

## 203. The idea of dynamics as flow

What new skills will I possess after completing this laboratory?

- **Recognising** bifurcation and limit cycles in continuous systems.
- **Applying** the flow concept in system dynamics.
- **Constructing** Kermack-McKendrick and Holling-Tanner population models.

Why do I need these skills?

Most important biochemical reactions are not elementary, and involve many nonlinear molecular interactions such as catalysis and inhibition. Ecological population models introduce us to the interesting varieties of behaviour that can arise in such nonlinear systems. We start by thinking about the **continuous logistic** population model:

$$(1) \quad \dot{x}(t) = rx(t)(1 - x(t)/K), \text{ where } r > 0 \text{ is a constant, and } t \in (0, \infty).$$

- To create the file **Populations.jl**, I simply copied the file **ReactionKinetics.jl**, then adapted it to a population model. I did not need to change the **demo()** method at all – only the definition of the model. What name do we give to this software development technique of partitioning code into separate blocks that we can change independently of each other?
- Run the Populations model now using the current settings of  $x_0 = 0.01$ ,  $r = 0.2$ ,  $K = 50$ . Substitute various values of  $r$  between 0.2 and 4.0 and observe what effect this has on the simulation output graph. What aspect of the curve does  $r$  determine, and what is the biological meaning of  $r$  in a real-life population?
- Now, keeping  $r$  constant at a value around 1.0, substitute various values of  $x_0$  between 0.001 and 4.0 and observe the effect on the output. What aspect of the curve does  $x_0$  determine, and what is the biological meaning of  $x_0$  in real-life populations?
- Now, keeping  $x_0$  constant at a value around 0.1, substitute various values of  $K$  between 1.0 and 100.0 and observe the effect on the output. What aspect of the curve does  $K$  determine, and what is the biological meaning of  $K$  in real-life populations?
- If we multiply out the bracket in (1), we obtain this form containing two terms:

$$(2) \quad \dot{x}(t) = rx(t)(1 - x(t)/K) = rx(t) - \frac{r}{K}x^2(t).$$

What is the biological meaning of the first of these two terms in real-life populations?

- What is the biological meaning of the *second* of the two terms in equation (2)?
- What are the **critical** points of equation (1), where  $\dot{x} = 0$ ?

Our first finding is that the logistic population growth model is extremely boring! Indeed, it is the simplest non-linear dynamical model that is analytic – that is, whose behaviour we can describe by combining a set of standard, closed functions:

More generally, nonlinear models can exhibit all kinds of exciting behaviour including chaotic behaviour. However, we need to wait a while before we can observe chaos, since the **Poincaré-Bendixson theorem** implies that chaos occurs only in continuous systems with three or more dimensions. As a lead-up to chaos, we first look at *limit cycles* and *bifurcation* ...

What is the structure of the skills?

The **Kermack-McKendrick** model is a dynamical model of the spread of either disease or ideas within a population  $P$  divided into three groups: *susceptibles* ( $S$ : individuals who are *susceptible* to an

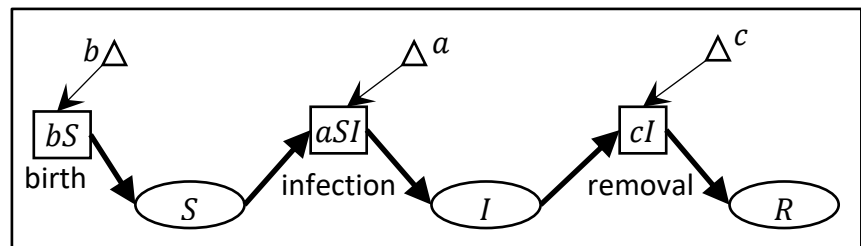
illness or an idea), *infectives* ( $I$ : those who are able/willing to pass on the disease or idea to other individuals), and those who are *removed* ( $R$ ) from the population due to immunity. The ODEs are:

$$(3) \quad P = S + I + R; \quad \dot{S} = b S(t) - a S(t)I(t); \quad \dot{I} = a S(t)I(t) - c I(t); \quad \dot{R} = c I(t)$$

where  $a$  is the infection rate,  $b$  the birth rate, and  $c$  is the recovery rate.

Notice two important features of the equations (3):

- First, there is a **flow** from group  $S$  to group  $I$  and from  $I$  to  $R$ . In other words, the terms that *deplete*  $S$  and  $I$  are respectively equal to the terms which *fill*  $I$  and  $R$ . This metaphor of flowing is central to system dynamics: always think of the thick arrows in an SPD as representing a flow of some material from one state variable to another, and *always* make sure that each flow in your diagram has a clear physical meaning.
- Second, the flow from  $S$  to  $I$  contains the product  $S \cdot I$ . As we know from the principle of mass action, this mathematical form implies a need for *contact* between two species: disease and ideas flow from one group to another through contact between  $I$  and  $S$  individuals.



