Problem sheet 2

Thomas E. Woolley

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1 Flattening the curve

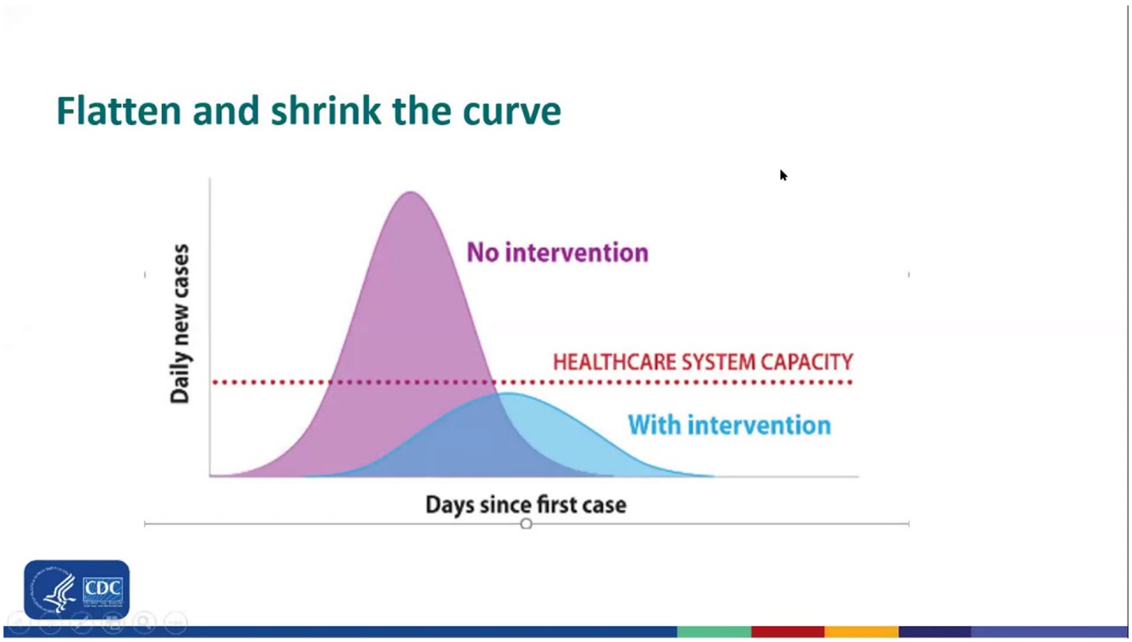


Figure 1: Image taken from the website of the "Centers for Disease Control and Prevention".

Consider the SIR equations for modelling an infectious disease and assume that the parameter values are such that we are in a pandemic scenario, *i.e.* $\rho = rS_0/a > 1$,

$$\dot{S} = -rSI, \quad S(0) = S_0, \tag{1}$$
$$\dot{I} = rSI - aI, \quad I(0) = I_0, \tag{2}$$
$$\dot{R} = aI, \quad R(0) = 0. \tag{3}$$

Note the following questions are easier if you have a good grip on the manipulations performed on the SIR model, as seen in the notes. Thus, this would be a good time to practice deriving the following quantities. However, if you are confident that you know what you are doing[1] then you can simply write down the required answers.

1. Write down expressions for the maximum number of infected people, $I_{\max}$, and total number of infected people, I_Σ, in terms of a, r, S_0, I_0 and S_∞.

2. Write down the expression that S_∞ must satisfy, call this the consistency equation.

3. Plot the left- and right-hand sides of the consistency equation on the same axes with S_∞ on the x-axis. Demonstrate that there are, generally, two possible roots and highlight which root we are interested in.

[1] Trust me, you don't.

In the early stages of the corona pandemic much was made of the "Flatten the Curve" idea. Namely, if you can reduce the infection rate then it was reported that although it would make the disease last longer it would reduce the maximum number of infections, thus, allowing the health care system to cope (see Figure 1).

4. Consider two infection rates r_1, r_2, such that $r_1 > r_2$. Show that $I_{\max}(r_1) > I_{\max}(r_2)$.

   Hint 1: we are considering a pandemic situation, so the reproduction number, ρ, is greater than one.

   Hint 2: consider the derivative of $I_{\max}(r)$ with respect to r.

As shown in the last question reducing the infection rate does reduce the maximum number of infections. However, it also extends the infection period (see Figure 1). Thus, are we sure that the total number of infectives is smaller? For example, instead of infecting 10 people in week 1 are we infecting 1 person per week and making the infection last 10 weeks? Namely, are we just delaying the inevitable, or does reducing the infection rate actually reduce total number of infectives?

5. Show that if $r_1 > r_2$ then $I_\Sigma(r_1) > I_\Sigma(r_2)$.

   Hint 1: Approach this equation graphically using the result from question 3.

