Mathematical Modelling in Biology
Lecture Notes

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Contents

Chapter 1: Discrete-time models for a single species

In this chapter we will explore models of a single species that can be assumed to evolve in discrete generations. We will look at some simple techniques to explore the behaviours that can be displayed by the models, before looking at bifurcations and oscillatory behaviour.

When there is no overlap in population numbers between each generation, it can be appropriate to apply a discrete-time model:

$$N_{t+1} = f(N_t) = N_t g(N_t). \tag{1.1}$$

1.1 Examples

Exponential growth

A simple example is

$$N_{t+1} = rN_t, \tag{1.2}$$

which implies

$$N_t = r^t N_0 \to \begin{cases} \infty & r > 1 \\ N_0 & r = 1 \\ 0 & r < 1 \end{cases}. \tag{1.3}$$

Ricker model

An extension of the simple exponential model is called the Ricker model and it includes a reduction of the growth rate for large N_t:

$$N_{t+1} = N_t \exp\left[r\left(1 - \frac{N_t}{K}\right)\right], \quad r > 0 \quad K > 0, \tag{1.4}$$

or, in non-dimensionalised form (letting $N_t = Ku_t$),

$$u_{t+1} = u_t \exp\left[r\left(1 - u_t\right)\right]. \tag{1.5}$$

1.2 Dynamic behaviour

Steady states. A *steady state*, N_s, for a discrete-time population model satisfies

$$N_s = f(N_s) = N_s g(N_s). \tag{1.6}$$

1.2.1 Cobwebbing

We can start developing an idea of how this system evolves in time via *cobwebbing*, a graphical technique, as shown in Figure 1.1 for the Ricker model. In particular, it is clear that the behaviour sufficiently close to a fixed point, N_s, depends on the value of $f'(N_s)$.

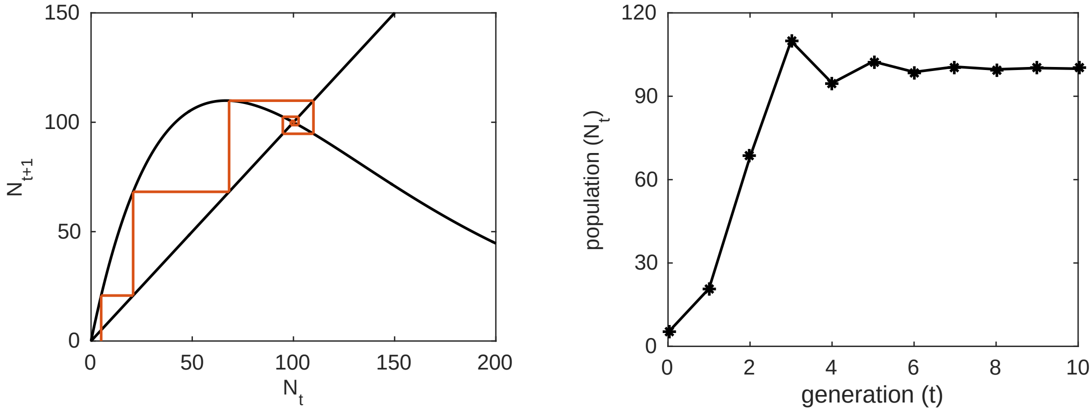
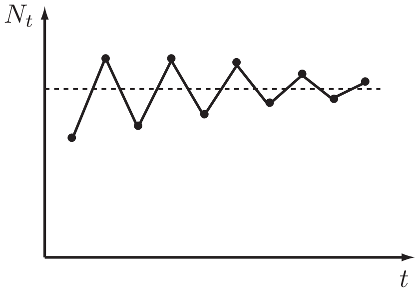
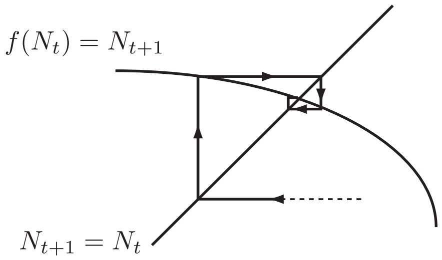


Figure 1.1: Dynamics of the Ricker model. The left-hand plot shows a plot of $N_{t+1} = N_t \exp\left[r\left(1 - N_t/K\right)\right]$ alongside $N_{t+1} = N_t$ with the cobwebbing technique shown. The right-hand plot shows N_t for successive generation times $t = 1, 2, \ldots, 10$. Parameters are: $N_0 = 5$, $r = 1.5$ and $K = 100$.

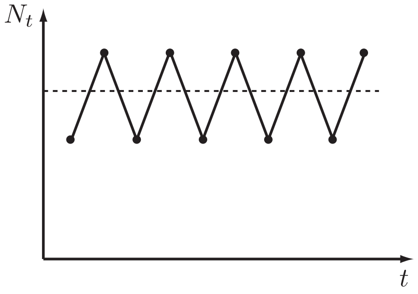
For example:

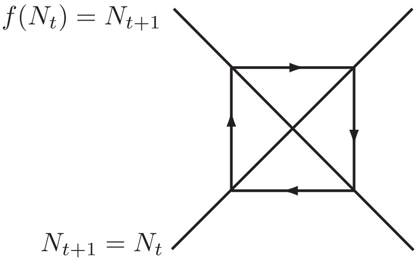
- $-1 < f'(u_s) < 0$



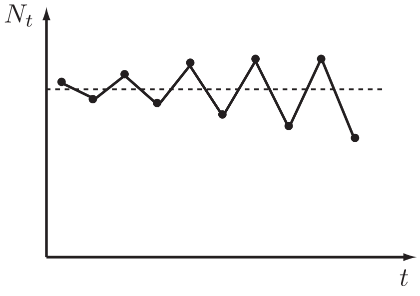


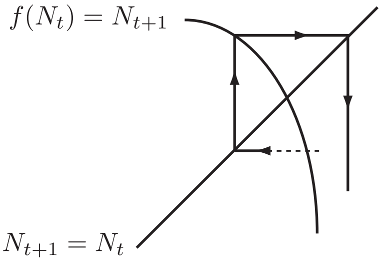
- $f'(u_s) = -1$





- $f'(u_s) < -1$





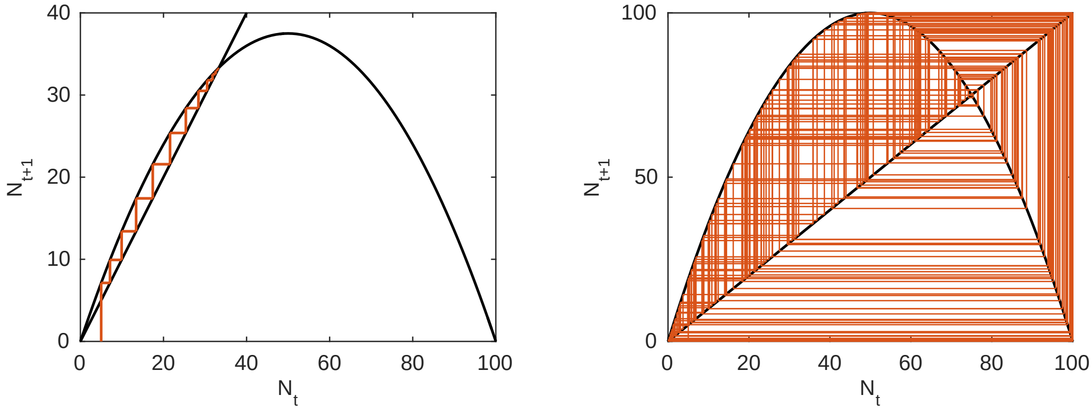


Figure 1.2: Dynamics of the discrete-time logistic model. The left-hand plot shows results for $r = 1.5$ whilst the right-hand plot shows results for $r = 4.0$. Other parameters are: $N_0 = 5$ and $K = 100$.

1.2.2 Linear stability

More generally, to consider the stability of a steady state algebraically, rather than graphically, we write

$$N_t = N_s + n_t, \tag{1.7}$$

where N_s is the steady state. Note that N_s is time independent and satisfies $N_s = f(N_s)$. Hence

$$N_{t+1} = N_s + n_{t+1} = f(N_s + n_t) = f(N_s) + n_t f'(N_s) + \mathcal{O}(n_t^2). \tag{1.8}$$

Consequently, we have

$$n_{t+1} = f'(N_s) n_t, \tag{1.9}$$

where $f'(N_s)$ is a constant, independent of t, and thus

$$n_t = \left[f'(N_s)\right]^t n_0. \tag{1.10}$$

This means that N_s is linearly stable if $|f'(N_s)| < 1$ and linearly unstable if $|f'(N_s)| > 1$.

1.3 Further investigation

The equations are not as simple as they seem. For example, from what we have seen thus far, the discrete-time logistic model seems innocuous enough.

$$N_{t+1} = rN_t\left(1 - \frac{N_t}{K}\right), \quad r > 0 \quad K > 0. \tag{1.11}$$

If we put in enough effort, one could be forgiven for thinking that the use of cobwebbing will give a simple representation of solutions of this equation. However, the effects of increasing r are stunning. Figure 1.2 shows examples of cobwebbing when $r = 1.5$ and $r = 4.0$. It should now be clear that even this simple equation does *not* always yield a simple solution! How do we investigate such a complicated system in more detail?

Bifurcation point. A *bifurcation point* is, in the current context, a point in parameter space where the number of steady state, or their stability properties, or both, change.

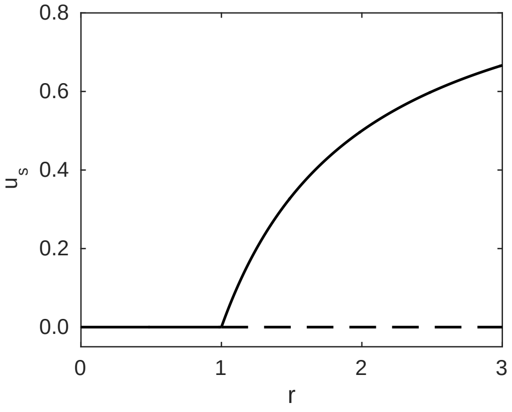


Figure 1.3: Bifurcation diagram for the non-dimensional discrete-time logistic model. The non-zero steady state is given, for $r > 1$, by $N^* = (r-1)/r$.

1.3.1 Bifurcations in the logistic growth model

We proceed to take a closer look at the non-dimensional discrete-time logistic growth model (again, let $N_t = Ku_t$):

$$u_{t+1} = ru_t\,(1-u_t) = f(u_t), \tag{1.12}$$

for different values of the parameter r, and, in particular, we seek the values where the number or stability nature of the steady states change. Note that we have steady states at $u_s = 0$ and $u_s = (r-1)/r$, and that $f'(u) = r(1-2u)$.

For $0 < r < 1$, we have:

- $u_s = 0$ is a stable steady state since $|f(0)| = |r| < 1$;
- the steady state at $u_s = (r-1)/r$ is unstable. It is also unreachable, and thus irrelevant, for physical initial conditions with $u_0 \geq 0$.

For $1 < r < 3$ we have:

- $u_s = 0$ is an unstable steady state since $|f'(0)| = |r| > 1$;
- $u_s = (r-1)/r$ is an stable steady state since $|f'((r-1)/r)| = |2-r| < 1$.

In Figure 1.3 we plot this information on a diagram of steady states, as a function of r, with stable steady states indicated by solid lines and unstable steady states by dashed lines. When $r = 1$ we have $(r-1)/r = 0$, so both steady states are at $u_s = 0$, with $f'(u_s = 0) = 1$. Clearly we have a switch in the stability properties of the steady states, and thus $r = 1$ is a bifurcation point.

