixed a which occur when $a = a_0$ and they take the form

$$a = a_0, \quad \theta(t) = g(a_0)t + \theta_0. \tag{12.33}$$

As an example we could choose

$$f(a) = a_0 - a, \quad g(a) = 1/a. \tag{12.34}$$

The first equation of (12.32) then becomes the logistic equation, if we choose a initial condition $a(t = 0) = 5a_0$ then

$$a(t) = \frac{5a_0e^{a_0t}}{5e^{a_0t} - 4}. \tag{12.35}$$

and

$$\theta(t) - \theta_0 = \int_0^t \frac{\mathrm{d}t}{a(t)} = \frac{t}{a_0} + \frac{4}{5a_0^2}\mathrm{e}^{-a_0t} \tag{12.36}$$

so now

$$u(t) = a(t)\cos(\theta(t)), \quad v(t) = a(t)\sin(\theta(t)). \tag{12.37}$$

Which is shown in Figure 12.3(b) to decay to its limit cycle. While in this case the functions u and v have negative values this could represent some variation around a mean value, i.e. it could be the fluctuating behaviour of some pair of species, be it physical or bio-chemical or some kind of signal (heart beat, nerve signalling rate).

Chapter 13

Spiral waves

13.1 Systems with spiral waves

Many systems exhibit spiral shape waves of high intensity with the kind of shape seen in Figure 13.1. Such patterns can be in Chemical systems, such as the famed Belousov-Zhabotinskii reaction, in electrochemical waves in the brain caused by lesions in the tissue and also mould growth due to spiral signalling patterns; this is what is shown in Figure 13.1. Each system (and there are more) has their own different drivers are modelled with a different set of equations, for example the FitzHugh-Nagamo model system, used to model neuron firing patterns, takes the form

$$\frac{\partial u}{\partial t} = u(a-u)(1-u) + v + D\nabla^2 u, \tag{13.1}$$

$$\frac{\partial v}{\partial t} = bu - \gamma v. \tag{13.2}$$

The spiral waves are surfaces where $u > a$, they appear as thin lines with spiral patterns of the type observed in Figure 13.1. Another model where such patterns are found takes the form

$$\frac{\partial u}{\partial t} = \nabla^2 u + \frac{1}{\epsilon}\left(u - u^3 - v\right), \tag{13.3}$$

$$\frac{\partial v}{\partial t} = \nabla^2 v + \epsilon\left(u + \beta - \frac{v}{2}\right). \tag{13.4}$$

which has been used to model the fibrillating heart. In this case the patterns are the peaks of travelling waves (like solutions gained with the substitution $v = x + ct$).

13.2 The f-g system spiral waves

The analysis of these systems is not trivial and in this section we focus on a spatial variant of the $f - g$ system introduced in the last chapter:

$$\frac{\partial}{\partial t}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} f(a) & -g(a) \\ g(a) & f(a) \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix} + D\nabla^2\begin{pmatrix} u \\ v \end{pmatrix}, \quad a^2 = u^2 + v^2. \tag{13.5}$$

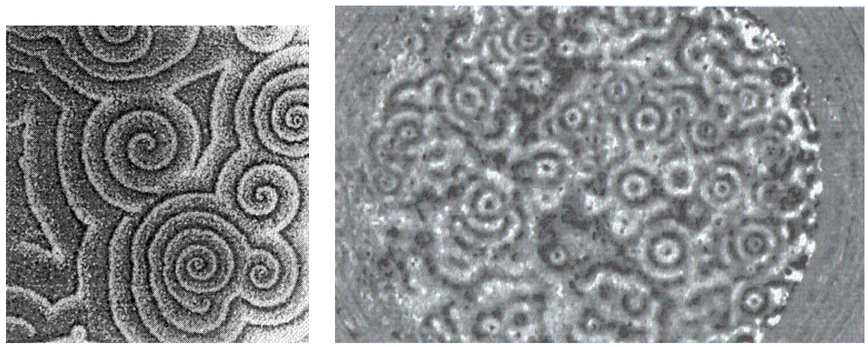


Figure 13.1: Spiral patterns caused by spiral wave signalling in the slime mould Dictyostelium discoideum.

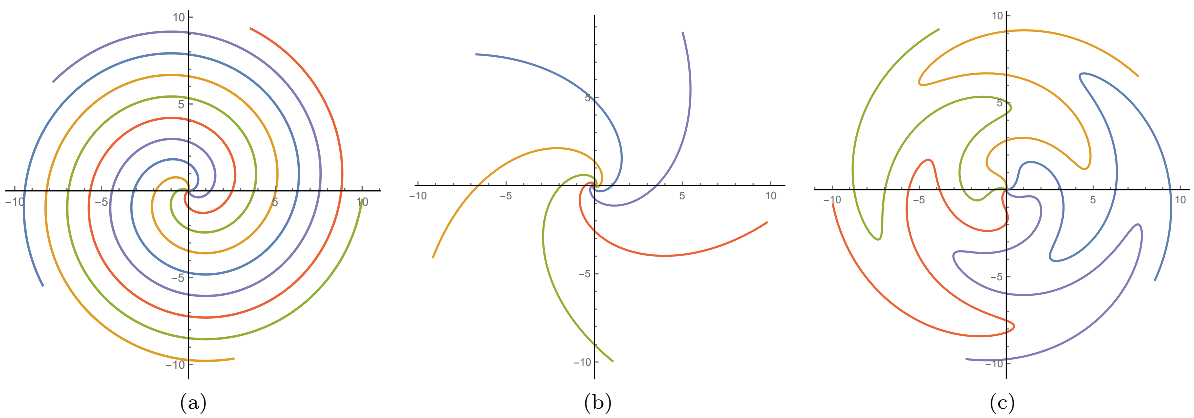


Figure 13.2: Spiral patterns for u obtained using $A(r) = r$ and $\psi(r) = r$ (a), $\psi(r) = \ln r$ (b) and $\psi(r) = \sin(r)$ (c).