- (viii) Use these ideas to build the Kermack-McKendrick model on the right. First, modify the code in **Populations.jl** by redefining the constant **model** as an array of named tuples, of which the first is the existing logistic model, and the second is your new model. You will also need to insert an integer argument into **demo()**, to specify which model to run.
- (ix) To run the model you will need actual numerical values. Typical values for the course of a disease in Australia might be:  $a = 7 \times 10^{-4}$ ,  $b = 12/1\,000$ ,  $c = 0.5$ ,  $S_0 = 20\,000$ ,  $I_0 = 5$  and  $R_0 = 2$ . Run the model over a duration of 500 years. Which system dynamics archetype does your Kermack-McKendrick model display?
- (x) Your K-M model displays a constant build-up of recovered individuals. Make the model more realistic by allowing recovered individuals to die at a constant rate with an average life-expectancy of 70 years. First make this change to the SPD, then implement the change in your simulation.
- (xi) First describe, and then explain, the similarities and differences between your Australia model and the case of Ethiopia, where  $b$  might be around  $36/1\,000$ .
- (xii) Do your findings change at all if you use more realistic death rates for Australia and Ethiopia?

### How can I extend my skills?

Now let's look at some of the interesting things that can happen with nonlinear DEs. You already know the Lotka-Volterra equations for the interactions between predators ( $y$ ) and their prey ( $x$ ). However, the L-V equations are rather unrealistic. For one thing, they assume that predators are capable of eating incredible amounts of prey: the contact term is proportional to the product  $xy$ , so if we multiplied the value of  $x$  by 1000, it should result in the predators suddenly eating 1000-times as many prey each day! This is clearly not what we observe in real life.

Holling and Tanner introduced the following equations to solve this modelling problem:

$$(4) \quad \dot{x} = r_1 x \left(1 - \frac{x}{k}\right) - \frac{wx}{d+x} y; \quad \dot{y} = r_2 y \left(1 - \frac{Ny}{x}\right)$$

In these equations, the term  $x(1 - x/k)$  represents logistic growth of the prey in isolation;  $\frac{wxy}{(1+x)}$  represents saturated predation (think of Hill functions!); and  $0.2y(1 - Ny/x)$  models logistic predator growth in which each predator requires  $N$  prey to survive.

- (xiii) The H-T equations contain six unspecified parameters, making them rather difficult to work with mathematically. However, each of these parameters has a biological meaning. Discuss with partners what each parameter means, and specify appropriate units for each parameter, assuming that we measure time in years.

For now, we assume that  $r_1 = 1$ ,  $k = 7$ ,  $w = \frac{6}{7}$ ,  $d = 1$  and  $r_2 = 0.2$ , giving us these equations:

$$(5) \quad \dot{x} = x \left( 1 - \frac{x}{7} \right) - \frac{6xy}{7+7x}; \quad \dot{y} = 0.2y \left( 1 - \frac{Ny}{x} \right)$$

- (xiv) Use flows to build this H-T model for the specific case  $N = 2.5$ . In your model, treat  $N$  as a parameter, and change **demo()** to draw an  $xy$  phase-plot of the two species  $x$  and  $y$ .
- (xv) Now use **plot!()** to plot a phase portrait of the H-T system that repeatedly adds trajectories to the current axes. Build up a portrait of the behaviour of the system by choosing various initial values for  $x$  and  $y$  covering the range  $[0,10] \times [0,5]$ . You should be able to observe two different types of critical points in your portrait.
- (xvi) Change the value of  $N$  to 0.5; what two critical points can you find now?

You have just discovered two important phenomena in dynamical systems. The behaviour in exercise (xv) cycles around a centre, and all trajectories converge to this cycle – hence it is called a **limit cycle**. Also, when  $N$  changes smoothly from 0.5 to 2.5, the behaviour of the system (5) changes suddenly from attraction to cycles. We call this rapid, qualitative change in the dynamics of a system a **bifurcation** (i.e., “branching in two”).

- (xvii) Explore the bifurcation of the H-T system (5). Substitute different values of  $N$  to look for the approximate value of  $N$  at which the bifurcation occurs, and describe in detail the story of how the transition from attraction to cycling occurs.

#### How can I deepen my practice of the skills?

- (xviii) Repeat the work of exercises (xv) to (xvii), using BOTGs instead of phase portraits to find the period of the limit cycles for  $N = 0.5$ . If we measure time in 6-month intervals, this model represents well the data for populations of lynx and hare. Which of the two representations, BOTG or phase-plot, is more convenient for which purposes?
- (xix) Imagine that two competing species are modelled by the equations  $\dot{x} = x(2 - x - y)$  and  $\dot{y} = y(c - y - c^2x)$ , where  $c$  is a constant parameter. Use the techniques of this lab to investigate, describe and explain the qualitative behaviour of this system as  $c$  varies.