What happens for $r > 3$? We have steady states at $u_s = 0$, $u = (r-1)/r$ and $f'(u_s = (r-1)/r) < -1$ so that both steady states are unstable. Hence if the system approaches one of these steady states the approach is only transient; it quickly moves away. We have a switch in the stability properties of the steady states, and thus $r = 3$ is a bifurcation point.

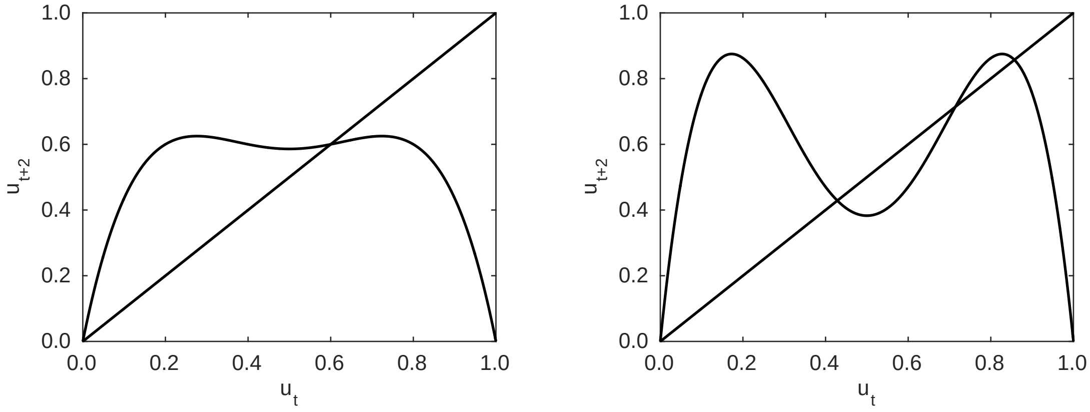


Figure 1.4: Dynamics of the non-dimensional discrete-time logistic model in terms of every second iteration. The left-hand plot shows results for $r = 2.5$ whilst the right-hand plot shows results for $r = 3.5$.

1.4 Periodic solutions

The m^{th} *composition* of the function f is given by

$$f_m(u) := \underbrace{[f \cdot f \ldots f \cdot f]}_{m \text{ times}}(u). \tag{1.13}$$

A point u is *periodic of period* m for the function f if

$$f_m(u) = u, \quad f_i(u) \neq u, \quad i \in \{1, 2, \ldots m-1\}. \tag{1.14}$$

We can determine the *linear stability* of the periodic solution in the same way as before: suppose u_0 is an steady state of period m for the function f and let $u_i = f_i(u_0)$ for $i \in \{1, 2, \ldots, m-1\}$. We define λ as

$$\begin{aligned} \lambda &= \frac{\mathrm{d}}{\mathrm{d}u} f_m(u)\bigg|_{u=u_0} \\ &= \frac{\mathrm{d}}{\mathrm{d}u}\left[f(Q(u))\right]\bigg|_{u=u_0} \\ &= f'(Q(u))\frac{\mathrm{d}Q}{\mathrm{d}u}\bigg|_{u=u_0} \\ &= f'(u_{m-1})\frac{\mathrm{d}}{\mathrm{d}u} f_{m-1}\bigg|_{u=u_0}, \end{aligned} \tag{1.15}$$

where $Q(u) = f_{m-1}(u)$. Hence, by iteration, we have that u_0 is linearly stable if

$$\prod_{i=0}^{m-1}\left[H'(u_i)\right] < 1. \tag{1.16}$$

1.4.1 Periodic solutions in the discrete-time logistic growth model

To consider the dynamics of this system once $r > 3$ we consider

$$u_{t+2} = f(u_{t+1}) = f\left[f(u_t)\right] := f_2(u_t) = r\left[ru_t(1-u_t)\right]\left[1 - ru_t(1-u_t)\right]. \tag{1.17}$$

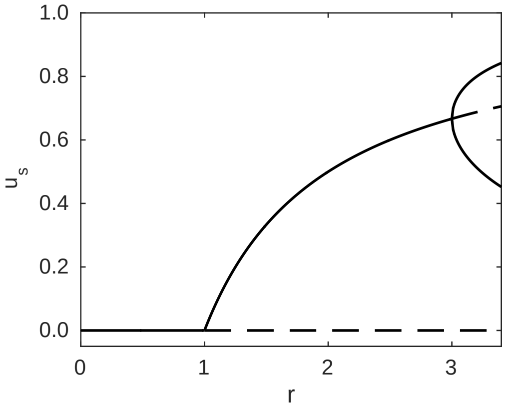


Figure 1.5: Bifurcation diagram for the non-dimensional discrete-time logistic model with inclusion of the period 2 solutions.

Figure 1.4 shows $f_2(u_t)$ for $r = 2.5$ and $r = 3.5$ and demonstrates the additional steady states that arise as r is increased past $r = 3$. The fixed points of f_2 satisfy $u_{2,s} = f_2(u_{2,s})$, which is a quartic equation in $u_{2,s}$. However, we know two solutions, the fixed points of f, *i.e.* 0 and $(r-1)/r$. Using standard techniques we can reduce the quartic to a quadratic, which can be solved to reveal the further fixed points of f_2, namely

$$u^{\pm}_{2,s} = \frac{r+1}{2r} \pm \frac{1}{2r}\sqrt{(r-1)^2 - 4}. \tag{1.18}$$

These roots are real if $(r-1)^2 > 4$, *i.e.* $r > 3$.

In this case, the points $u^{\pm}_{2,s}$ are points of period 2 for the function f with

$$u^{-}_{2,s} = f\left(u^{+}_{2,s}\right), \qquad u^{+}_{2,s} = f\left(u^{-}_{2,s}\right). \tag{1.19}$$

For stability we require

$$\left|f'\left(u^{+}_{2,s}\right) f'\left(u^{-}_{2,s}\right)\right| < 1. \tag{1.20}$$

We can substitute to show that the steady states

$$u^{\pm}_{2,s} = \frac{r+1}{2r} \pm \frac{1}{2r}\sqrt{(r-1)^2 - 4}, \tag{1.21}$$

are linearly stable for the dynamical system $u_{t+1} = f_2(u_t)$, with $r > 3$, $(r-3) \ll 1$.

We plot the fixed points of f_2, which we now know to be stable, in addition to the fixed points of f_1, in Figure 1.5. The upper branch, $u^{+}_{2,s}$, is given by the positive root of equation (1.21) whilst the lower branch, $u^{-}_{2,s}$, is given by the negative root. We have $u^{-}_{2,s} = f(u^{+}_{2,s})$, $u^{+}_{2,s} = f(u^{-}_{2,s})$. Thus a stable, period 2, oscillation is present, at least for $(r-3) \ll 1$. Any solution that gets sufficiently close to either $u^{+}_{2,s}$ or $u^{-}_{2,s}$ stays close.

Subsequent bifurcations

For higher values of r, there is a bifurcation point for f_2; we can then find a stable fixed point for $f_4(u) := f_2[f_2(u)]$ in a similar manner. Increasing r further there is a bifurcation point for $f_4(u)$. To bring further understanding to this complex system, we can think an orbits: an *orbit* generated by the point u_0 is the set points $\{u_0, u_1, u_2, , u_3, \ldots\}$ where $u_i = f_i(u) = f(u_{i-1})$. We

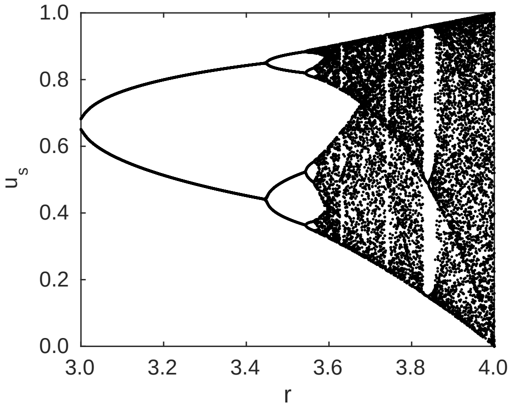


Figure 1.6: The orbit diagram of the logistic map. For each value of $r \in [3,4]$ along horizontal axis, points on the large time orbits of the logistic map are plotted.

are primarily interested in the large time behaviour of these systems in the context of biological applications. Thus, for a fixed value of r, we start with a reasonable initial seed, say $u_s = 0.5$, and plot the large time asymptote of the orbit of u_s, *i.e.* the points $f_i(u_s)$ once i is sufficiently large for there to be no transients. This gives an intriguing plot; see Figure 1.6. In particular, we have regions where, for r fixed, there are three points along the vertical corresponding to period 3 oscillations. This means any period of oscillation exists and we have a chaotic system[1].

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[1] This can be proved using Sharkovskii's theorem. See P. Glendinning, Stability, Instability and Chaos for more details on chaos and chaotic systems.

Chapter 2: Discrete-time models for interacting species

We will first explore models that explicitly take into account different ages within a population. These models will consist of different species that represent different age categories. Although not strictly "interacting species", such models can be analysed in much the same way as more traditional interacting species models such as predator-prey. We will consider these models in the second half of this chapter.

2.1 Discrete-time age-structured models

The models that we have looked at thus far describe populations for which it is sensible to assume that, for example, birth and death rates of individuals do not depend on age, sex or genetic make up. In this section we will look at a simple model that takes into account variation in birth and death rates depending on the age of the individual.

2.1.1 A simple example

Suppose that a population can be divided into two age classes that differ in their reproduction rates. Denoting n_t^1 as the number of individuals in age class 1 at time t, and n_t^2 as the number of individuals in age class 2 at time t we can write

$$\begin{aligned} n_{t+1}^1 &= f_1 n_t^1 + f_2 n_t^2, \qquad (2.1) \\ n_{t+1}^2 &= s_1 n_t^1, \qquad (2.2) \end{aligned}$$

where f_1 and f_2 are the reproductive rates of individuals in age classes 1 and 2, respectively, and s_1 is the survival probability for individuals in age class 1 to reach age class 2. Our goal for this simple model will be to analyse the population growth rate.

2.1.2 Leslie matrix

More generally, and with ω classes within the population, we can write an age-structured model in the general form

$$\boldsymbol{n}_{t+1} = \mathcal{L}\boldsymbol{n}_t \quad \text{where} \quad \mathcal{L} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{\omega-1} & f_\omega \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{\omega-1} & 0 \end{pmatrix} \quad \Longrightarrow \quad \boldsymbol{n}_t = \mathcal{L}^t \boldsymbol{n}_0, \qquad (2.3)$$

where $\boldsymbol{n} = [n^1, n^2, \ldots, n^\omega]^T$. In the above, the s_i are the probabilities of surviving from age i to age $i+1$ and each individual of age i produces f_i offspring on average over a generation. The matrix $\mathcal{L}$ is knows as a *Leslie matrix* or population projection matrix.

Theorem. For any Leslie matrix $\mathcal{L}$, there exists a real positive eigenvalue λ_1 that is a simple root of the characteristic equation

$$\det(\mathcal{L} - \lambda \mathcal{I}) = 0. \tag{2.4}$$

This eigenvalue, which is called the *dominant eigenvalue*, is strictly greater in magnitude than any other eigenvalue. The associated right eigenvector $\boldsymbol{w}_1$ and left eigenvector $\boldsymbol{v}_1$ are both real and the only strictly positive right and left eigenvectors of $\mathcal{L}$.

Corollary. The dominant eigenvalue determines the long time properties of the population:

- if $\lambda_1 > 1$ then $\boldsymbol{n}_t \to A\lambda_1^t \boldsymbol{v}_1$;
- if $\lambda_1 < 1$ then $\boldsymbol{n}_t \to 0$ as $t \to \infty$.