Before we search for the type of solutions we want, we first build up a little relevant spiral geometry. We can write this as a complex equation by writing $w = u + \mathrm{i}v$ so that

$$\frac{\partial w}{\partial t} = (f + \mathrm{i}g)w + D\nabla^2 w. \tag{13.6}$$

so that the real part gives the first line of (13.5) the imaginary part the second. As in the previous chapter this suggests solutions in the form

$$w(\mathbf{x}, t) = A(\mathbf{x}, t)\mathrm{e}^{\mathrm{i}\phi(\mathbf{x},t)}. \tag{13.7}$$

We substitute this into (13.6) to obtain P.D.E's for A and ϕ. We find

$$\frac{\partial w}{\partial t} = \frac{w}{A}\frac{\partial A}{\partial t} + \mathrm{i}w\frac{\partial \phi}{\partial t}.$$
$$\nabla w = \frac{w}{A}\nabla A + \mathrm{i}w\nabla\phi,$$
$$\nabla^2 w = \nabla\cdot\nabla w = \frac{w}{A^2}(\nabla A)^2 + \frac{\mathrm{i}w}{A}\nabla\phi\cdot\nabla A - \frac{w}{A^2}(\nabla A)^2 + \frac{w}{A}\nabla^2 A - w(\nabla\phi)^2 + \frac{\mathrm{i}w}{A}\nabla\phi\cdot\nabla A + \mathrm{i}w\nabla^2\phi.$$

where $(\mathbf{A})^2 = \mathbf{A}\cdot\mathbf{A}$. If we substitute these expressions into (13.6) and collect the parts prefaced by i and not, we obtain the following system of equations.

$$\frac{\partial A}{\partial t} = D\nabla^2 A + Af - DA(\nabla\phi)^2, \tag{13.8}$$
$$\frac{\partial \phi}{\partial t} = D\nabla^2\phi + g + 2\frac{D}{A}\nabla A\cdot\nabla\phi. \tag{13.9}$$

which is a system of diffusion equations with coupled source terms.

13.2.1 Fixed shape spiral waves

We now search for spirals by seeking a very specific set of limit-cycle solutions to this equation. Similar to the temporal version of this system we seek limit cycles with the functions A and ϕ taking the form

$$A = A(r), \quad \phi(r, \theta, t) = \Omega t + m\theta + \psi(r). \tag{13.10}$$

(to be clear the only t dependence anywhere is the Ωt term). Here we have chosen to focus on a 2-D system with radial coordinates (r, θ). The parameter Ω will represent the temporal rotation of the spiral (constant). The function m dictates the number of spiral arms of the pattern and $\psi(r)$ in controls the form of the spirals. For example lets say $u(r, \theta, t) = A(r)\cos(\phi(r, \theta, t))$ is the density which produces the visible spiral pattern. Lets say it only becomes visible when $u > u_c$ some fixed value. For fixed r hence fixed A this is a cosine wave which will rise above u_c m times, particularly it has a maximum at $\theta = 2\pi/m$ when $t = 0$. Then as t increases it has maxima at $\theta + \Omega t = 2\pi/m$ hence the spiral arms (regions above which $u > u_c$) will rotate.

For example if we set $A = r$, and $\psi = ar$ then $u = \mathrm{Re}(w)$, would, for fixed θ values make a sprial pattern as shown in Figure (13.2)(a) (this shows the lines maxima of u). Other patterns for $\psi = \ln r$ (b) and $\psi = \sin(r)$ are shown in Figures (13.2)(b) and (c), the curves in case (b) are logarithmic or Archimedian spirals, shapes frequently found in nature (*e.g* Roman/Romanesco cabbage!) .

Both cases (a) and (b) are quite typical of the patterns which can be found experimentally in the Belousov-Zhabotinskii reaction setting, the third is just for fun (to the best of my knowledge).

Of course we have a specific set of equations (13.8) to determine our functions A and ψ. Substituting (13.10) into (13.8) and using

$$\nabla f = \frac{\partial f}{\partial r}\hat{\mathbf{r}} + \frac{1}{r}\frac{\partial f}{\partial \theta}\hat{\theta}, \quad \nabla^2 f = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial f}{\partial r}\right) + \frac{1}{r^2}\frac{\partial^2 f}{\partial \theta^2}. \tag{13.11}$$

we obtain

$$D\left(\frac{\mathrm{d}^2 A}{\mathrm{d}r^2} + \frac{1}{r}\frac{\mathrm{d}A}{\mathrm{d}r}\right) + A\left[f - D\left(\frac{\mathrm{d}\psi}{\mathrm{d}r}\right)^2 - \frac{Dm^2}{r^2}\right] = 0, \tag{13.12}$$

$$D\frac{\mathrm{d}^2\psi}{\mathrm{d}r^2} + D\left[\frac{1}{r} + \frac{2}{A}\frac{\mathrm{d}A}{\mathrm{d}r}\right]\frac{\mathrm{d}\psi}{\mathrm{d}r} = \Omega - g. \tag{13.13}$$

Now we have a system of O.D.E's, but they are non-linear. However, we can obtain an integral equation for ψ as a function of A. We multiply the second equation by $rA^2(r)$ and integrate,

$$D\int_0^r sA^2\frac{\mathrm{d}^2\psi}{\mathrm{d}s^2}\mathrm{d}s + D\int_0^r \mathrm{d}s\left[A^2 + 2sA\frac{\mathrm{d}A}{\mathrm{d}s}\right]\frac{\partial\psi}{\partial s} = \int_0^r sA^2(\Omega - g(s))\mathrm{d}s. \tag{13.14}$$

Using integration by parts on the first term we get

$$\int_0^r sA^2\frac{\mathrm{d}^2\psi}{\mathrm{d}s^2}\mathrm{d}s = \frac{\mathrm{d}\psi}{\mathrm{d}r}rA^2 - \int_0^r\left[A^2 + 2As\frac{\mathrm{d}A}{\mathrm{d}s}\right]\frac{\partial\psi}{\partial s}\mathrm{d}s. \tag{13.15}$$

so that (13.14) can be re-written as

$$\frac{\mathrm{d}\psi}{\mathrm{d}r} = \frac{1}{DrA^2}\int_0^r sA^2(\Omega - g)\mathrm{d}s. \tag{13.16}$$

One can then substitute this into the first equation to obtain a rather nasty integral-differential equation for A. Before analysing this equation we need to consider our boundary conditions. We would expect our solutions to be well behaved at the origin. So.

$$A(0) = 0, \quad \text{and } \frac{\mathrm{d}\psi}{\mathrm{d}r}(0) = 0. \tag{13.17}$$

If A is not zero there is spurious interchange in behaviour of u and v as a function of θ at the origin, which explains the first condition. The ψ derivative condition just makes ψ a smooth function there. A second slightly more delicate argument allows us to set the value of Ω. We would like $\frac{\mathrm{d}\phi}{\mathrm{d}r}$ to be bounded as $r \to \infty$, else u and v begin to oscillate at an infinite rate. In this limit we would also like $A_\infty = A(\lim r \to \infty)$ to remain bounded, for obvious reasons. If we assume A adopts sufficiently regular behaviour as $r \to \infty$ then

$$\int_0^r sA^2(\Omega - g(s))\mathrm{d}s \sim \int_0^r sA_\infty^2(\Omega - g_\infty)\mathrm{d}s \tag{13.18}$$

