

# MATH40004 - Calculus and Applications:

## Unseen Questions 5: Nonlinear systems of differential equations: The Lotka-Volterra equations

### 1 The Lotka-Volterra (predator-prey) equations

The **Lotka-Volterra** equations are a pair of first order **nonlinear** differential equations. In lectures you have seen how to solve **linear** systems of differential equations - here you will see some techniques for dealing with nonlinear systems. These techniques will be introduced as we explore the Lotka-Volterra equations.

The Lotka-Volterra equations are used to explain the dynamics of biological systems in which two species interact, one as a predator the other as the prey, which is why they are sometimes referred to as the predator-prey equations. They have also found use in economic theory. The equations are

$$\frac{dx}{dt} = ax - bxy, \quad (1)$$

$$\frac{dy}{dt} = cxy - dy, \quad (2)$$

where  $x$  represents the number (or population) of the prey (e.g. rabbits) at time  $t$ ,  $y$  represents the population of predators (e.g. foxes) at time  $t$  and  $a$ ,  $b$ ,  $c$  and  $d$  are **positive** real numbers.

### 2 Eliminating $t$ from the equations

Since the equations are nonlinear, one thing we can try to do first is to eliminate the variable  $t$  from the equations.

- (a). By dividing the two Lotka-Volterra equations (1) and (2) together show that  $x$  and  $y$  satisfy the relationship

$$cx - d \log x + by - a \log y = K, \quad (3)$$

where  $K$  is an arbitrary constant.

- (b). Using any computational method you prefer (MATLAB, Python, Wolfram Alpha, Maple, a graphics calculator, etc.) plot the curve (3) in the case where  $a = b = c = d = 1$  with several different choices of  $K$  in the range  $2 < K < K_{\max}$ ; choosing  $K_{\max} \approx 4$  should give a nice range of results.

### 3 Population Equilibrium

From the solution curves plotted in part (b) in the last exercise what did you notice happened as  $K$  approached 2? In fact when  $K = 2$  the curve disappears and only the point  $(x, y) = (1, 1)$  remains! For the case when  $a = b = c = d = 1$  this point is called a **population equilibrium**. In other words this is a point where once the populations of  $x$  and  $y$  simultaneously arrive there, they remain there for the rest of time (the populations are in equilibrium there).

The equilibria of a system can be found from setting the right hand sides of the differential equations to zero. In other words, if once the populations arrive at the point, they remain there, then this is equivalent to the derivatives  $\frac{dx}{dt}$  and  $\frac{dy}{dt}$  being equal to zero at that point.

- (a). By setting the derivatives on the LHS to zero, show that the equilibria of the Lotka-Volterra system (1)-(2) are

$$(x_0, y_0) = (0, 0), \quad \text{and} \quad (x_0, y_0) = (d/c, a/b). \quad (4)$$

## 4 Linearisation

Nonlinear systems are in general harder to deal with than linear systems for which you know how to solve and understand the dynamics using techniques from lectures. So wouldn't it be great if we could somehow make our nonlinear system of equations into a linear one? If we focus on what happens very close to the equilibria it turns out we can make the system of equations linear. This allows us to study the stability of the equilibria. The basic recipe goes as follows:

**Steps of a linear stability analysis:** For a nonlinear system of equations

- Find all the equilibria of the system  $(x_0, y_0)$ .
- For each one, make a small change to this equilibria, mathematically we write

$$(x, y) = (x_0, y_0) + \epsilon(x_1, y_1), \quad \epsilon \ll 1, \quad (5)$$

and substitute this expression into the system of equations, retaining all the terms of size  $\epsilon$  (or  $\mathcal{O}(\epsilon)$  if you have seen this notation). Throw away any terms that are much smaller (size  $\epsilon^2$  or smaller).

- Solve the resulting system of equations (which will now be linear) to find out how  $(x_1, y_1)$  change with  $t$ .
- If  $(x_1, y_1)$  grows in  $t$  we say the equilibrium point is unstable, if they decay in time we say the equilibrium point is stable.

### 4.1 Exercise: Linearisation of the Lotka-Volterra equations

- Linearise the Lotka-Volterra equations (1)-(2) around each of the system equilibria in turn (found in section 3 question (a).) and solve the resulting linear systems in each case. Draw a phase plane showing how the system behaves near to each equilibrium.
- For the equilibria at  $(x_0, y_0) = (d/c, a/b)$ :
  - Explain why the local solutions indicate that the predator population follows a similar trend to the prey population but with a time lag of  $\pi/2$ .
  - Show that the local solution curves in the phase plane are ellipses.
- For a given  $K$  explain the shape of the curve (3) plotted in section 2 part (b) from a physical context. In other words, thinking back to the physical situation these equations represent (a predator and a prey population) explain from a physical point of view why the curves might be of this general shape. Use the findings from the phase plane analysis in part (a) here to decide the direction of the trajectories.

## 5 Extension: The Competitive Lotka-Volterra equations

The system of equations

$$\frac{dx}{dt} = \alpha x(1 - x/M) - \gamma xy, \quad (6)$$

$$\frac{dy}{dt} = \beta y(1 - y/N) - \delta xy, \quad (7)$$

are called the **competitive Lotka-Volterra** equations. Here  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$ ,  $M$  and  $N$  are **positive** real numbers. The equations are a modification of the usual Lotka-Volterra system to have a logistic model growth rather than an exponential one.

(a). Consider the competitive Lotka-Volterra model

$$\frac{dx}{dt} = \alpha x(1 - x) - xy, \quad (8)$$

$$\frac{dy}{dt} = \beta y(1 - y) - xy. \quad (9)$$

For each of the cases:

(i).  $\alpha = 2$ ,  $\beta = 3$ ,

(ii).  $\alpha = 1/2$ ,  $\beta = 1/3$ .

Find the equilibrium points of the system and linearise the system around each point in turn. Analyse the resulting linear systems with a phase plane analysis for each. Piece these together to conclude what happens to the populations  $x$  and  $y$  in the long run.