The right eigenvector is proportional to the stable age distribution. It can be rescaled to give either the proportion or the percentage of individuals in each age class. The left eigenvector is the reproductive value of the population. That is the number of offspring that an individual may expect to have in the future at their current age. This vector may be scaled so that its first element is one.

2.2 A discrete-time predator-prey model

We will consider interactions between predators, P, and prey, N, of the form

$$\begin{aligned} N_{t+1} &= rN_t f(N_t, P_t), & (2.5) \\ P_{t+1} &= N_t g(N_t, P_t). & (2.6) \end{aligned}$$

Here, $r > 0$ is the net linear birth rate of prey, and f is represents the influence of the predator on the birth rate. The function g describes the efficiency with which the predator searches for the prey.

We will first consider a model where the predators search over a constant area, and have an unlimited capacity for consuming prey:

$$\begin{aligned} N_{t+1} &= rN_t e^{-aP_t}, & (2.7) \\ P_{t+1} &= N_t \left(1 - e^{-aP_t}\right), & (2.8) \end{aligned}$$

where $a > 0$ represents the strength of the predation effect.

2.2.1 Linear stability analysis

The model has steady states

$$(N^*, P^*) = (0, 0) \qquad \text{and} \qquad (N^*, P^*) = \left(\frac{\ln r}{a}, \frac{r \ln r}{a(r-1)}\right), \tag{2.9}$$

where the second steady state exists only for $r > 1$.

We can explore the linear stability of these steady states by writing

$$N_t = N^* + n_t, \qquad P_t = P^* + p_t, \tag{2.10}$$

substituting into equations (2.7)-(2.8) and keeping terms up to first order.

For the trivial steady state we have

$$n_{t+1} = rn_t, \qquad p_{t+1} = 0. \tag{2.11}$$

Hence for $r < 1$ the steady state $(N^*, P^*) = (0, 0)$ is linearly stable, whilst for $r > 1$ it is unstable.

For the non-zero steady state we can write

$$\begin{pmatrix} n_{t+1} \\ p_{t+1} \end{pmatrix} = \begin{pmatrix} 1 & -N^*a \\ 1-1/r & N^*a/r \end{pmatrix} \begin{pmatrix} n_t \\ p_t \end{pmatrix}. \tag{2.12}$$

We seek solutions of the form

$$\begin{pmatrix} n_t \\ p_t \end{pmatrix} = B \begin{pmatrix} 1 \\ 1 \end{pmatrix} \lambda^t, \tag{2.13}$$

where B is an arbitrary, constant 2×2 matrix. Substituting into equation (2.12) shows that for a non-trivial solution we require

$$\det(A - \lambda\mathcal{I}) = 0 \quad \Longrightarrow \quad \det \begin{pmatrix} 1-\lambda & -N^*a \\ 1-1/r & N^*a/r - \lambda \end{pmatrix} = 0, \tag{2.14}$$

and so

$$\lambda_{1,2} = \frac{1}{2}\left[1 + \frac{\ln r}{r-1} \pm \sqrt{\left(1 + \frac{\ln r}{r-1}\right)^2 - 4\frac{r\ln r}{r-1}}\right]. \tag{2.15}$$

The term under the square root is negative, so $\lambda_{1,2}$ are complex conjugates, and

$$|\lambda_1|^2 = \frac{r\ln r}{r-1} > 1 \quad \text{for} \quad r > 1. \tag{2.16}$$

This means that n_t and p_t become unbounded at $t \to \infty$ and so the non-zero steady state is unstable. Since $\lambda_{1,2}$ are complex conjugates then n_t and p_t increase in an oscillatory manner.

The take home message from this simple example, is that this model is too simple (neglects key biological phenomena) to be useful in modelling any real, practical situation.

2.2.2 A modified predator-prey model

One simple assumption of the previous model was that the prey grows unboundedly in the absence of predators (consider the linear stability of the trivial steady state for $r > 1$). A more realistic model could include saturation in the prey population. For example:

$$\begin{aligned} N_{t+1} &= rN_t \exp\left[r\left(1 - \frac{N_t}{K}\right) - aP_t\right], \qquad (2.17) \\ P_{t+1} &= N_t\left(1 - e^{-aP_t}\right). \qquad (2.18) \end{aligned}$$

In the absence of predators, growth of the prey population is governed by the Ricker model, equation (1.4). It can be shown that there is a steady state with both prey and predator populations non-zeros, that is linearly stable for some $r > 0$.

Chapter 3: Continuous-time models for a single species

We will now move to look at modelling the dynamics of biological populations using continuous-time models. Such models can be used to describe the dynamics of a far wider range of biological phenomena. In this chapter we will consider models for a single species, taking into account the effects of other species (for example, predatory effects or harvesting) in a simple way. We will conclude with a brief look at the role of delays.

3.1 Introduction

A core feature of population dynamics models is the conservation of population number, *i.e.*

$$\begin{aligned}\text{rate of increase of population} &= \text{birth rate} - \text{death rate} \\ &\quad + \text{rate of immigration} - \text{rate of emigration.}\end{aligned} \tag{3.1}$$

We will make the assumption the system is closed and thus there is no immigration or emigration. Let $N(t)$ denote the population at time t. Equation (3.1) can be written

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N) = Ng(N), \tag{3.2}$$

where $g(N)$ is defined to be the *intrinsic growth rate.*

3.1.1 Simple examples

The Malthus (exponential) model

In the Malthus model, we have

$$f(N) = (b-d)N := rN, \tag{3.3}$$

where b and d are constant birth and death rates. Thus, the population grows (or decays) exponentially,

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN \qquad \Longrightarrow \qquad N(t) = N_0 e^{rt}. \tag{3.4}$$

The Verhulst (logistic) model

In the logistic model we have

$$f(N) = rN\left(1 - \frac{N}{K}\right). \tag{3.5}$$

Here, r is defined to be the *linear birth rate* and K is defined to be the *carrying capacity.* We can non-dimensionalise by taking $N = Ku$ and $t = \tau/r$, so that

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = u(1-u). \tag{3.6}$$

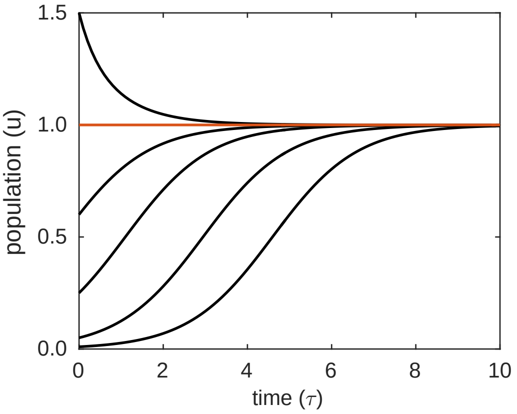

Figure 3.1: Logistic growth for $u_0 < 1$ and $u_0 > 1$.

For $u \ll 1$ (equivalently, $N \ll K$) the growth rate is approximately linear in u,

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} \approx u \qquad \Longrightarrow \qquad u \approx u_0 e^t, \tag{3.7}$$

and as $u \to 1$ (equivalently, $N \to K$),

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} \to 0. \tag{3.8}$$

We have can solve explicitly to give

$$u(t) = \frac{u_0 e^t}{1 + u_0(e^t - 1)} \to 1 \quad \text{as} \quad t \to \infty. \tag{3.9}$$

Sketching $u(\tau)$ against time, τ yields solutions as plotted in Figure 3.1: solutions monotonically relax to $u = 1$ as $\tau \to \infty$.

3.1.2 Investigating model dynamics

There are two techniques we can use to investigate the model

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N) = Ng(N). \tag{3.10}$$

Analytic solution

For the initial conditions $N(0) = N_0$, with N_0 fixed, we can we formally integrate equation (3.10) to give $N(t) = N^*(t)$, where $N^*(\cdot)$ is the inverse of the function $F(\cdot)$ defined by

$$F(x) = \int_{N_0}^{x} \frac{1}{f(s)}\,\mathrm{d}s. \tag{3.11}$$

However, unless integrating and finding the inverse function is straightforward, there is an easier way to determine the dynamics of the system.

Sketch the graph of $f(N)$

Plot $\mathrm{d}N/\mathrm{d}t = f(N) = Ng(N)$ as a function of N. For example, with

$$f(N) = Ng(N) = N(6N^2 - N^3 - 11N + 6) = N(N-1)(N-2)(3-N), \tag{3.12}$$

we have the plot shown in Figure 3.2. We see that:

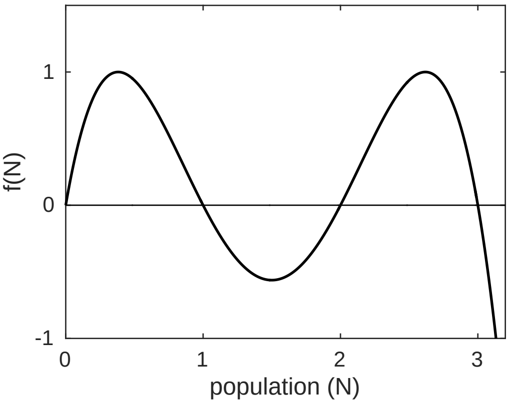

Figure 3.2: Growth according to the dynamics $f(N) = N(N-1)(N-2)(3-N)$.

- when $N_0 \in (0,2)$ the large time asymptote is $N(\infty) = 1$;
- for $N_0 > 2$ the large time asymptote is $N(\infty) = 3$;
- $N(t) \equiv 0$ if $N(0) = 0$.

3.2 Steady states and linear stability

The two main aspects of the model we generally wish to understand are the steady states and their stability.

Steady states. A *steady state* is a point where the dynamics does not change in time. Thus, in our specific context of $\mathrm{d}N/\mathrm{d}t = f(N)$, the steady states, N_s, are such that $f(N_s) = 0$.

Stability. Such a steady state is *stable* if a solution starting sufficiently close to the steady state remains close to the steady state. A rigorous definition is as follows: let $N_{N_0}(t)$ denote the solution to $\mathrm{d}N/\mathrm{d}t = f(N)$ with initial condition $N(0) = N_0$. A steady state N_s is stable if, and only if, for all $\epsilon > 0$ there exists a δ such that if $|N_s - N_0| < \delta$ then $|N_{N_0}(t) - N_s| < \epsilon$.

3.2.1 Linear stability

Suppose N_s is a steady state of $\mathrm{d}N/\mathrm{d}t = f(N)$. We wish to determine its *linear stability*, and we do so by making a small perturbation about N_s:

$$N(t) = N_s + n(t), \quad |n(t)| \ll N_s. \tag{3.13}$$

We have, by using a Taylor expansion of $f(N)$ and denoting $' = \mathrm{d}/\mathrm{d}N$, that

$$f\left(N(t)\right) = f\left(N_s + n(t)\right) = f(N_s) + n(t)f'(N_s) + \frac{1}{2}n(t)^2 f''(N_s) + \ldots, \tag{3.14}$$

and hence

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \frac{\mathrm{d}N}{\mathrm{d}t} = f\left(N(t)\right) = f(N_s) + n(t)f'(N_s) + \frac{1}{2}n(t)^2 f''(N_s) + \ldots. \tag{3.15}$$

The linearisation of $\mathrm{d}N/\mathrm{d}t = f(N)$ about the steady state N_s is given by neglecting higher order (and thus smaller) terms to give

$$\frac{\mathrm{d}n}{\mathrm{d}t} = f'(N_s)n(t) \qquad \Longrightarrow \qquad n(t) = n(0)\exp\left[t\frac{\mathrm{d}f}{\mathrm{d}N}(N_s)\right]. \tag{3.16}$$

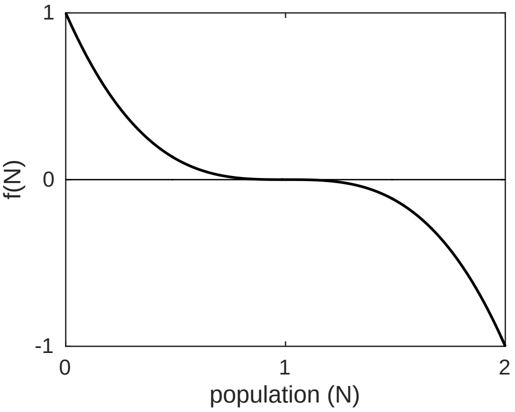

Figure 3.3: Growth according to the dynamics $f(N) = (1 - N)^3$.