The symbol $\sim$ means on the order of, the ratio of the two terms $A \sim B$ A/B is constant in the limit (this is the same as saying A is $\mathcal{O}(B)$). So we can integrate to obtain

$$\int_0^r sA_\infty^2(\Omega - g_\infty)\mathrm{d}s = \frac{1}{2}r^2 A_\infty(\Omega - g_\infty) \tag{13.19}$$

and

$$\left.\frac{\mathrm{d}\psi}{\mathrm{d}r}\right|_{r\to\infty} \sim \frac{[\Omega - g_\infty]\, r}{2D} \tag{13.20}$$

The only way this can be bounded is if $\Omega = g_\infty$. So this argument allows use to determine the termporal rate of oscillation of our system Ω. In turn if we are assuming $A \to A_\infty$ (so that the r derivatives of A vanish) then

$$\left.\frac{\mathrm{d}\psi}{\mathrm{d}r}\right|_{r\to\infty} = \left(\frac{f(A_{\infty)}}{D}\right)^{1/2}. \tag{13.21}$$

We would also like to get some idea of the permissible behaviour of A near the origin $r = 0$. To do so we treat $A(r)$ locally as a series solution

$$A(r) \sim r^c \sum_{n=0}^{\infty} a_n r^n, \text{ as } r \to 0. \tag{13.22}$$

We substitue this into (13.12) and equate coefficients, the lowest order coefficient r^{c-2} yeilds an equation

$$c(c-1) + c - m^2 = 0 \tag{13.23}$$

So $c = \pm m$. An in the limit $r \to 0$ we want A to be non-singular so $c = m$. This implies that, as $r \to 0$ and $A(r)$ starts to be dominated by its lowest order corefficient, *i.e.*

$$A(r) \sim a_0 r^m, \text{ as } r \to 0. \tag{13.24}$$

So we now have four potential boundary or limiting conditions for the system. In Cohen *et al* showed that with these assumptions, that as $r \to \infty$ the function ψ takes both the linear and log forms shown in Figures 13.2(a) and (b).

13.3 The f-g system as an asymptoptic limt for general reaction diffusion equation.

The systems mentioned at the start of this chapter are examples of the general reaction-diffusion equations which take the from

$$\begin{aligned} \frac{\partial u}{\partial t} &= D_1 \nabla^2 u + F(u_1, u_2, \lambda), \\ \frac{\partial v}{\partial t} &= D_2 \nabla^2 v + G(u_1, u_2, \lambda). \end{aligned} \tag{13.25}$$

To the best of my knowledge there is no known model of a real physical system which fits exactly the pattern indicated by (13.5). However, we can show that in some sense (13.5) is embedded in all systems (13.25), and further, for the right parameters, its behaviour will be the dominant behaviour in the system. This would explain why spiral patterns are so prevalent. To demonstrate this is the case we will use a technique known as a *weakly non-linear analysis* (sometimes a *multi-scale* analysis). The basic idea is that there are two timescales on which the system operates when it has a spiral. The first assumes the spiral pattern stays fixed over fast times scales. The second assumes the system evolves slowly over a much longer timescale. The difference in time scale is such that the two behaviours can be considered separate. More concretely we consider solutions which take the form

$$u \equiv R(\beta, \tau)P(t^*), \text{ and similar for v.} \tag{13.26}$$

Where $t^* = (1 + \epsilon\omega)^{-1}t$ with ω of order $\mathcal{O}(\epsilon)$ and $\tau = \epsilon^2 t$. t^* is the *fast* timescale and τ the *slow* timescale. If ϵ is a small number then even if t is quite big τ will be very small and hence the R, the changing amplitude, will evolve very slowly as a function of t. Also $\beta = \epsilon\mathbf{x}$, β is a parameter which varies slowly across space, functions of β will tend to vary only on a long length-scale. If our system is to have spiral behaviour then there will be some parameter value λ_0 at which the linearised system's eigenvalues become purely imgainary (we find a Hopf-bifurcation) and the system switches form having a steady state (time derivatives are zero) to exhibiting a limit cycle. The idea is that we seek behaviour for $\lambda = \epsilon + \lambda_0$ with ϵ very small, so that we might still expect to be close to a steady cycle (we assume sufficiently smoothness in λ for this to be the case). The value of λ_0 could of course be found by a linear stability analysis.

We further assume that we can write

$$F(\lambda, u, v) = f(\lambda)u - g(\lambda)v + \gamma(\lambda, u, v), \tag{13.27}$$

$$G(\lambda, u, v) = g(\lambda)u - h(\lambda)v + \Sigma(\lambda, u, v). \tag{13.28}$$

Where γ and Σ are order u^2 and v^2 in u and v. For a differentiable function this can be done using the Taylor method but this is not a restrictive assumption, even for continous functions. We then assume $u = v = 0$ for the initial stable state (again no real loss of generality but the algebra is easier than the no zero case). With this we can expand u and v in terms of ϵ.

$$u = u(\beta, \tau, t^*) = \epsilon F_1(\beta, \tau, t^*) + \epsilon^2 F_2(\beta, \tau, t^*) + \epsilon^3 F_3(\beta, \tau, t^*) \tag{13.29}$$

$$v = v(\beta, \tau, t^*) = \epsilon G_1(\beta, \tau, t^*) + \epsilon^2 G_2(\beta, \tau, t^*) + \epsilon^3 G_3(\beta, \tau, t^*) \tag{13.30}$$

We are assuming all F_i and G_i have the form (13.26). In what follows we will have no need to go beyond order ϵ^3. We also expand f, g and h as

$$f \approx f_0 + \epsilon^2 f_2 + \epsilon^3 f_3 + \mathcal{O}(\epsilon^4), \tag{13.31}$$

$$g \approx g_0 + \epsilon^2 g_2 + \epsilon^3 g_3 + \mathcal{O}(\epsilon^4), \tag{13.32}$$

$$h \approx h_0 + \epsilon^2 h_2 + \epsilon^3 h_3 + \mathcal{O}(\epsilon^4). \tag{13.33}$$

