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Lotka-Volterra (Predator prey)

Examples of prey and predators.

Bacteria and amoebas

Food fish and sharks

Aphids and lady bugs

Rabbit and wolves

The Lotka-Volterra equations, also know as the predator prey equations, are a pair of first-order nonlinear differential equations.

Predator:

Predator is an organism that hunts, kills and eats other organisms to survive.

Prey:

Prey is an organism which gets hunted and taken as food by other organisms.

"The Lotka-Volterra (predator-prey) system discovered separately by Alfred J. Lotka (1910) and Vito Volterra (1926)."

Predator-Prey (ladybirds / greenflies)

$x(t)$ = population of prey (greenflies)
$y(t)$ = population of predator (ladybirds)

Without interaction between predator and prey:

$$\frac{dx}{dt} = ax \qquad \frac{dy}{dt} = -cy$$

Prey has unlimited resources — Only food soure is prey.

We assume the number of "interactions" is proportional to $x(t)\ y(t)$.

Each interaction decrease the number of prey, and provides food for the predator, increasing their propulation.

So, we have a coupled set of ordinary differential equations:

$$\frac{dx}{dt} = ax - bxy \qquad a, b, c, d > 0$$

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

These are the Lotka-Volterra Equation.

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Suppose that populations of ladybirds and greenflies are described by the Lotka - Volterra equations with:

$$a=2 \quad b=0.01 \quad c=0.5 \quad d=0.0001$$

A) Find the constant solution (called the equilibrium solutions) and explain their significance.

With the given values of a, b, c, d, the Lotka - Volterra equations become:

$$\frac{dx}{dt} = 2x - 0.01xy = 0$$

$$\frac{dy}{dt} = -0.5y + 0.0001xy = 0$$

or

$$x(2-0.01y) = 0 \qquad x=0$$

$$y(-0.5+0.0001x) = 0 \qquad y=0$$

equilibrium Solution.

This make sense. If there are no ladybirds or greenflies, the populations are certainly not going to grow. We also get:

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$$2-0.01y=0$$
$$-2 \qquad\qquad -2$$

$$\frac{-0.01y}{-0.01}=\frac{-2}{-0.01}$$
$$y=200$$

$$-0.5+0.0001x=0$$
$$+0.5 \qquad\qquad +0.5$$

$$\frac{0.0001x}{0.0001}=\frac{0.5}{0.0001}$$

$$x=5000$$

So $x=5000$ and $y=200$ is also an equilibrimm solution. This tells us that population of 5000 greenflies and 200 ladybirds is stable.

This mean that 5000 greenflies are enough to support a constant ladybirds populations of 200.

B) Find an expression for $\frac{dy}{dx}$:

We use the Chain Rule

$$\frac{dy}{dx} = \frac{\frac{dy}{dt}}{\frac{dx}{dt}} = \frac{-0.5y + 0.0001xy}{2x - 0.01xy}$$

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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.*

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

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.

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

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

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

So we have a coupled set of ordinary differential equations

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

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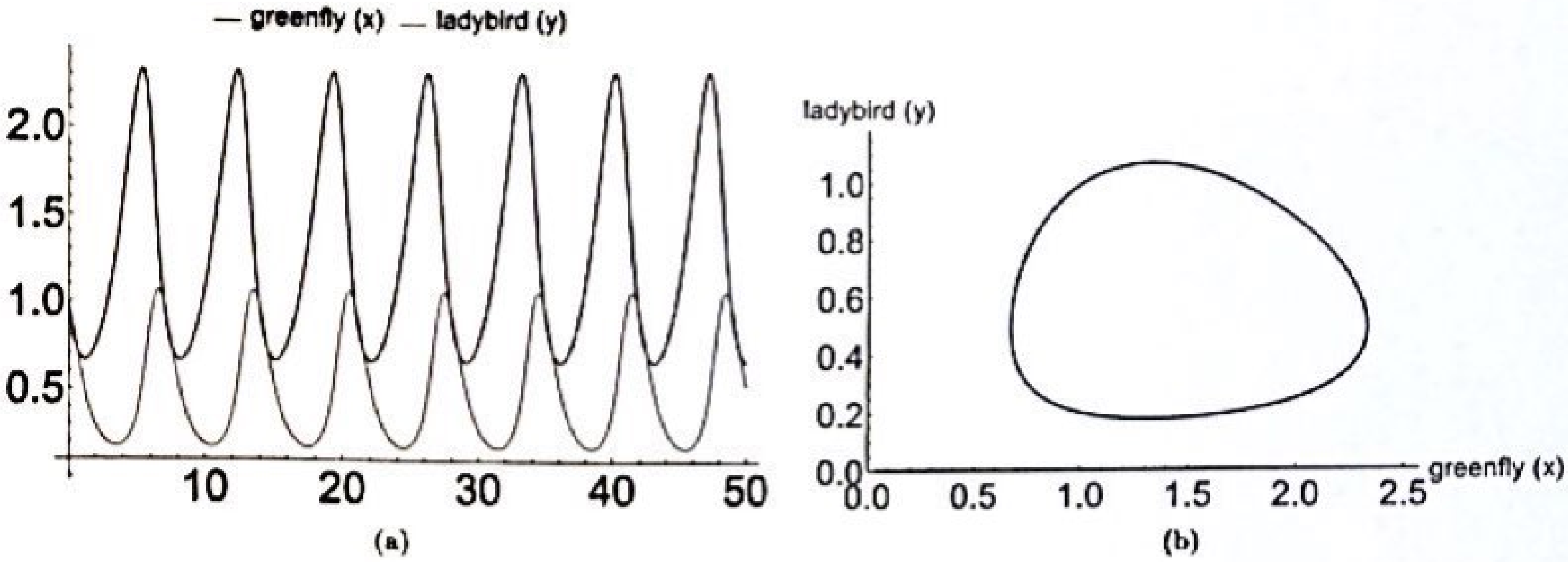