The steady state N_s is *linearly stable* if $n(t) \to 0$ as $t \to \infty$. In other words, N_s is linearly stable if

$$\frac{\mathrm{d}f}{\mathrm{d}N}(N_s) < 0. \tag{3.17}$$

Example 1

To understand which of the steady states of the system

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N) = N(N-1)(N-2)(3-N), \tag{3.18}$$

are linearly stable, we consider the graph of $f(N)$. Steady states with negative gradient are linearly stable (see Figure 3.2).

Example 2

Plotting $f(N)$ for the logistic model shows that $N_s = 0$ is unstable, whilst $N_s = K$ is stable.

Example 3

Note that we can find functions $f(N)$ such that $\mathrm{d}N/\mathrm{d}t = f(N)$ has a steady state which is stable and *not* linearly stable. For example, the function

$$f(N) = (1-N)^3, \tag{3.19}$$

gives $f'(1) = 0$ and is therefore not linearly stable (see Figure 3.3).

3.3 Models of predation

In this section we will consider two models that include the effects of predation upon population evolution and persistence.

3.3.1 The Allee effect

The Allee effect is the phenomenon that individuals within a species generally require the assistance of another for more than simple reproductive reasons in order to persist. Examples of these can easily be seen in animals that hunt for prey or defend against predators as a group.

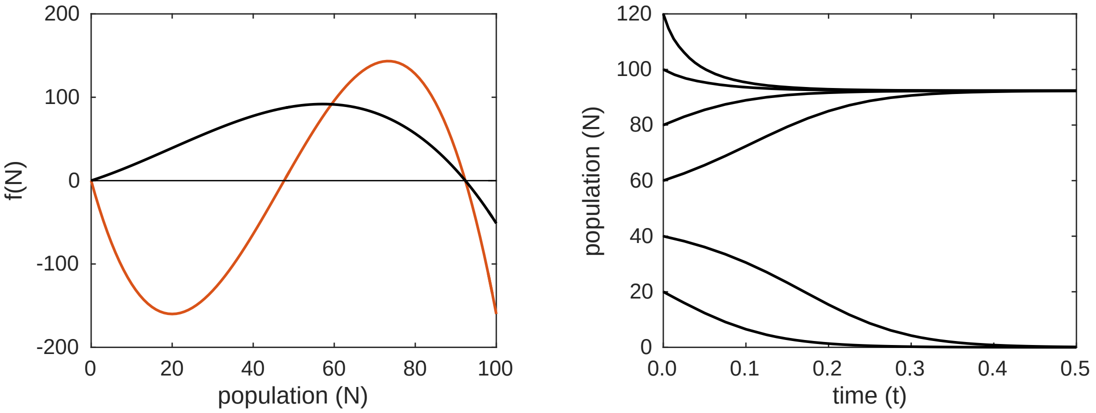

Figure 3.4: The Allee effect. Left: orange – strong Allee effects; black – weak Allee effects. Right: time series in the strong Allee effect case. Parameters for the strong Allee case are $\alpha = 0.004$ and $\eta = 70$, while in the weak case they are $\alpha = 0.0005$ and $\eta = 29.1$. In both cases $r = 2$.

A simple model that includes the Allee affect can be written

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left(r - \alpha\left(N-\eta\right)^2\right). \tag{3.20}$$

The system has steady states $N_s = 0$, $N_s = \eta + \sqrt{r/\alpha}$ and $N_s = \eta - \sqrt{r/\alpha}$, where the final steady state exists only when $\eta > \sqrt{r/\alpha}$. We can use graphical means to determine stability of the steady states as α and η are varied. Figure 3.4 shows that for $\eta < \sqrt{r/\alpha}$ the dynamics look very similar to the logistic case, with $N_s = 0$ unstable and $N_s = \eta + \sqrt{r/\alpha}$ stable. However, for $\eta > \sqrt{r/\alpha}$, we have $N_s = 0$ stable, and the intermediate steady state, $N_s = \eta - \sqrt{r/\alpha}$, unstable. This means that if the population falls below $N_s = \eta - \sqrt{r/\alpha}$ (due to, for example, fluctuations) then the model predicts the species will become extinct.

3.3.2 The spruce budworm model

First introduced by Ludwig in 1978, the model supposes budworm population dynamics can be modelled by the following equation:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = r_B N\left(1 - \frac{N}{K_B}\right) - p(N), \qquad p(N) := \frac{BN^2}{A^2+N^2}. \tag{3.21}$$

The first term of the right-hand side assumes logistic growth of the population, with carrying capacity K_B and linear growth rate r_B. The function $p(N)$ is taken to represent the effect predation by birds upon the budworm population.

Non-dimensionalisation

Let

$$N = N^* u, \quad t = t^*\tau, \tag{3.22}$$

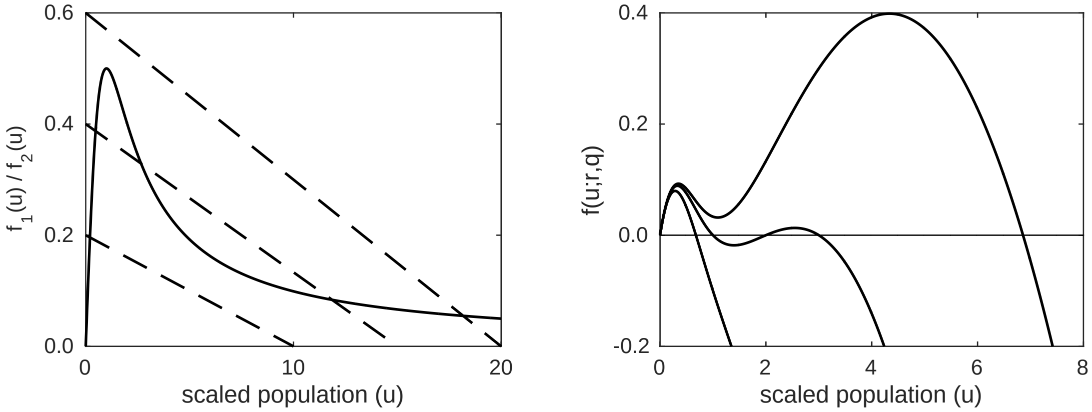

Figure 3.5: Dynamics of the non-dimensional insect outbreak model. Left: plots of the functions $f_1(u)$ (dashed line) and $f_2(u)$ (solid line) with parameters $r = 0.2, 0.4, 0.6$, $q = 10, 15, 20$, respectively. Right: plot of $f(u; r, q)$ with parameters $r = 0.6$ and $q = 3, 6, 9$.

where N^*, N have units of biomass, and t, t^* have units of time, with N^* and t^* constant. Then

$$\frac{N^*}{t^*}\frac{\mathrm{d}u}{\mathrm{d}\tau} = r_B N^* u\left(1-\frac{N^*u}{K_B}\right) - \frac{B(N^*)^2u^2}{A^2+(N^*)^2u^2}, \tag{3.23}$$

$$\Longrightarrow \quad \frac{\mathrm{d}u}{\mathrm{d}\tau} = r_B t^* u\left(1-\frac{N^*u}{K_B}\right) - \frac{BTN^*u^2}{A^2+(N^*)^2u^2}. \tag{3.24}$$

Hence with

$$N^* = A, \qquad t^* = \frac{A}{B}, \qquad r = r_B t^* = \frac{r_B A}{B}, \qquad q = \frac{K_B}{N^*} = \frac{K_B}{A}, \tag{3.25}$$

we have

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = ru\left(1-\frac{u}{q}\right) - \frac{u^2}{1+u^2} := f(u; r, q). \tag{3.26}$$

Thus we have reduced the number of parameters in our model from four to two, which substantially simplifies our subsequent study.

Steady states

The steady states are given by the solutions of

$$ru\left(1-\frac{u}{q}\right) - \frac{u^2}{1+u^2} = 0. \tag{3.27}$$

Clearly $u_s = 0$ is a steady state. We proceed graphically to consider the other steady states which are given by the intersection of the graphs

$$f_1(u) = r\left(1-\frac{u}{q}\right) \quad \text{and} \quad f_2(u) = \frac{u}{1+u^2}. \tag{3.28}$$

The top left plot of Figure 3.5 shows plots of $f_1(u)$ and $f_2(u)$ for different values of r and q. We see that, depending on the values of r and q, we have either one or three non-zero steady states. Noting that

$$\left.\frac{\mathrm{d}f(u; r, q)}{\mathrm{d}u}\right|_{u=0} = r > 0, \tag{3.29}$$

typical plots of $\mathrm{d}u/\mathrm{d}\tau$ as a function of u are shown in Figure 3.5 for a range of values of r and q.

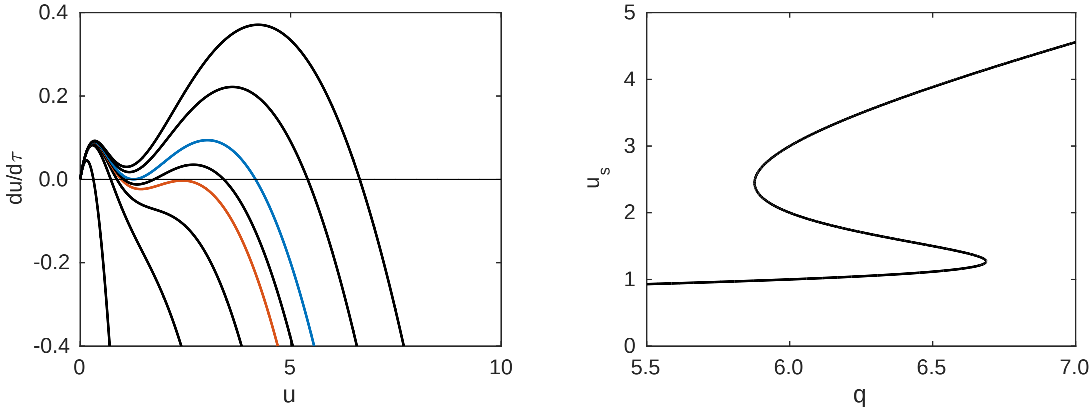

Figure 3.6: Left: $\mathrm{d}u/\mathrm{d}\tau = f(u; r, q)$ in the non-dimensional insect outbreak model as q is varied. For small q there is one, small, steady state, for $q \in (q_1, q_2)$ there are three non-zero steady states and for large q there is one, large, steady state. Right: the steady states plotted as a function of the parameter q reveals the hysteresis loop.