1.1 Answers

1. Since we are considering the pandemic scenario then from the lecture notes

$$I_{\max} = I_0 + S_0 - \frac{a}{r} + \frac{a}{r}\ln\left(\frac{a}{rS_0}\right), \tag{4}$$

$$I_\Sigma = R_\infty = S_0 + I_0 - S_\infty = N - S_\infty, \tag{5}$$

   where all terms are defined as in the notes.

2.

$$S_\infty - \frac{a}{r}\ln(S_\infty) = N - \frac{a}{r}\ln(S_0). \tag{6}$$

3. See Figure 2. The two roots are circled in red and labelled $S_{L\infty} < S_{R\infty}$. Since the susceptible population is always decreasing $S_{L\infty}$ is the correct root to choose.

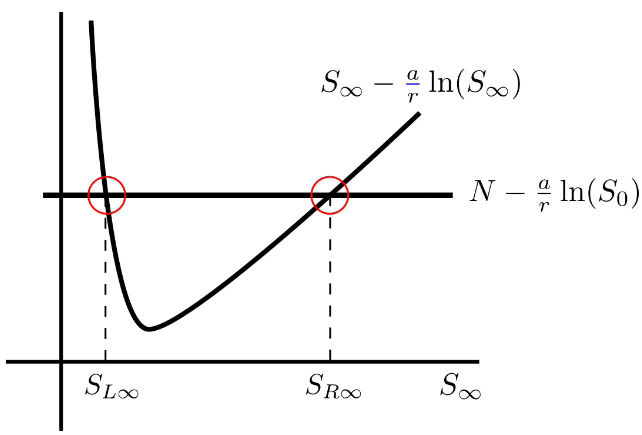


Figure 2: Plotting the left- and right-hand sides of equation (6).

4. Take the derivative of equation (4) with respect to r,

$$\frac{\mathrm{d}I_{\max}}{\mathrm{d}r} = \frac{a}{r^2} - \frac{a}{r^2}\ln\left(\frac{a}{rS_0}\right) - \frac{a}{r^2} = -\frac{a}{r^2}\ln\left(\frac{a}{rS_0}\right). \tag{7}$$

   Since we are in a pandemic $\rho = rS_0/a > 1$, meaning that $0 < a/rS_0 < 1$, thus $\ln(a/rS_0) < 0$. Hence, $\mathrm{d}I_{\max}/\mathrm{d}r > 0$. This means $I_{\max}$ is an increasing function with respect to r, which implies that if $r_1 > r_2$ then $I_{\max}(r_1) > I_{\max}(r_2)$. Thus, proving the desired result.

5. We want to plot the left- and right-hand sides of equation (6) for two different values of r. First thing to note is that all the $S_\infty - (a/r)\ln(S_\infty)$ curves meet at $S_\infty = 1$. Further, if $r_1 > r_2$ then $N - (a/r_1)\ln(S_0) > N - (a/r_2)\ln(S_0)$ and

$$S_\infty - (a/r_1)\ln(S_\infty) > S_\infty - (a/r_2)\ln(S_\infty) \text{ for } S_\infty > 1, \tag{8}$$

$$S_\infty - (a/r_1)\ln(S_\infty) < S_\infty - (a/r_2)\ln(S_\infty) \text{ for } S_\infty < 1. \tag{9}$$

Figure 3 illustrates all of this information on one set of axes, where we have zoomed in on the left-hand roots. Clearly we see that $S_\infty(r_1) < S_\infty(r_2)$ leading to the result that

$$I_\Sigma(r_1) = N - S_\infty(r_1) > N - S_\infty(r_2) = I_\Sigma(r_2). \tag{10}$$

Thus, decreasing r does indeed reduce the maximum number of infectives as well as reduce the entire total number of infected. Flattening the curve is a good idea.