(we ignore the linear order correction for the sake of simplicity, but it does not affect the conclusions). We also assume $f_0 = h_0 = 0$. We have the freedom to do so. With our assumptions on the timescales τ, t^*, we note that, for any function $f(\tau, t^*)$

$$\frac{\partial f}{\partial t} = \frac{\partial f}{\partial t^*}\frac{\mathrm{d}t^*}{\mathrm{d}t} + \frac{\partial f}{\partial \tau}\frac{\mathrm{d}\tau}{\mathrm{d}t} = (1 + \epsilon\omega)^{-1}\frac{\partial f}{\partial t^*} + \epsilon^2\frac{\partial f}{\partial \tau}. \tag{13.34}$$

so

$$\frac{\partial}{\partial t} = (1 + \epsilon\omega)^{-1}\frac{\partial}{\partial t^*} + \epsilon^2\frac{\partial}{\partial \tau} \tag{13.35}$$

or if we use the binomial series for $(1 + \epsilon\omega)^{-1}$

$$\frac{\partial}{\partial t} = (1 - \omega_0\epsilon^2 + \mathcal{O}(\epsilon^3))\frac{\partial}{\partial t^*} + \epsilon^2\frac{\partial}{\partial \tau} \tag{13.36}$$

(we will only need up to ϵ^2 as the u and v expansions are order ϵ). Also

$$\nabla_x = \epsilon \nabla_\beta \quad \text{where e.g.} \nabla_\beta = \frac{\partial}{\partial \beta_1} + \frac{\partial}{\partial \beta_2} + \dots \frac{\partial}{\partial \beta_n} \text{ in Cartesian coordinates.} \tag{13.37}$$

So up to order $\mathcal{O}(\epsilon^3)$ we have

$$\frac{\partial u}{\partial t} = \frac{\partial F_1}{\partial t^*}\epsilon + \frac{\partial F_2}{\partial t^*}\epsilon^2 + \left(\frac{\partial F_3}{\partial t^*} - \omega_0 \frac{\partial F_1}{\partial t^*} + \frac{\partial F_1}{\partial \tau}\right)\epsilon^3 + \mathcal{O}(\epsilon^4), \tag{13.38}$$

$$\frac{\partial v}{\partial t} = \frac{\partial G_1}{\partial t^*}\epsilon + \frac{\partial G_2}{\partial t^*}\epsilon^2 + \left(\frac{\partial G_3}{\partial t^*} - \omega_0 \frac{\partial G_1}{\partial t^*} + \frac{\partial G_1}{\partial \tau}\right)\epsilon^3 + \mathcal{O}(\epsilon^4), \tag{13.39}$$

$$\nabla_x^2 u = \epsilon^3 \nabla_\beta^2 F_1 + \mathcal{O}(\epsilon^4), \quad \nabla_x^2 v = \epsilon^3 \nabla_\beta^2 + G_1 + \mathcal{O}(\epsilon^4), \tag{13.40}$$

$$fu = f_2 F_1 \epsilon^3 + \mathcal{O}(\epsilon^4), \quad hv = h_2 G_1 \epsilon^3 + \mathcal{O}(\epsilon^4), \tag{13.41}$$

$$gu = g_0 F_1 \epsilon + (g_2 F_1 + g_0 F_3)\epsilon^3 + \mathcal{O}(\epsilon^4) \quad gv = g_0 G_1 \epsilon + (g_2 G_1 + g_0 G_3)\epsilon^3 + \mathcal{O}(\epsilon^4).$$

We also expand the functions γ and Σ about λ_0. The zeroth order term must be zero for equilibrium of the original system as F and G must be zero at $\lambda = \lambda_0$, $u_0 = 0$, $v_0 = 0$. Also we note that γ and Σ must be at at least quadratic order in u and v. so we can expect terms of no less than quadratic order in ϵ, *i.e.*

$$\gamma(\beta, \tau, t^*) = \gamma_2(\beta, \tau, t^*)\epsilon^2 + \gamma_3(\beta, \tau, t^*)\epsilon^3, \tag{13.42}$$

$$\Sigma(\beta, \tau, t^*) = \Sigma_2(\beta, \tau, t^*)\epsilon^2 + \Sigma_3(\beta, \tau, t^*)\epsilon^3, \tag{13.43}$$

13.3.1 Solving over each scale

We have now determined the expansion of all terms in (13.25), based on our separated scale assumptions. We substitute all the expansions back into (13.25) and collect terms at $\mathcal{O}(\epsilon)$, $\mathcal{O}(\epsilon^2)$ and $\mathcal{O}(\epsilon^3)$, ... Each equation at each order must equate to zero. We now solve these equations sequentially.

So, collecting all terms of $\mathcal{O}(\epsilon)$ we have

$$\frac{\partial F_1}{\partial t^*} = -g(\lambda_0) G_1, \tag{13.44}$$

$$\frac{\partial G_1}{\partial t^*} = g(\lambda_0) F_1. \tag{13.45}$$

For which the solutions will take the from

$$F_1 = A(\beta, \tau) \cos\left(g(\lambda_0) t^* + \Theta(\beta, \tau)\right), \tag{13.46}$$

$$G_1 = A(\beta, \tau) \sin\left(g(\lambda_0) t^* + \Theta(\beta, \tau)\right).$$

But we note this is just the fast time scale t^* behaviour of F_1 and G_1. The functional dependence on β and τ, the slow timescale is not yet determined.

At $\mathcal{O}(\epsilon^2)$ (not actually very important here),

$$\frac{\partial F_2}{\partial t^*} = \gamma_2(\beta, \tau, t^*), \quad F_2 = \int_0^{t^*} \gamma_2(\beta, \tau, s) \mathrm{d}s \tag{13.47}$$

$$\frac{\partial G_2}{\partial t^*} = \Sigma_2(\beta, \tau, t^*), \quad G_2 = \int_0^{t^*} \Sigma_2(\beta, \tau, s) \mathrm{d}s \tag{13.48}$$

Crucially at $\mathcal{O}(\epsilon^3)$ we have the slow timescale derivatives (in β and τ) for the functions F_1 and G_1

$$\frac{\partial F_3}{\partial t^*} - \omega_0 \frac{\partial F_1}{\partial t^*} + \frac{\partial F_1}{\partial \tau} = D_1 \nabla_\beta^2 F_1 + f_2 F_1 - g_2 G_1 - g_0 G_3 + \gamma_3(\beta, \tau, t^*), \tag{13.49}$$

$$\frac{\partial G_3}{\partial t^*} - \omega_0 \frac{\partial G_1}{\partial t^*} + \frac{\partial G_1}{\partial \tau} = D_2 \nabla_\beta^2 G_1 + g_2 F_1 + g_0 F_3 + h_2 G_1 + \Sigma_3(\beta, \tau, t^*). \tag{13.50}$$