Hysteresis

A system displaying *hysteresis* exhibits a response to the increase of a driving variable which is not precisely reversed as the driving variable is decreased. Suppose that we fix $r = 0.6$ in the insect outbreak model. For small values of q there is only one non-zero steady state, S_1. As q is increased past q_1, three non-zero steady states exist, S_1, S_2, S_3, but the system stays at S_1. As q is increased further, past q_2, the upper steady state S_3 is all that remains and hence the system moves to S_3. If q is now decreased past q_2, three non-zero steady states (S_1, S_2, S_3) exist but the system remains at S_3 until q is decreased past q_1. Figure 3.6 shows $f(u; r, q)$ for different values of q. The red line shows a plot for $q = q_1$ whilst the blue line shows a plot for $q = q_2$. We could ask “What is the biological interpretation of the presence of hysteresis in this model?” If the carrying capacity, q, is accidentally manipulated such that an outbreak occurs ($S_1 \to S_3$) then reversing this change is not sufficient to reverse the outbreak.

3.4 Harvesting

We wish to consider simple models of harvesting and determine the maximum sustainable yield. We will look at two different types harvesting: constant yield, Y; and constant effort, E.

First, we will briefly discuss the notion of recovery times. Suppose, in the absence of harvesting, we have

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right). \tag{3.30}$$

We consider a perturbation from the non-zero steady state, $N = K$. Thus we write $N = K + n$, and find, on linearising,

$$\frac{\mathrm{d}n}{\mathrm{d}t} = -rn \quad \Rightarrow \quad n = n(0)e^{-rt}. \tag{3.31}$$

Hence, defining the *recovery time* to be the time for a perturbation to decrease by a factor of e according to the linearised equations about the non-zero steady state, we see that the system returns to equilibrium on a timescale of $T_R(0) = \mathcal{O}(1/r)$.

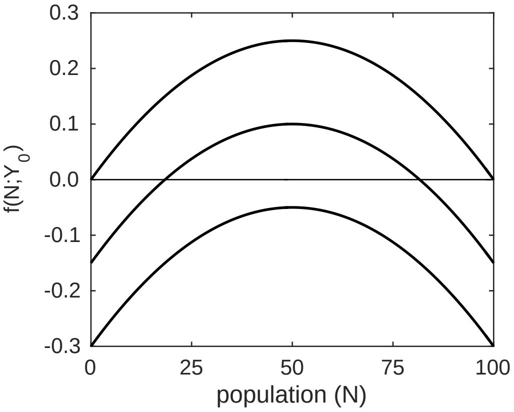

Figure 3.7: Dynamics of the constant yield model for $Y_0 = 0.00, 0.15, 0.30$. As Y_0 is increased beyond a critical value the steady states disappear and $N \to 0$ in finite time. Parameters are: $K = 100$ and $r = 0.01$.

3.4.1 Constant yield

For a constant yield, $Y = Y_0$, we have

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) - Y_0 := f(N; Y_0). \tag{3.32}$$

Plotting $\mathrm{d}N/\mathrm{d}t$ as a function of N reveals (see Figure 3.7) that the steady states disappear as Y_0 is increased beyond a critical value, and then $N \to 0$ in finite time.

The steady states are given by the solutions of

$$rN_s - \frac{rN_s{}^2}{K} - Y_0 = 0 \quad \Rightarrow \quad N_s = \frac{r \pm \sqrt{r^2 - 4rY_0/K}}{2r/K}. \tag{3.33}$$

Therefore extinction will occur once

$$Y_0 > \frac{rK}{4}. \tag{3.34}$$

3.4.2 Constant effort

For harvesting at constant effort we have

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) - EN := f(N; E) = N(r - E) - \frac{rN^2}{K}, \tag{3.35}$$

where the yield is $Y(E) = EN$. The question is: how do we maximise $Y(E)$ such that the steady state still recovers?

The steady states, N_s, are such that $f(N_s; E) = 0$ (see Figure 3.8). Thus

$$N_s(E) = \frac{(r - E)K}{r} = \left(1 - \frac{E}{r}\right)K, \tag{3.36}$$

and hence

$$Y_s(E) = EN_s(E) = \left(1 - \frac{E}{r}\right)KE. \tag{3.37}$$

Maximum yield

The maximum yield, $Y_s^{\max}$, and corresponding value of N_s, are given by the value of E such that

$$\frac{\mathrm{d}Y_s}{\mathrm{d}E} = 0 \quad \Rightarrow \quad E = \frac{r}{2}, \qquad Y_s^{\max} = \frac{rK}{4}, \qquad N_s^{\max} = \frac{K}{2}. \tag{3.38}$$

We linearise about the steady state $N_s(E)$ by letting $N = N_s(E) + n$ to give

$$\frac{\mathrm{d}n}{\mathrm{d}t} \simeq f(N_s; E) + \left.\frac{\mathrm{d}f(N;E)}{\mathrm{d}N}\right|_{N=N_s} n + \ldots = -(r-E)n + \ldots \tag{3.39}$$

We see that the recovery time is given by

$$T_R(E) = \frac{1}{r-E}, \tag{3.40}$$

and hence, at the maximum yield state,

$$T_R(E) = \frac{2}{r} \quad \text{since} \quad E = \frac{r}{2} \text{ at maximum yield.} \tag{3.41}$$

As we measure Y it is useful to rewrite E in terms of Y to give the ratio of recovery times in terms of the yield, $Y(E)$, and the maximum yield, $Y_s^{\max}$. At steady state, we have

$$\frac{K}{r}E^2 - KE + Y_s = 0 \quad \text{as} \quad Y_s = EN_s = KE\left(1 - \frac{E}{r}\right). \tag{3.42}$$

This gives

$$E = \frac{r \pm r\sqrt{1 - 4Y_s/Kr}}{2} \qquad \Longrightarrow \qquad r - E = \frac{r}{2}\left[1 \mp \sqrt{1 - \frac{Y_s}{Y_s^{\max}}}\right]. \tag{3.43}$$

Substituting into equation (3.40) gives

$$\frac{T_R(Y)}{T_R(0)} = \frac{2}{1 \pm \sqrt{1 - Y/Y_s^{\max}}}. \tag{3.44}$$

Plotting $T_R(Y)/T_R(0)$ as a function of $Y/Y_s^{\max}$ yields some interesting observations, as shown in Figure 3.8. For example, as T_R increases the population recovers less quickly, and therefore spends more time away from the steady state, N_s. The biological implication of this is that, in order to maintain a constant yield, E must be increased. This, in turn, implies T_R increases, resulting in a positive feedback loop that can have disastrous consequences upon the population.

3.5 Delays

A disadvantage of simple population models is that they do not take account of time delays. These arise, for example, due to the time taken for an organism to reach maturity or due to finite gestation periods. Delays can be incorporated by using the framework of *delay differential equations* models of the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f\left(N, N(t-T)\right), \tag{3.45}$$

where $T > 0$ is the delay.

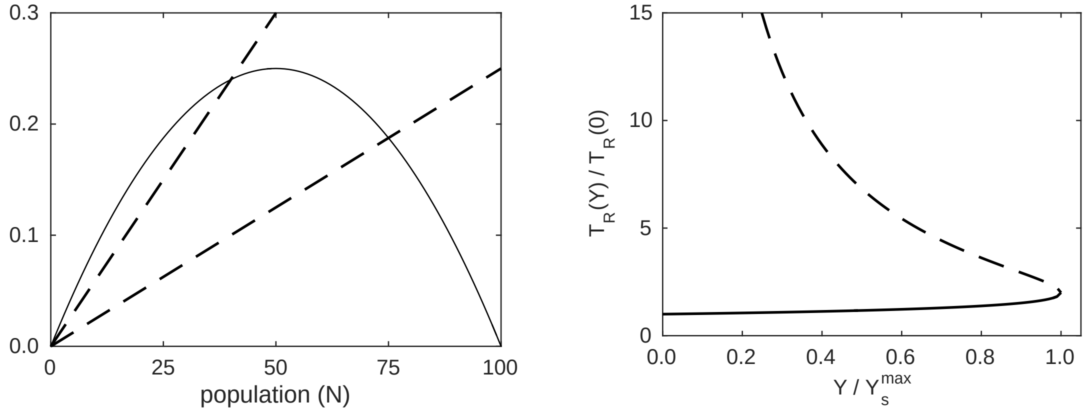

Figure 3.8: Dynamics of the constant effort model. Left: the logistic growth curve (solid line) and the yield, $Y = EN$ (dashed lines), for two values of E. Right: the ratio of recovery times, $T_R(Y)/T_R(0)$, with the negative root plotted as a dashed line and the positive root as a solid line. Parameters are: $K = 100$ and $r = 0.01$.

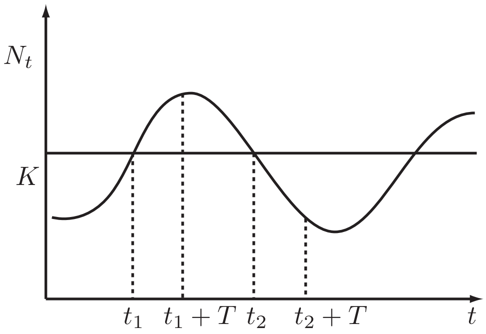

Figure 3.9: Schematic of the oscillatory nature of solutions.

3.5.1 The delayed logistic model

A commonly used example of a delay model is the delayed logistic model:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(t)\left(1 - \frac{N(t-T)}{K}\right), \tag{3.46}$$

where the constants are as defined previously. Note that to compute the solution we need to specify $N(t)$ for $-T \leq t \leq 0$.

We can get some idea of the possible behaviour of the model using heuristic reasoning (see Figure 3.9). Suppose that at $t = t_1$, $N(t_1) = K$, and that for some time $t < t_1$, $N(t-T) < K$. Then at this time t, $\mathrm{d}N/\mathrm{d}t > 0$ and so $N(t)$ is increasing. Also, when $t = t_1 + T$, $\mathrm{d}N/\mathrm{d}t = 0$. For $t_1 + T < t < t_2$, $\mathrm{d}N/\mathrm{d}t < 0$ and so $N(t)$ decreases until $t = t_2 + T$ when $\mathrm{d}N/\mathrm{d}t = 0$ again. Therefore there is the possibility of oscillatory behaviour. We expect that the period of these limit cycle solutions will be approximately $4T$.

The solutions of (3.46) can exhibit *stable limit cycle* periodic solutions for a large range of values of rT. This means that if t_p is the period then $N(t + t_p) = N(t)$, and if the perturbation is imposed then the solution returns to the original periodic behaviour as $t \to \infty$ (although a *phase shift* may occur).

Note. Single species populations models without delays cannot exhibit limit cycle behaviour.

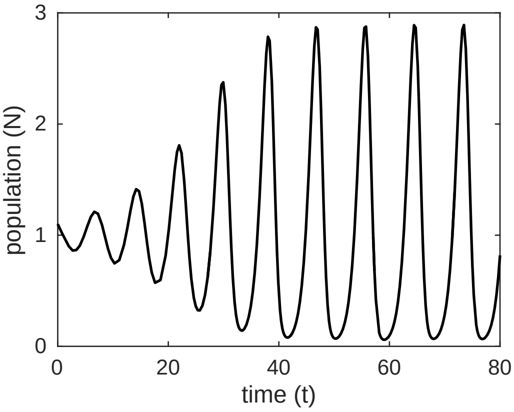

Figure 3.10: Dynamics of the non-dimensional delayed logistic model with $T = 2$ and $N(t) = 1$ for $-2 \le t \le 0$.

To see this, suppose that such a model as equation (3.2) has a periodic solution with period t_p. Then

$$\int_t^{t+t_p} \left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)^2 \mathrm{d}t = \int_t^{t+t_p} f(N)\frac{\mathrm{d}N}{\mathrm{d}t}\mathrm{d}t = \int_{N(t)}^{N(t+t_p)} f(N)\mathrm{d}N = 0, \tag{3.47}$$

since $N(t + t_p) = N(t)$. Since the left-hand-most term in above is non-negative this means that $\mathrm{d}N/\mathrm{d}t \equiv 0$ and hence we have a contradiction.