Figure 1.1: (a) A plot of the solutions $x(t)$ and $y(t)$ for $t \in [0, 50]$, for the set $(a, b, c, d) = (2/3, 4/3, 1, 1)$, $x(0) = 1$, $y(0) = 1$. (b) the phase plot of (a).

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

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

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

where

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

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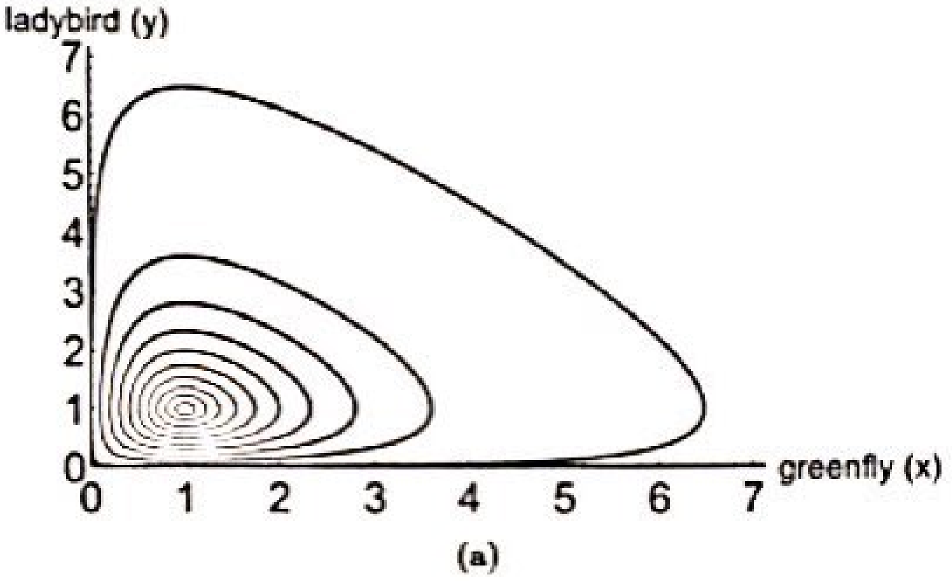

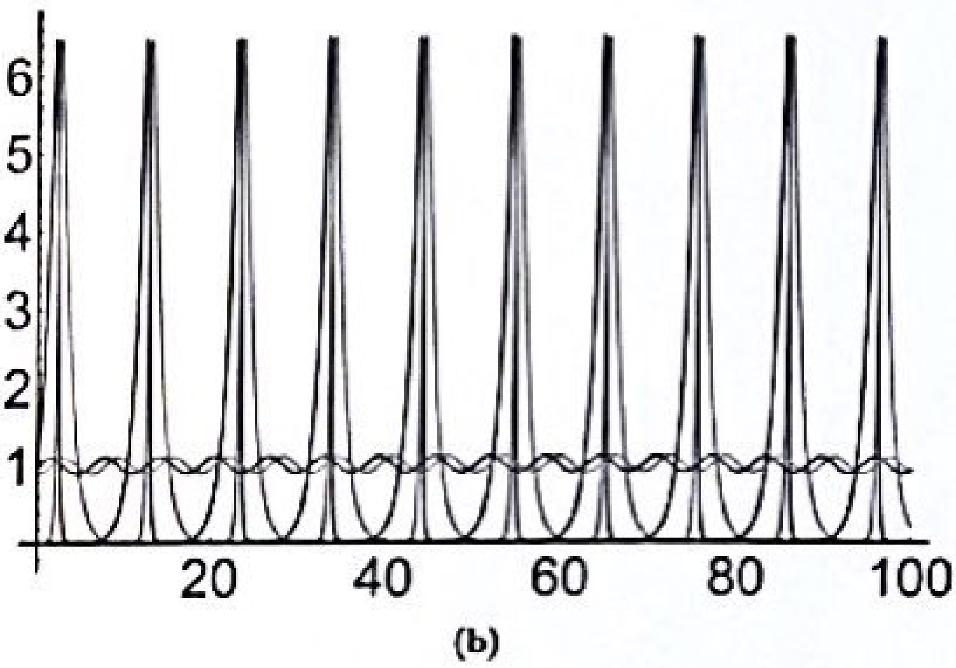

Figure 1.2: Phase and parametric solutions to the scaled Lotka-Volterra equation (1.6). (a) show phase curves for $\gamma = 1$, $\beta = 1$, $x(0) = 1$ and $y(0)$ a set of values from 0.01, the outer curve, to 0.9 the inner curve, all of which circle the equilibrium $x = y = 1$ with decreasing radius.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

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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.