With some re-arranging we see we have a pair of inhomogenous ordinary differential equations for F_3 and G_3, *i.e.*.

$$\frac{\partial F_3}{\partial t^*} + g_0(\lambda_0) G_3 = M, \tag{13.51}$$
$$\frac{\partial G_3}{\partial t^*} - g_0(\lambda_0) F_3 = N.$$

Where the functionals M and N take the form.

$$M(F_1, G_1) = -\frac{\partial F_1}{\partial \tau} + D_1 \nabla_\beta^2 F_1 + f_2 F_1 - g_2 G_1 - \omega_0 g_0 G_1 + \gamma_3(\beta, \tau, t^*), \tag{13.52}$$

$$N(F_1, G_1) = -\frac{\partial G_1}{\partial \tau} + D_2 \nabla_\beta^2 G_1 + g_2 F_1 + h_2 G_1 + \omega_0 g_0 F_1 + \Sigma_3(\beta, \tau, t^*). \tag{13.53}$$

We can eliminate F_3 from (13.51) to give

$$\frac{\partial^2 G_3}{\partial (t^*)^2} + g_0^2(\lambda_0) G_3 = \frac{\partial N}{\partial t^*} + g_0 M. \tag{13.54}$$

An inhomogenous O.D.E for G_3. The homogenous part G_3^h (set the R.H.S to zero) has solutions in the form

$$B\cos(g_0 t^* + \Theta(\beta, \tau)) \text{ and } B\sin(g_0 t^* + \Theta(\beta, \tau)). \tag{13.55}$$

The solvability conditions for the inhomogenous O.D.E (13.51) are

$$\int_0^{2\pi/g_0} \cos(g_0 t^* + \Theta(\beta, \tau)) \left(\frac{\partial N}{\partial t^*} + g_0 M \right) \mathrm{d}t^* = \int_0^{2\pi/g_0} \sin(g_0 t^* + \Theta(\beta, \tau)) \left(\frac{\partial N}{\partial t^*} + g_0 M \right) \mathrm{d}t^* = 0. \tag{13.56}$$

We explain where these come from in the following chapter, for now it suffices to say we **cannot** solve (13.54) if (13.56) does not hold. We note that

$$\frac{\partial N}{\partial t^*} = g_0 \left[-\frac{\partial F_1}{\partial \tau} + D_2 \nabla_\beta^2 F_1 + h_2 F_1 - g_2 G_1 - \omega_0 g_0 G_1 \right] + \frac{\partial \Sigma_3}{\partial t^*}. \tag{13.57}$$

so

$$\frac{\partial N}{\partial t^*} + g_0 M = 2g_0 \left[-\frac{\partial F_1}{\partial \tau} + D \nabla_\beta^2 F_1 - g_2 G_1 - \omega_0 g_0 G_1 \right] + g_0(f_2 + h_2) F_1 + g_0 \gamma_3 + \frac{\partial \Sigma_3}{\partial t^*}. \tag{13.58}$$

where $D = (D_1 + D_2)/2$. With a little effort we can also find

$$\frac{\partial F_1}{\partial \tau} = \frac{\partial A}{\partial \tau} \frac{F_1}{A} - \frac{\partial \Theta}{\partial \tau} G_1, \tag{13.59}$$

$$\nabla_\beta^2 F_1 = \frac{\nabla_\beta^2 A}{A} F_1 - \frac{2\nabla_\beta \Theta \cdot \nabla_\beta A}{A} G_1 - \nabla_\beta^2 \Theta G_1 - (\nabla_\beta \Theta)^2 F_1. \tag{13.60}$$

So we can write

$$\frac{\partial N}{\partial t} + g_0 M = \sigma_f \cos(g_0 t^* + \Theta(\beta,\tau)) + \sigma_g \sin(g_0 t^* + \Theta(\beta,\tau)) + g_0\gamma_3 + \frac{\partial \Sigma_3}{\partial t}, \tag{13.61}$$

$$\sigma_f = 2g_0\left[-\frac{\partial A}{\partial \tau} + D\nabla_\beta^2 A - DA(\nabla_\beta\Theta)^2 + (f_2+h_2)A\right], \tag{13.62}$$

$$\sigma_g = 2g_0 A\left[\frac{\partial \Theta}{\partial \tau} - D\frac{2\nabla_\beta\Theta\cdot\nabla_\beta A}{A} - D\nabla_\beta^2\Theta - g_2 - \omega_0 g_0\right] \tag{13.63}$$

Before we apply the solvability conditions we make one further observation. Both γ_3 and Σ_3 are periodic functions of t^*, as u and v are. Further, we now know that this period is $2\pi/g_0$. This implies we can write both γ and Σ as Fourier series

$$\gamma_3(\tau,\beta,t^*) = \sum_{n=0}^{\infty} \gamma_{3n}^c(\tau,\beta)\cos(ng_0t^* + \Theta(\beta,\tau)) + \gamma_{3n}^s(\tau,\beta)\sin(ng_0t^* + \Theta(\beta,\tau)), \tag{13.64}$$

$$\Sigma_3(\tau,\beta,t^*) = \sum_{n=0}^{\infty} \Sigma_{3n}^c(\tau,\beta)\cos(ng_0t^* + \Theta(\beta,\tau)) + \Sigma_{3n}^s(\tau,\beta)\sin(ng_0t^* + \Theta(\beta,\tau)). \tag{13.65}$$

where

$$\gamma_{3n}^c = \int_0^{2\pi/g_0} \gamma_3\cos(ng_0t^* + \Theta(\beta,\tau))\mathrm{d}t^*, \quad \gamma_{3n}^s = \int_0^{2\pi/g_0} \gamma_3\sin(ng_0t^* + \Theta(\beta,\tau))\mathrm{d}t^* \tag{13.66}$$

So further we can write

$$\frac{\partial N}{\partial t} + g_0 M = \sigma_f^\dagger \cos(g_0 t^* + \Theta(\beta,\tau)) + \sigma_g^\dagger \sin(g_0 t^* + \Theta(\beta,\tau)) + \text{ higher harmonics and constant term }, \tag{13.67}$$

$$\sigma_f^\dagger = 2g_0\left[-\frac{\partial A}{\partial \tau} + D\nabla_\beta^2 A - DA(\nabla_\beta\Theta)^2 + (f_2+h_2)A\right] + g_0(\Sigma_{31}^s + \gamma_{31}^c), \tag{13.68}$$

$$\sigma_g^\dagger = 2g_0 A\left[\frac{\partial \Theta}{\partial \tau} - D\frac{2\nabla_\beta\Theta\cdot\nabla_\beta A}{A} - D\nabla_\beta^2\Theta - g_2 - \omega_0 g_0\right] + g_0(\gamma_{31}^s - \Sigma_{31}^c). \tag{13.69}$$