3.5.2 Linear analysis of delayed population models

We will use the delayed logistic model as an example, and investigate the linear stability of the steady states $N = K$ and $N = 0$. We non-dimensionalise as before by letting $N = KN^*$, $t = t^*/r$ and $T = T^*/r$ to give (dropping the asterisks for notational convenience):

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(t)\left[1 - N(t-T)\right], \tag{3.48}$$

and steady states $N = 0$ and $N = 1$. First we linearise about the steady state $N = 1$ by writing $N(t) = 1 + n(t)$ so that

$$\frac{\mathrm{d}n(t)}{\mathrm{d}t} \approx -n(t-T). \tag{3.49}$$

Seeking solutions of the form $n(t) = c\exp(\lambda t)$ gives

$$\lambda = -e^{-\lambda t}. \tag{3.50}$$

This is a transcendental equation for λ that has infinitely many roots. To determine the linear stability we require an understanding of whether there are solutions with $Re(\lambda) > 0$. To investigate, we let $\lambda = \mu + i\omega$. Taking the modulus of both sides of equation (3.50) gives

$$|\lambda| = e^{-\mu t}. \tag{3.51}$$

If $|\lambda| \to \infty$ then $\mu \to -\infty$. This means that there exists μ_0 such that $Re(\lambda) < \mu_0$.

Substituting into equation (3.50) we have

$$\begin{aligned} \mu &= -e^{\mu t}\cos(\omega T), & (3.52)\\ \omega &= e^{\mu t}\sin(\omega T). & (3.53) \end{aligned}$$

We would like to determine the range of values for T such that $\mu < 0$. Suppose first that $\omega = 0$. Then equation (3.53) is satisfied, and equation (3.52) gives $\mu = -\exp(\mu t)$ which has no positive roots. Suppose now that $\omega \neq 0$. If ω is a solution then so is $-\omega$, so without loss of generality let $\omega > 0$. From equation (3.52), $\mu < 0$ (stability) requires $\omega T < \pi/2$. Substituting into equation (3.53) and multiplying by T gives

$$Te^{-\mu t}\sin(\omega T) = \omega T < \frac{\pi}{2} \quad \Longrightarrow \quad 0 < T < \frac{\pi}{2}. \tag{3.54}$$

Going back to the dimensional model, this means that the steady state $N(t) = K$ is stable if $0 < rT < \pi/2$ and unstable for $rT > \pi/2$, and we anticipate stable limit cycle behaviour in the latter case. Figure 3.10 illustrates the stable limit cycle behaviour that can arise in the delayed logistic model. We see oscillations that gradually increase to have stable amplitude, with period approximately $4T$.

Chapter 4: Continuous-time models for interacting species

We begin this chapter with a brief recap of the "recipe" for determining linear stability for a two-species model. We then consider three types of canonical interactions between two species.

4.1 Introduction

We will consider models of two species, u and v, whose dynamics can be described using a system of coupled ordinary differential equations:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = f(u,v), \tag{4.1}$$

$$\frac{\mathrm{d}v}{\mathrm{d}t} = g(u,v), \tag{4.2}$$

where f and g are prescribed functions that model the interactions between the species. Our "recipe" for analysing these models is to find their steady states, conduct a linear stability analysis and sketch the phase plane.

4.1.1 Steady states

The *steady states*, (u_s, v_s), satisfy $f(u_s, v_s) = 0$ and $g(u_s, v_s) = 0$. We can often make progress in determining the number and nature of steady states by drawing the *null clines*. These are defined as the curves in phase space where either $\mathrm{d}u/\mathrm{d}t = 0$ or $\mathrm{d}v/\mathrm{d}t = 0$. The steady states are then given by the intersections of the u and v null clines.

4.1.2 Linear stability analysis

We analyse the linear stability of any steady states by making small perturbations about the steady states: let

$$u(t) = u_s + \tilde{u} \qquad \text{and} \qquad v(t) = v_s + \tilde{v}. \tag{4.3}$$

Substituting into equations (4.1)-(4.2) and retaining only first order terms in $\tilde{u}$, $\tilde{v}$ we have

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} &= \begin{pmatrix} f(u_s+\tilde{u}, v_s+\tilde{v}) \\ g(u_s+\tilde{u}, v_s+\tilde{v}) \end{pmatrix} & (4.4)\\
&= \begin{pmatrix} f(u_s, v_s) \\ g(u_s, v_s) \end{pmatrix} + \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)} \begin{pmatrix} u_s \\ v_s \end{pmatrix} & (4.5)\\
&= \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)} \begin{pmatrix} u_s \\ v_s \end{pmatrix}. & (4.6)
\end{aligned}$$

As in the Differential Equations I course, we determine linear stability by consider the eigenvalues of the (constant) Jacobian matrix

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)}. \tag{4.7}$$

4.2 Predator-prey models

The most common predator-prey model is the Lotka-Volterra model. With N the number of prey and P the number of predators, this model can be written

$$\frac{\mathrm{d}N}{\mathrm{d}t} = aN - bNP, \tag{4.8}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = cNP - dP, \tag{4.9}$$

with a, b, c, d positive parameters and $c < b$.

4.2.1 Non-dimensionalisation

Non-dimensionalising with $u = (c/d)N$, $v = (b/a)P$, $\tau = at$ and $\alpha = d/a$, we have

$$\frac{1}{1/a}\frac{d}{c}\frac{\mathrm{d}u}{\mathrm{d}\tau} = \frac{ad}{c}u - \frac{bd}{c}\frac{a}{b}uv \quad \Rightarrow \quad \frac{\mathrm{d}u}{\mathrm{d}\tau} = u - uv = u(1-v) \coloneqq f(u,v), \tag{4.10}$$

$$\frac{1}{1/a}\frac{a}{b}\frac{\mathrm{d}v}{\mathrm{d}\tau} = c\frac{d}{c}\frac{a}{b}uv - d\frac{a}{b}v \quad \Rightarrow \quad \frac{\mathrm{d}v}{\mathrm{d}\tau} = \alpha(uv - v) = \alpha v(u-1) \coloneqq g(u,v). \tag{4.11}$$

4.2.2 Linear stability analysis

There are steady states at $(u,v) = (0,0)$ and $(u,v) = (1,1)$. The Jacobian, $\boldsymbol{J}$, is given by

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)} = \begin{pmatrix} 1 - v_s & -u_s \\ \alpha v_s & \alpha(u_s - 1) \end{pmatrix}. \tag{4.12}$$

At $(0,0)$ we have

$$\boldsymbol{J} = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}, \tag{4.13}$$

with eigenvalues 1, $-\alpha$. Therefore the steady state $(0,0)$ is an unstable saddle.

At $(1,1)$ we have

$$\boldsymbol{J} = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}, \tag{4.14}$$

with eigenvalues $\pm i\sqrt{\alpha}$. Therefore the steady state $(1,1)$ is a centre (not linearly stable).

4.2.3 Analytic solution

These equations are special in that we can integrate them once, as follows, to find a conserved constant:

$$\frac{\mathrm{d}u}{\mathrm{d}v} = \frac{u(1-v)}{\alpha(u-1)v} \quad \Rightarrow \quad \int \frac{u-1}{u}\mathrm{d}u = \int \frac{1-v}{\alpha v}\mathrm{d}v. \tag{4.15}$$

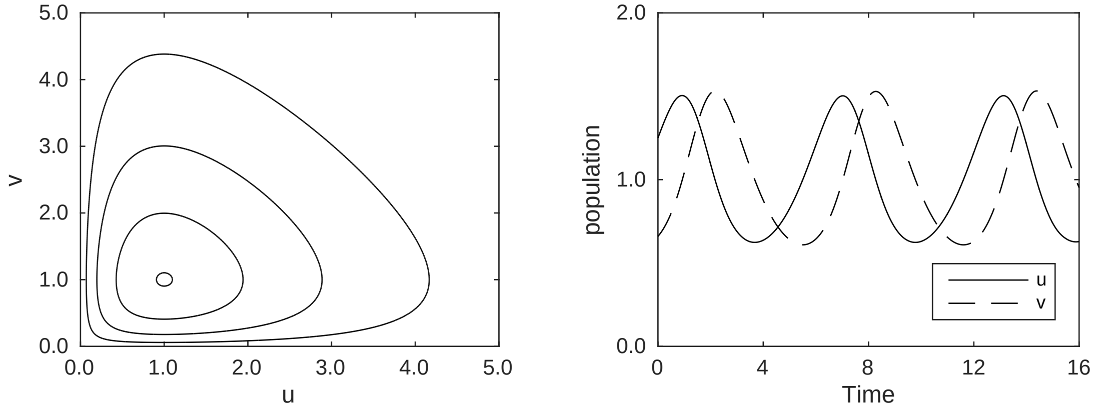

Figure 4.1: Dynamics of the non-dimensional Lotka-Volterra system for $\alpha = 1.095$ and $H = 2.1, 2.4, 3.0, 4.0$. The left-hand plot shows the dynamics in the (u, v) phase plane whilst the right-hand plot shows the temporal evolution of u and v.

Hence

$$H = \text{constant} = \alpha u + v - \alpha \ln u - \ln v. \tag{4.16}$$

This can be rewritten as

$$\left(\frac{e^v}{v}\right)\left(\frac{e^u}{u}\right)^{\alpha} = e^H, \tag{4.17}$$

from which we can deduce that the trajectories in the (u, v) plane take the form shown in Figure 4.1. Thus u and v exhibit temporal oscillations, though not in phase, and hence we have a prediction; predators and prey population numbers oscillate out of phase. There are often observations of this *e.g.* hare-lynx interactions.

4.3 Finite predation

The common predator-prey model assumes that as $N \to \infty$ the rate of predation per predator becomes unbounded, as does the rate of increase of the predator's population. However, with an abundance of food, these quantities will saturate rather than become unbounded. Thus, a more realistic incorporation of an abundance of prey requires a refinement of the Lotka-Volterra model. A suitable, simple, model for predator-prey interactions under such circumstances would be (after non-dimensionalisation)

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = f(u, v) = u(1-u) - \frac{auv}{d+u}, \tag{4.18}$$

$$\frac{\mathrm{d}v}{\mathrm{d}\tau} = g(u, v) = bv\left(1 - \frac{v}{u}\right), \tag{4.19}$$

where a, b, d are positive constants. Note the effect of predation per predator saturates at high levels of u whereas the predator levels are finite at large levels of prey and drop exceedingly rapidly in the absence of prey.