Now, the solvability conditions (13.56) depend on integrals in the form

$$\int_0^{2\pi/g_0} \sin(g_0nt^* + \Theta)\sin(g_0mt^* + \Theta)\mathrm{d}t^* = \pi\delta_{mn},$$
$$\int_0^{2\pi/g_0} \cos(g_0nt^* + \Theta)\cos(g_0mt^* + \Theta)\mathrm{d}t^* = \pi\delta_{mn},$$

where $\delta_{nn} = 1$, $\delta_{mn} = 0$ if $n \neq m$. Thus the only contibutions (13.56) to which are not guaranteed to be zero are

$$\int_0^{2\pi/g_0} \cos^2(g_0t^* + \Theta)\sigma_f^\dagger \mathrm{d}t^*. \tag{13.70}$$

and

$$\int_0^{2\pi/g_0} \sin^2(g_0t^* + \Theta)\sigma_g^\dagger \mathrm{d}t^*. \tag{13.71}$$

So we require $\sigma_f^\dagger = 0$ and $\sigma_g^\dagger = 0$. Finally we point out that the functions $\Sigma_{31}^{s/c}$ and $\gamma_{31}^{s/c}$ are functions of A. As Σ_3 and γ_3 are functions of u and v we could have expanded Σ and γ in terms of u and v, *e.g.*

$$\Sigma \approx \Sigma_{u2}(\lambda)u^2 + \Sigma_{v2}(\lambda)v^2 + \Sigma_{uv}(\lambda)uv + \Sigma_{u2v}(\lambda)u^2v + \Sigma_{uv2}(\lambda)uv^2 + \Sigma_{u3}(\lambda)u^3 + \Sigma_{v3}(\lambda)v^3 + \dots \tag{13.72}$$

On can then expand the λ functions about $\lambda = \lambda_0$. The point being we have a power series in F_1, F_2, G_1, G_2 which will have order ϵ^2 and ϵ^3 terms. Since F_1 and G_1 are functions of A and $\sin(g_0mt^* + \Theta)$, $\cos(g_0mt^* + \Theta)$, the functions F_2 and G_2 will also be representable as a Fourier series through (13.47). So the whole third order correction must form a Fourier series with all coefficients functions of A, hence $\Sigma_{31}^{s/c}$ and $\gamma_{31}^{s/c}$ are functions of A.

An example will perhaps make this clearer, this is taken from a nerve-firing model. If we had the case for which

$$F(u, v, \lambda) = \alpha(\lambda)u - \beta v - \lambda u^3 \Rightarrow \gamma = -\lambda u^3, \tag{13.73}$$

$$G(u, v, \lambda) = \beta u - \gamma(\lambda)v - \mu\lambda u^2 \Rightarrow \Sigma = -\mu\lambda u^2 v. \tag{13.74}$$

so

$$\gamma \approx -(\lambda_0 + \epsilon + ..)(F_1^3\epsilon^3 + \dots) = -\lambda_0 F_1^3 \epsilon^3 + \mathcal{O}(\epsilon^4), \tag{13.75}$$

$$\Sigma \approx -\mu(\lambda_0 + \epsilon + ..)(F_1^2\epsilon^2 + ...)(G_1\epsilon + G_2\epsilon^2 + ...) = -\mu\lambda_0 G_1 F_1^2 \epsilon^3 + \mathcal{O}(\epsilon^4), \tag{13.76}$$

so

$$\gamma_3 = -\lambda_0 A^3 \cos^3(\beta t^* + \Theta) \Rightarrow \gamma_{31}^c = -\frac{3\lambda_0}{4}A^3, \quad \gamma_{31}^s = 0 \tag{13.77}$$

$$\Sigma_3 = -\mu\lambda_0 A^3 \sin(\beta t^* + \Theta)\cos^2(\beta t^* + \Theta) \Rightarrow \Sigma_{31}^c = 0, \quad \Sigma_{31}^s = -\lambda_0\mu A^3/4, \tag{13.78}$$

(here we have expanded $\cos^3()$ and $\sin^2()\cos()$and taken the coefficients of the relevant terms).

So, in general the solvability condition for (13.54) takes the form

$$\frac{\partial A}{\partial \tau} = D\nabla_\beta^2 A - DA(\nabla_\beta\Theta)^2 + p(A), \tag{13.79}$$

$$\frac{\partial \Theta}{\partial \tau} = D\frac{2\nabla_\beta\Theta \cdot \nabla_\beta A}{A} + D\nabla_\beta^2\Theta + q(A). \tag{13.80}$$

with $p(A)$ and $q(A)$ arising soley from the non-linearity of F and G the original source terms of (13.25). These equations in the same form as (13.8). Specifically this system could be written as

$$\frac{\partial}{\partial \tau}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} p/A & -q \\ q & p/A \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix} + \nabla^2\begin{pmatrix} u \\ v \end{pmatrix}. \tag{13.81}$$

with $u = A\cos(g_0 t + \Theta), v = A\sin(g_0 t + \Theta)$. So now we have determined the behaviour on both the fast (t^*) and slow τ time scales of the order ϵ term of the series for u and v. We expect the spiral wave type behaviour in the neigbourhood of the parameter domain $\lambda = \lambda_0$; *i.e.*spiral wave behaviour in the parameter domain where our error of approximation is $\mathcal{O}(\epsilon^2)$ very small. Any changing behaviour of the shape of the spiral is on the timescale τ and length scale β which are both very large. Thus we would expect any spiral wave type behaviour to persist for a long time.

This result is very significant. The set of equations (13.25) cover a huge range of applications, heart modelling, pattern formation in biology, chemical and enzyme reaction systems, population modelling. What we have shown is that if, there is some parameter at which a Hopf-bifurcation occurs (the linearised eigenvalues go from real to purely imaginary) the f-g system we have studied is the dominant behavour of these more general systems in the neighborhood of this point in the λ parameter space (the error is $\mathcal{O}(\epsilon^2)$). Thus determining the existence and form of spiral waves in any such system can be boiled down to studying this one system and its conclusions apply to a huge range of biologically applicable systems.

Chapter 14

The Fredholm alternative

The solvability conditions (13.56) in the last chapter were presented without explanation. They come from a very general theorem on linear operators, *the Fredholm alternative.* We first illustrate its consequences with a relevant example. Consider the inhomogenous O.D.E

$$\frac{\mathrm{d}^2 y}{\mathrm{d}x^2} + g_0^2 y = \eta(x). \tag{14.1}$$

we consider the problem of periodic boundary condtions

$$y(0) = y(2\pi/g_0), \quad \frac{\mathrm{d}y}{\mathrm{d}x}(0) = \frac{\mathrm{d}y}{\mathrm{d}x}(2\pi/g_0). \tag{14.2}$$

The complementary solution y_c to the problem

$$\frac{\mathrm{d}^2 y_c}{\mathrm{d}x^2} + g_0^2 y_c = 0, \quad y_c(0) = y_c(2\pi/g_0), \quad \frac{\mathrm{d}y_c}{\mathrm{d}x}(0) = \frac{\mathrm{d}y_c}{\mathrm{d}x}(2\pi/g_0). \tag{14.3}$$

is

$$y_c(x) = A\sin(g_0 x) + B\cos(g_0 x). \tag{14.4}$$

We now consider the case $\eta(x) = \sin(x)$, and seek a particular solution in the form $y_p = C\sin(x)$, so

$$\frac{\mathrm{d}^2 y_p}{\mathrm{d}x^2} + g_0^2 y_p = \sin(x) \Rightarrow -C + Cg_0^2 = 1 \quad C = \frac{1}{g_0^2 - 1}. \tag{14.5}$$

The general solution in this case is

$$y(x) = A\sin(g_0 x) + B\cos(g_0 x) + \frac{1}{g_0^2 - 1}\sin(x). \tag{14.6}$$

Applying the first boundary condition we obtain

$$y(0) = y(2\pi/g_0) \Rightarrow B = B + \frac{1}{g_0^2 - 1}\sin(2\pi/g_0). \tag{14.7}$$

So generally we cannot satisfy the boundary conditions of this problem. However, if we consider the case $\eta(x) = \sin(2g_0x)$, we try the particular solution $y_p = C\sin(2g_0x)$,

$$\frac{\mathrm{d}^2y_p}{\mathrm{d}x^2} + g_0^2y_p = \sin(2g_0x) \Rightarrow -C4g_0^2 + Cg_0^2 = 1 \quad C = \frac{-1}{3g_0^2} \tag{14.8}$$

so

$$y(x) = A\sin(g_0x) + B\cos(g_0x) - \frac{1}{3g_0^2}\sin(2g_0x). \tag{14.9}$$

Applying the first boundary condition we obtain

$$y(0) = y(2\pi/g_0) \Rightarrow B = B. \tag{14.10}$$

Then

$$\frac{\mathrm{d}y}{\mathrm{d}x} = g_0(A\cos(g_0x) - B\sin(g_0x)) - \frac{2}{3g_0}\cos(2g_0x). \tag{14.11}$$

Applying the second boundary condition we obtain

$$\frac{\mathrm{d}y}{\mathrm{d}x}(0) = \frac{\mathrm{d}y}{\mathrm{d}x}(2\pi/g_0) \Rightarrow g_0A - \frac{2}{3g_0} = g_0A - \frac{2}{3g_0} \tag{14.12}$$

So we have a non-unique solution to the problem, neither A or B are determined by the boundary conditions. Of course in this case it was easy to find the particular solution as the equation/problem was linear with constant coefficients. In general it may not be easy to find a particular solution, it may well be the problem has to be solved numerically; indeed, we have seen it is not always even worth trying in the first case. The Fredholm alternative helps tell us whether we **can** expect a solution? Still further, if we can, will it be unique?

Before we start we introduce some definitions and notations. A linear operator L acting on a function f satisfies

$$L(af + bg) = aL(f) + bL(g). \tag{14.13}$$

where a and b are real constants. In our example $L = \frac{\mathrm{d}^2}{\mathrm{d}x^2} + g_0^2$. We consider the periodic problem

$$Ly = \eta(x) \quad y(0) = y(p), \quad \frac{\mathrm{d}y}{\mathrm{d}x}(0) = \frac{\mathrm{d}y}{\mathrm{d}x}(p). \tag{14.14}$$

where $x \in [0, p]$ is the domain. We define the (Hilbert) inner product $\langle f, g\rangle$ for two functions which are square integrable ($\int_0^p f^2\mathrm{d}x < \infty$), to be

$$\langle f, g\rangle = \int_0^p fg\,\mathrm{d}x. \tag{14.15}$$

We define the adjoint operator $L^\dagger$ through

$$\langle Lf, g\rangle = \left\langle f, L^\dagger g\right\rangle. \tag{14.16}$$

Some examples should help make the notion of an adjoint operator clear. The term g_0^2 is the operation of multiplying by a constant. By our definition (14.16) we have

$$\int_0^p L(f)g\,\mathrm{d}x = \int_0^p g_0^2fg\,\mathrm{d}x = \int_0^p fL^\dagger(g)\,\mathrm{d}x, \Rightarrow L^\dagger(g) = g_0^2. \tag{14.17}$$

This property, the adjoint operator being the same as the original, is known as *self-adjointness* (the operator is *self-adjoint*). This is certainly not always the case. Consider the operator $L = \frac{\mathrm{d}}{\mathrm{d}x}$, using integration by parts we have

$$\int_0^p \frac{\mathrm{d}f}{\mathrm{d}x} g \,\mathrm{d}x = [fg]_0^p - \int_0^p f \frac{\mathrm{d}g}{\mathrm{d}x} \,\mathrm{d}x = \int_0^p f L^\dagger(g) \,\mathrm{d}x. \tag{14.18}$$

Using periodic B.C.'s for the operator Lf the boundary term becomes

$$f(0) \left[g(p) - g(0)\right]. \tag{14.19}$$

which is zero if g is also periodic. In this case we see $L^\dagger = -\frac{\mathrm{d}}{\mathrm{d}x}$. This raises a crucial point. The notion of an adjoint in this context depends on the choice of the boundary conditions, not just the operator. As the far as the Fredholm alternative is concerned the boundary conditions are part and parcel of the operator. Finally for our example operator $L = \frac{\mathrm{d}^2}{\mathrm{d}x^2} + g_0^2$ we need to know the adjoint of the second derivative. Again using integration by parts we have

$$\int_0^p \frac{\mathrm{d}^2 f}{\mathrm{d}x^2} g \,\mathrm{d}x = \left[\frac{\mathrm{d}f}{\mathrm{d}x} g\right]_0^p - \left[f \frac{\mathrm{d}g}{\mathrm{d}x}\right]_0^p + \int_0^p f \frac{\mathrm{d}^2 g}{\mathrm{d}x^2} \,\mathrm{d}x = \int_0^p f L^\dagger(g) \,\mathrm{d}x, \tag{14.20}$$

$$= \frac{\mathrm{d}f}{\mathrm{d}x}(0) \left[g(p) - g(0)\right] - f(0) \left[\frac{\mathrm{d}g}{\mathrm{d}x}(p) - \frac{\mathrm{d}g}{\mathrm{d}x}(0)\right] + \int_0^p f \frac{\mathrm{d}^2 g}{\mathrm{d}x^2} \,\mathrm{d}x \tag{14.21}$$