4.3.1 Linear stability analysis

There is one non-trivial steady state, (u_s, v_s), satisfying

$$v_s = u_s \quad \text{where} \quad (1 - u_s) = \frac{au_s}{d + u_s}, \tag{4.20}$$

and hence

$$u_s = \frac{1}{2}\left[-(a+d-1) + \sqrt{(a+d-1)^2 + 4d}\right]. \tag{4.21}$$

The Jacobian at (u_s, v_s) is

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)} \tag{4.22}$$

where

$$\frac{\partial f}{\partial u}(u_s, v_s) = 1 - 2u_s - \frac{au_s}{d+u_s} + \frac{au_s v_s}{(d+u_s)^2} = -u_s + \frac{a(u_s)^2}{(d+u_s)^2}. \tag{4.23}$$

$$\frac{\partial f}{\partial v}(u_s, v_s) = -\frac{au_s}{d+u_s}, \tag{4.24}$$

$$\frac{\partial g}{\partial u}(u_s, v_s) = \frac{b(v_s)^2}{(u_s)^2} = b, \tag{4.25}$$

$$\frac{\partial g}{\partial v}(u_s, v_s) = b\left(1 - 2\frac{v_s}{u_s}\right) = -b. \tag{4.26}$$

The eigenvalues satisfy

$$\left(\lambda - \frac{\partial f}{\partial u}\right)\left(\lambda - \frac{\partial g}{\partial v}\right) - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u} = 0 \quad \Longrightarrow \quad \lambda^2 - \left(\frac{\partial f}{\partial u} + \frac{\partial g}{\partial v}\right)\lambda + \left(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u}\right) = 0. \tag{4.27}$$

Hence

$$\lambda^2 - \alpha\lambda + \beta = 0 \quad \Longrightarrow \quad \lambda = \frac{\alpha \pm \sqrt{\alpha^2 - 4\beta}}{2}, \tag{4.28}$$

where

$$\alpha = -u_s + \frac{au_s^2}{(u_s+d)^2} - b, \quad \beta = b\left(u_s - \frac{au_s^2}{(u_s+d)^2} - (u_s - 1)\right). \tag{4.29}$$

Note that

$$\beta = 1 - \frac{au_s^2}{(u_s+d)^2} = 1 - \frac{u_s(1-u_s)}{(u_s+d)} = \frac{(u_s+d) - u_s + u_s^2}{u_s+d} = \frac{d + (u_s)^2}{d+u_s} > 0. \tag{4.30}$$

Thus, if $\alpha < 0$ we have either a stable node ($\alpha^2 - 4\beta > 0$) or stable focus ($\alpha^2 - 4\beta < 0$) at the steady state (u_s, v_s). If $\alpha > 0$ we have an unstable steady state at (u_s, v_s).

4.3.2 Phase plane

The u null clines are given by

$$f(u,v) \equiv 0 \qquad \Longrightarrow \qquad u \equiv 0 \quad \text{and} \quad v = \frac{1}{a}(1-u)(u+d). \tag{4.31}$$

The v null clines are given by

$$g(u,v) \equiv 0 \qquad \Longrightarrow \qquad v \equiv 0 \quad \text{and} \quad v = u. \tag{4.32}$$

A sketch of the null clines and the behaviour of the phase plane trajectories is shown in Figure 4.2.

4.3.3 Limit cycle dynamics

In this model, $\alpha > 0$ implies we have limit cycle dynamics. This is because for $\alpha > 0$ the steady state is an unstable node or spiral. Further, we can find a simple, closed boundary curve, $\mathcal{C}$, in the positive quadrant of the (u,v) plane such that on $\mathcal{C}$ phase trajectories always point into the domain, $\mathcal{D}$, enclosed by $\mathcal{C}$. Applying the Poincaré-Benedixon Theorem gives the existence of a limit cycle[1]. This means that the predator and prey population densities oscillate out-of-phase.

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[1] See J. D. Murray, Mathematical Biology Volume I (Chapter 3.4) for more details.

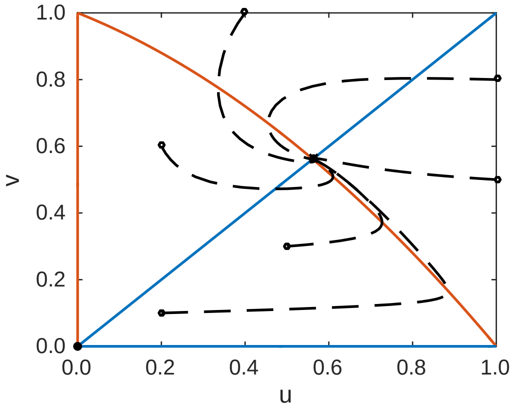

Figure 4.2: The (u, v) phase plane for the finite predation model when the steady state is stable. The u null clines are plotted in orange and the v null clines in blue. Trajectories for a number of different initial conditions are shown as dashed lines. Parameters are: $a = 2.0$, $b = 0.1$, $d = 2.0$.

4.4 Competitive exclusion

We consider an ordinary differential equation model of two competitors. An example might be populations of red squirrels and grey squirrels. Here, both populations compete for the same resources and a typical model for their dynamics is

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{4.33}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right), \tag{4.34}$$

where K_1, K_2, r_1, r_2, b_{12}, b_{21} are positive constants. Let us associate N_1 with red squirrels and N_2 with grey squirrels in our example.

In particular, given a range of parameter values and some initial values for N_1 and N_2 at $t = 0$, we would typically like to know if the final outcome is one of the following possibilities:

- the reds become extinct, leaving the greys;
- the greys become extinct, leaving the reds;
- both reds and greys become extinct;
- the reds and greys co-exist. If this system is perturbed in any way will the reds and greys continue to coexist?

This model can be non-dimensionalised to give

$$\frac{\mathrm{d}u_1}{\mathrm{d}\tau} = u_1(1 - u_1 - \alpha_{12}u_2) := f_1(u_1, u_2), \tag{4.35}$$

$$\frac{\mathrm{d}u_2}{\mathrm{d}\tau} = \rho u_2(1 - u_2 - \alpha_{21}u_1) := f_2(u_1, u_2), \tag{4.36}$$

where $\rho = r_2/r_1$.

4.4.1 Linear stability analysis

The steady states are

$$(u_{1,s}, u_{2,s}) = (0,0), \quad (u_{1,s}, u_{2,s}) = (1,0), \quad (u_{1,s}, u_{2,s}) = (0,1), \tag{4.37}$$

and

$$(u_{1,s}, u_{2,s}) = \frac{1}{1-\alpha_{12}\alpha_{21}}(1-\alpha_{12}, 1-\alpha_{21}), \tag{4.38}$$

if $\alpha_{12} < 1$ and $\alpha_{21} < 1$ *or* $\alpha_{12} > 1$ and $\alpha_{21} > 1$.

The Jacobian is

$$\mathbf{J} = \begin{pmatrix} 1-2u_1-\alpha_{12}u_2 & -\alpha_{12}u_1 \\ -\rho\alpha_{21}u_2 & \rho(1-2u_2-\alpha_{21}u_1) \end{pmatrix}. \tag{4.39}$$

Steady state $(u_{1,s}, u_{2,s}) = (0,0)$**.**

$$\mathbf{J} - \lambda\mathbf{I} = \begin{pmatrix} 1-\lambda & 0 \\ 0 & \rho-\lambda \end{pmatrix} \quad \Rightarrow \quad \lambda = 1, \rho. \tag{4.40}$$

Therefore $(0,0)$ is an unstable node.

Steady state $(u_{1,s}, u_{2,s}) = (1,0)$**.**

$$\mathbf{J} - \lambda\mathbf{I} = \begin{pmatrix} -1-\lambda & -\alpha_{12} \\ 0 & \rho(1-\alpha_{21})-\lambda \end{pmatrix} \quad \Rightarrow \quad \lambda = -1, \rho(1-\alpha_{21}). \tag{4.41}$$

Therefore $(1,0)$ is a stable node if $\alpha_{21} > 1$ and a saddle point if $\alpha_{21} < 1$.

Steady state $(u_{1,s}, u_{2,s}) = (0,1)$**.**

$$\mathbf{J} - \lambda\mathbf{I} = \begin{pmatrix} 1-\alpha_{12}-\lambda & 0 \\ -\rho\alpha_{21} & -\rho-\lambda \end{pmatrix} \quad \Rightarrow \quad \lambda = -\rho, 1-\alpha_{12}. \tag{4.42}$$

Therefore $(0,1)$ is a stable node if $\alpha_{12} > 1$ and a saddle point if $\alpha_{12} < 1$.

Steady state $(u_{1,s}, u_{2,s}) = \frac{1}{1-\alpha_{12}\alpha_{21}}(1-\alpha_{12}, 1-\alpha_{21})$**.**

$$\mathbf{J} - \lambda\mathbf{I} = \frac{1}{1-\alpha_{12}\alpha_{21}} \begin{pmatrix} \alpha_{21}-1-\lambda & \alpha_{12}(\alpha_{12}-1) \\ \rho\alpha_{21}(\alpha_{21}-1) & \rho(\alpha_{21}-1)-\lambda \end{pmatrix}. \tag{4.43}$$

Stability depends on α_{12} and α_{21}.

There are several different possible behaviours. The totality of all behaviours of the above model is reflected in how one can arrange the null clines within the positive quadrant. However, for competing populations these straight line null clines have negative gradients. Figure 4.3 shows the model behaviour for different sets of parameter values.

Note. In ecology the concept of *competitive exclusion* is that two species competing for exactly the same resources cannot stably coexist. One of the two competitors will always have an ever so slight advantage over the other that leads to extinction of the second competitor in the long run (or evolution into distinct ecological niches).

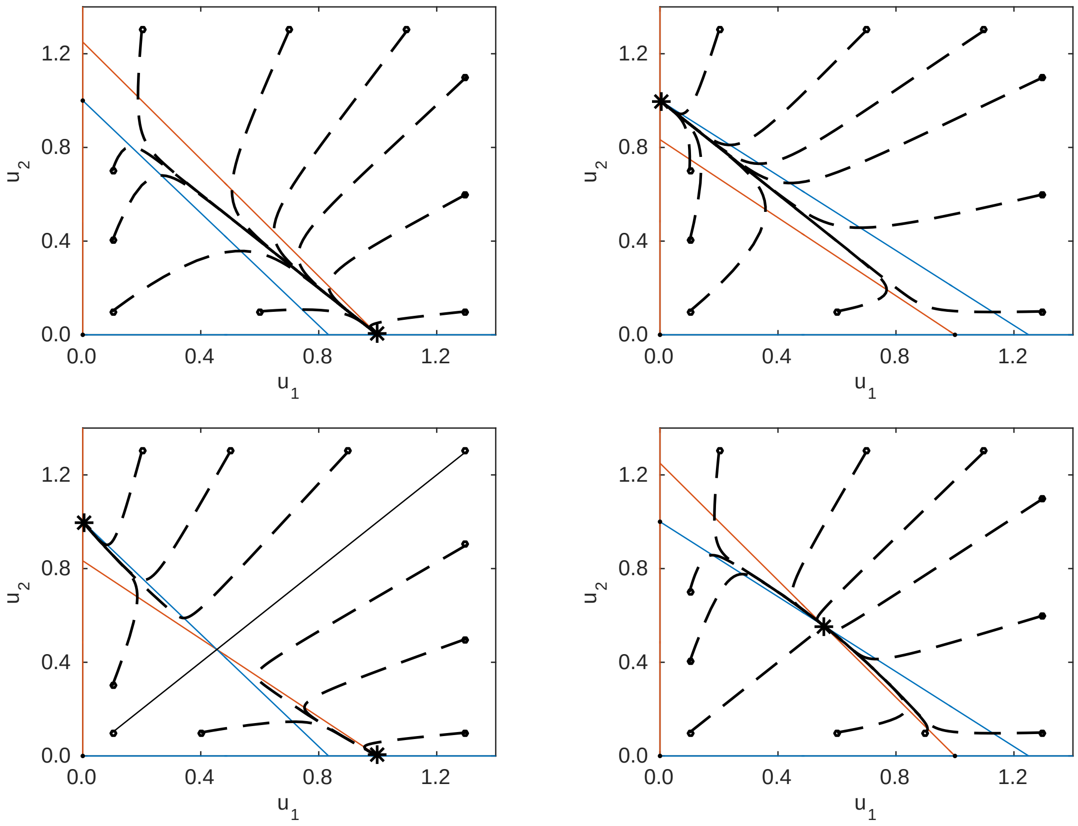

Figure 4.3: Dynamics of the non-dimensional competitive exclusion system. Top left: $\alpha_{12} = 0.8 < 1$, $\alpha_{21} = 1.2 > 1$ and u_2 is excluded. Top right: $\alpha_{12} = 1.2 > 1$, $\alpha_{21} = 0.8 < 1$ and u_1 is excluded. Bottom left: $\alpha_{12} = 1.2 > 1$, $\alpha_{21} = 1.2 > 1$ and exclusion is dependent on the initial conditions. Bottom right: $\alpha_{12} = 0.8 < 1$, $\alpha_{21} = 0.8 < 1$ and we have coexistence. The stable steady states are marked with $*$'s and $\rho = 1.0$ in all cases. The orange lines indicate $f_1 \equiv 0$ whilst the blue lines indicate $f_2 \equiv 0$.