If we assume periodic boundary conditions for g, $g(0) = g(p)$ and $\frac{\mathrm{d}g}{\mathrm{d}x}(0) = \frac{\mathrm{d}g}{\mathrm{d}x}(p)$, then we see that the second derivative operator is also self adjoint, thus

$$\text{if } L = \frac{\mathrm{d}^2}{\mathrm{d}x^2} + g_0^2 \text{ with periodic boundary conditions,} \quad L^\dagger = \frac{\mathrm{d}^2}{\mathrm{d}x^2} + g_0^2 \text{ with the same periodic boundary conditions,} \tag{14.22}$$

and the operator is self-adjoint. We are now ready for the theorem:

The alternative statement

Either

1. The homogenous problem $L^\dagger y = 0$ has a non-trivial solution.
2. The inhomogenous boundary value problem $Ly = \eta(x)$, with relevant boundary conditions has a unique solution.

This is the alternative, either 1 or 2 is true, but never simultaneously. If it is the case 1. then there is a further alternative. If $y_c^\dagger$ is the complementary solution to $L^\dagger y = 0$, then either

1. $$\int_0^p y_c^\dagger \eta(x) \mathrm{d}x = 0 \tag{14.23}$$

   and there is a non-unique solution to the problem $Ly = \eta(x)$, with relevant boundary conditions.
2. Or, this integral does not vanish and there is no solution to the problem $Ly = \eta(x)$, with relevant boundary conditions.

Returing to our example should give some clarity. As discussed above our operator L is self adjoint. Thus the complementary adjoint $y_c^\dagger$ is

$$y_c^\dagger = A\sin(g_0 x) + B\cos(g_0 x). \tag{14.24}$$

So in our first alternative we have 1: the complementary solution to the adjoint problem is non-trivial. Thus in order to have any (non-unique) solutions we must have

$$\int_0^p \sin(g_0 x)\eta(x)\mathrm{d}x = 0 \text{ and } \int_0^p \cos(g_0 x)\eta(x)\mathrm{d}x = 0 \tag{14.25}$$

We see for the case $\eta = \sin(x)$ neither of these integrals will vanish (unless $g_0 = 0$). But for the case $\eta(x) = \sin(2g_0 x)$ they do (see the orthogonality identities **??**), which is why we could solve the problem but not determine the constants A and B. We finally add that this is the problem we were considering in (13.51) hence the solvability conditions (13.56).

We give one more example, for which the second case of the alternative holds. Consider the problem

$$\frac{\mathrm{d}^2 y}{\mathrm{d}x^2} = \mathrm{e}^{2x} \quad y(0) = 0, \quad y(1) = 0. \tag{14.26}$$

We look for the adjoint,

$$\int_0^1 \frac{\mathrm{d}^2 y}{\mathrm{d}x^2} g\mathrm{d}x = \left[\frac{\mathrm{d}y}{\mathrm{d}x} g\right]_0^1 - \left[y\frac{\mathrm{d}g}{\mathrm{d}x}\right]_0^1 + \int_0^1 y\frac{\mathrm{d}^2 g}{\mathrm{d}x^2}\mathrm{d}x. \tag{14.27}$$

the second boundary term vanishes as $y = 0$ on both boundaries. As there is no condition on the derivatives $\frac{\mathrm{d}y}{\mathrm{d}x}$ we require $g(0) = g(1) = 0$ for the first boundary term to vanish, so the problem is again self-adjoint. The complementary solution to the adjoint problem solves

$$\frac{\mathrm{d}^2 y_c^\dagger}{\mathrm{d}x^2} = 0, \quad y_c^\dagger(0) = 0, \quad y_c^\dagger(1) = 0, \tag{14.28}$$

so

$$y_c^\dagger(x) = ax + b, \quad y_c^\dagger(0) = 0, \rightarrow b = 0, \quad y_c^\dagger(1) = 0, \rightarrow a = 0. \tag{14.29}$$

Thus the complementary solution of $L^\dagger y_c^\dagger = 0$ is trivial and we are in the second branch of the Fredholm alternative: there is a unique solution to the problem $Ly = e^{2x}$. This would be

$$y(x) = \mathrm{e}^{2x}/4 + (1/4 - \mathrm{e}^2/4)x - 1/4. \tag{14.30}$$

[NEM The actual Fredholm alternative is much more general than described here. In general it is true of any dimension (linear P.D.E's). We can have matrix equations and integral equations. The set of functions, which are basically defined by the definition of the norm $< f, g >$ can be drawn from any Banach space. The statement (the alternative) is usually expressed in terms of the kernel of the operator ($Ly = 0$ is the kernel of L in our case). It should be made clear we **always** need the linearity of the operator (the condition (14.13) should hold).]

A brief outline of the reason for the alternative

[NEM A hand-wavy explanation is as follows (this is not examinable). Consider the adjoint identity

$$\langle Lf, g \rangle = \left\langle f, L^{\dagger} g \right\rangle \tag{14.31}$$

If $L^{\dagger}g = 0$ then $\langle Lf, g \rangle = 0$. If $g = g_c^{\dagger}$ is non trivial *i.e.* 1. of our first alternative. This seems to imply $Lf = 0$, in which case we cannot solve $Lf = \eta(x)$. But of course if $\left\langle Lf, g_c^{\dagger} \right\rangle = \left\langle \eta(x), g_c^{\dagger} \right\rangle = 0$ for some non-trivial $g_c^{\dagger}$, Lf doesn't have to be zero. This implies the condition (14.23) which only constrains L_f up to a constant due to linearity (condition (14.13)).

On the other hand if g were originally trivial then there is no constraint on Lf as $< Lf, 0 >= 0$ whatever Lf is and no reason it cannot solve $L(f) = \eta(x)$. That this condition, $L^{\dagger}g = 0$ only if g is trivial, implies we can always solve $Lf = \eta$ and that the solution is unique is somewhat tougher to show (it relies on the relationship between the kernel of $L^{\dagger}$ and the range of L).]