4.5 Mutualism (symbiosis)

We consider a very similar ordinary differential equation model for two species, but this time with positive interactions,

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}\right), \tag{4.44}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_2}\right), \tag{4.45}$$

where K_1, K_2, r_1, r_2, b_{12}, b_{21} are positive constants. The model can be non-dimensionalised to give

$$\frac{\mathrm{d}u_1}{\mathrm{d}\tau} = u_1(1 - u_1 + \alpha_{12}u_2) := f_1(u_1, u_2), \tag{4.46}$$

$$\frac{\mathrm{d}u_2}{\mathrm{d}\tau} = \rho u_2(1 - u_2 + \alpha_{21}u_1) := f_2(u_1, u_2). \tag{4.47}$$

In this model of symboisis, the straight line null clines will have positive gradients. There are three steady states that have either u_1 or u_2, or both, equal to zero. As additional steady state

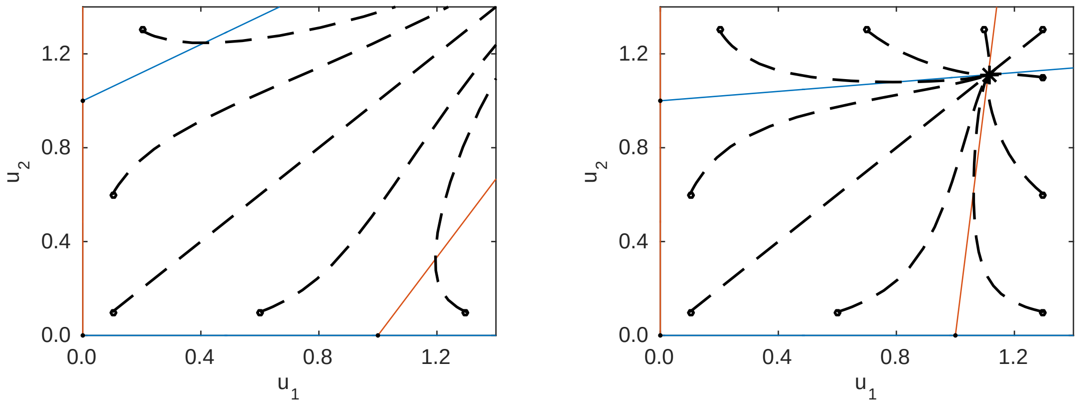

Figure 4.4: Dynamics of the non-dimensional symbiotic system. The left-hand figure shows population explosion ($\alpha_{12} = 0.6 = \alpha_{21}$) whilst the right-hand figure shows population coexistence ($\alpha_{12} = 0.1 = \alpha_{21}$). The stable steady states are marked with $*$'s and $\rho = 1.0$ in all cases. The orange lines indicate $f_1 \equiv 0$ whilst the blue lines indicate $f_2 \equiv 0$.

with both u_1 and u_2 non-zero exists in some parameter regimes. The two possible behaviours displayed by the model are shown in Figure 4.4. We see that when a non-zero steady state exists it is stable, and the populations coexist. However, when this steady state does not exist, but populations grow unboundedly.

Chapter 5: Infectious disease modelling

Finally, we will look briefly at models of infectious diseases. The study of infectious diseases has a long history and there are numerous detailed models of a variety of epidemics and epizootics (*i.e.* animal epidemics). We can only possibly scratch the surface. In the following, we consider a simple model but even this is capable of highlighting general aspects of epidemics and, in fact, approximately describes some specific epidemics.

5.1 The SIR model

Consider a disease for which the population can be placed into three compartments:

- the susceptible compartment, S, who can catch the disease;
- the infective compartment, I, who have and transmit the disease;
- the removed compartment, R, who have been isolated, or who have recovered and are immune to the disease, or have died due to the disease during the course of the epidemic.

5.1.1 Assumptions

- The epidemic is of short duration course so that the population is constant (counting those who have died due to the disease during the course of the epidemic).
- The disease has a negligible incubation period.
- If a person contracts the disease and recovers they are immune (and hence remain in the removed compartment).
- The rate at which new infections occur is proportional to the number of contacts between infectives and susceptibles.
- Infectives recover (and become immune) or die at a constant rate.

5.1.2 The model

The equations describing the time evolution of numbers in the susceptible, infective and removed compartments are given by

$$\frac{\mathrm{d}S}{\mathrm{d}t} = -rIS, \tag{5.1}$$

$$\frac{\mathrm{d}I}{\mathrm{d}t} = rIS - aI, \tag{5.2}$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aI, \tag{5.3}$$

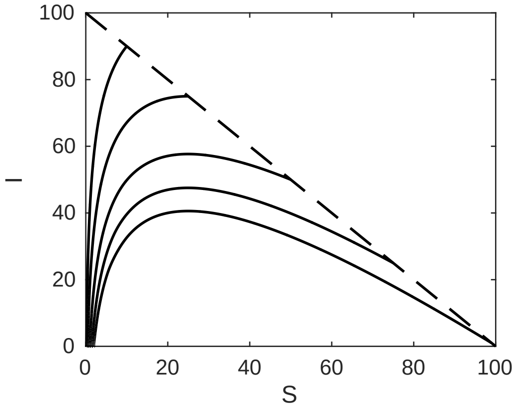

Figure 5.1: Numerical solution of the SIR model, equations (5.1)-(5.3), where the solid lines indicate the phase trajectories and the dashed line $S + I = S_0 + I_0$. Parameters are as follows: $r = 0.01$ and $a = 0.25$.

subject to

$$S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0. \tag{5.4}$$

Note that, as we would expect from the assumptions,

$$\frac{\mathrm{d}}{\mathrm{d}t}(S + I + R) = 0 \quad \Longrightarrow \quad S + I + R = S_0 + I_0. \tag{5.5}$$

5.1.3 Key questions

The key dynamics of the model can be seen by looking at the phase plane dynamics, shown in Figure 5.1. However, we can also gain quantitative insights into the model behaviour by investigating the questions outlined below.

Question 1. First, we would like to know whether the disease will spread, *i.e.* will the number of infectives increase, at least in the short-term?

From equations (5.1)-(5.2) we have that

$$\frac{\mathrm{d}S}{\mathrm{d}t} = -rIS \quad \Longrightarrow \quad S \text{ is decreasing and therefore } S \leq S_0. \tag{5.6}$$

$$\frac{\mathrm{d}I}{\mathrm{d}t} = I(rS - a) < I(rS_0 - a). \tag{5.7}$$

Therefore, if $S_0 < a/r$ the infectives never increase, at least initially.

The parameter $\rho \coloneqq a/r$ is sometimes called the *relative removal rate*, and the parameter $R_0 \coloneqq rS_0/a$ the *basic reproductive rate*. This is the average number of secondary infections produced by one primary infection in a wholly susceptible population. From our analysis, we see that if $R_0 > 1$ then an epidemic occurs.

Question 2. Secondly, if the disease spreads, what will be the maximum number of infectives at any given time?

Again, using equations (5.1)-(5.2), we can write

$$\frac{\mathrm{d}I}{\mathrm{d}S} = -\frac{(rS - a)}{rS} = -1 + \frac{\rho}{S}. \tag{5.8}$$

Integrating gives

$$I + S - \rho \ln S = I_0 + S_0 - \rho \ln S_0, \tag{5.9}$$

and so, noting that $\mathrm{d}I/\mathrm{d}S = 0$ for $S = \rho$, the maximum number of infectives is given by

$$I_{max} = \begin{cases} I_0 & S_0 \leq \rho \\ I_0 + S_0 - \rho \ln S_0 - \rho \ln \rho - \rho & S_0 > \rho \end{cases}. \tag{5.10}$$

Question 3. Finally, how many people in total catch the disease?

From the first question, we know that $I \to 0$ as $t \to \infty$. Therefore the total number who catch the disease is

$$R(\infty) = N_0 - S(\infty) - I(\infty) = N_0 - S(\infty), \tag{5.11}$$

where $S(\infty) < S_0$ is the root of

$$S_\infty - \rho \ln S_\infty = N_0 - \rho \ln S_0, \tag{5.12}$$

obtained by setting $S = S_\infty$ and $N_0 = I_0 + S_0$ in equation (5.9).

5.2 Incubation periods

Suppose now that the disease has a small incubation period, τ, where $0 < \tau \ll 1$, such that a susceptible who has been infected only enters the infective compartment a time τ after they are exposed to the disease. In this case, the model becomes

$$\begin{aligned} \frac{\mathrm{d}S}{\mathrm{d}t} &= -rI(t-\tau)S(t-\tau), & (5.13)\\ \frac{\mathrm{d}I}{\mathrm{d}t} &= rI(t-\tau)S(t-\tau) - aI(t), & (5.14)\\ \frac{\mathrm{d}R}{\mathrm{d}t} &= aI(t), & (5.15) \end{aligned}$$

along with suitable initial conditions.

We can make progress in analysing the dynamics of the model by writing

$$\begin{aligned} I(t-\tau)S(t-\tau) &= I(t)S(t) - \tau I'(t)S(t) - \tau I(t)S'(t) + \mathcal{O}(\tau^2) & (5.16)\\ &= I(t)S(t) - (I(t)S(t))' + \mathcal{O}(\tau^2). & (5.17) \end{aligned}$$

We have that

$$\begin{aligned} \tau\,(I(t)S(t))' &= rI(t)S(t)[S(t) - I(t)] + r\tau[I(t) - S(t)](I(t)S(t))' & (5.18)\\ &= \frac{I(t)S(t)[r(S(t) - I(t)) - a]}{1 - r\tau(I(t) - S(t))}. & (5.19) \end{aligned}$$

Substituting into equations (5.13)-(5.14) gives

$$\begin{aligned} \frac{\mathrm{d}S}{\mathrm{d}t} &= -rIS - \tau ISf(I,S,r,a), & (5.20)\\ \frac{\mathrm{d}I}{\mathrm{d}t} &= rIS - aI + \tau ISf(I,S,r,a), & (5.21) \end{aligned}$$

where

$$\frac{r[r(S-I) - a]}{1 - r\tau(I - S)}. \tag{5.22}$$

We can then divide one by the other and collect terms to give

$$\frac{\mathrm{d}I}{\mathrm{d}S} = \frac{rS - a}{-rS}\left(1 + \mathcal{O}(a\tau, \tau^2)\right). \tag{5.23}$$

This means that if we neglect terms that are $\mathcal{O}(a\tau)$ and $\mathcal{O}(\tau^2)$ the dynamics are the same as in the non-delayed case.

5.2.1 Quarantine and the number of infected individuals

Suppose that a quarantine is imposed once the number of infected individuals reaches some threshold value I^*. Then using previous results, we know that I^* satisfies

$$S^* - \rho \ln S^* = N_0 - I^* - \rho \ln S_0, \tag{5.24}$$

and so the total number that catch the disease is

$$\begin{aligned} N_{disease} &= S_0 - S^* + \int_0^\tau rI(t^* - q)S(t^* - q)\mathrm{d}q && (5.25)\\ &\approx S_0 - S^* + r\tau I^* S^* + \mathcal{O}\left(\tau^2\right). && (5.26)\end{aligned}$$

where t^* is the time that the quarantine is imposed.