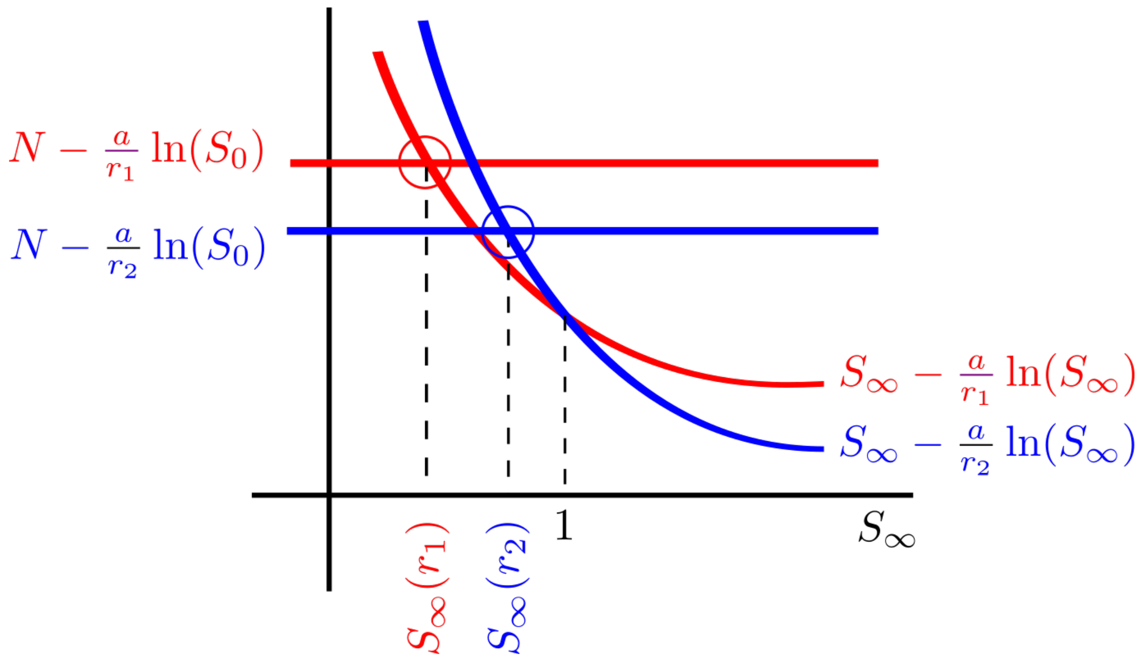


Figure 3: Plotting the left- and right-hand sides of equation (6) for two different values of r.

2 Discrete dynamics

Consider the following discrete evolution equation of a population N_t at generation t,

$$N_{t+1} = \frac{bN_t^2}{1+N_t^2} - EN_t = f(N_t), \tag{11}$$

where $b > 2$ and $E > 0$ are constants.

1. Suggest a biological interpretation of equation (11).
2. Determine the three steady states of equation (11). Define them to be $N_0 < N_- \leq N_+$. You should be able to show that $N_\pm$ only exist if $E < (b-2)/2 = E_M$.
3. Draw (x, y) graphs of

$$y = \frac{bx^2}{1+x^2} \text{ and } y = Ex \tag{12}$$

for a variety of b and E. Using these graphs draw three (N_t, N_{t+1}) plots for the three cases

(a) $E < E_M$,

(b) $E = E_M$,

(c) $E > E_M$.

4. Focusing now on the case of $E < E_M = (b-2)/2$. Show by cob-webbing, or otherwise, that the model is realistic only if the population, N_t, always lies between the two positive values $[N_-, N_2]$, where you should analytically derive the form of N_2.

5. By cobwebbing, or otherwise, discuss the stability of the steady states $N_0, N_\pm$.

2.1 Answers

1. The
$$\frac{bN^2}{1+N_t^2} \tag{13}$$
term is positive but it saturates for large N_t. Hence, it represents reproduction with competition. The $-EN_t$ term suggests that a constant proportion of the population is removed during each generation. Thus, the dynamics could be harvesting of a farmed species, for example, fish stocks.

2. Steady states are when $N_t = N$ for all t. Thus, the steady states satisfy
$$N = \frac{bN^2}{1+N^2} - EN.$$
By inspection $N = 0$ is a solution. Call this solution N_0. Cancel the Ns on both sides to get
$$1 + E = \frac{bN}{1+N^2},$$
$$\implies N^2(1+E) - bN + (1+E) = 0,$$
$$\implies N_\pm = \frac{b \pm \sqrt{b^2 - 4(1+E)^2}}{2(1+E)}.$$
The roots $N_\pm$ only exist when they are real, thus,
$$b^2 > 4(1+E)^2,$$
$$\implies b > 2(1+E),$$
$$\implies E_M = \frac{b-2}{2} > E. \tag{14}$$

3. After some sketching you should come to realise that you do not need to vary both parameters. Thus, we can cover all possible outcomes by varying E (see Figure 4).

   The top image of Figure 4 shows that as E increases the line Ex gets steeper. For $E < E_M$ the two curves cross three times (black and red curves in top figure). At $E = E_M$ the two curves cross twice times (black and blue curves in top figure). For $E > E_M$ the two curves cross once (black and green curves in top figure). The coloured lines in the top graph then corresponds to the coloured curves in the bottom graphs. Namely, if $E < E_M$ then N_0, N_- and N_+ all exist. If $E = E_M$ then N_0 and $N_- = N_+$ exist. If $E > E_M$ then only N_0 exists.

4. From cobwebbing in multiple places we see that the starting points must be between N_- and N_2 (green region in Figure 5). If you start with initial conditions outside of this region (red region in Figure 5) the trajectories end up going negative, which is unrealistic for a population model.

   To calculate N_2 we realise that it satisfies $f(N_2) = N_-$. Further, from considering Figure 5 we know there must be three roots $N_1 < 0 < N_- < N_2$. We also note that, by definition, N_- satisfies
$$N_- = \frac{bN_-^2}{1+N_-^2} - EN_-. \tag{15}$$
   Using this information we derive
$$\frac{bN_-^2}{1+N_-^2} - EN_- = N_- = f(N) = \frac{bN^2}{1+N^2} - EN. \tag{16}$$

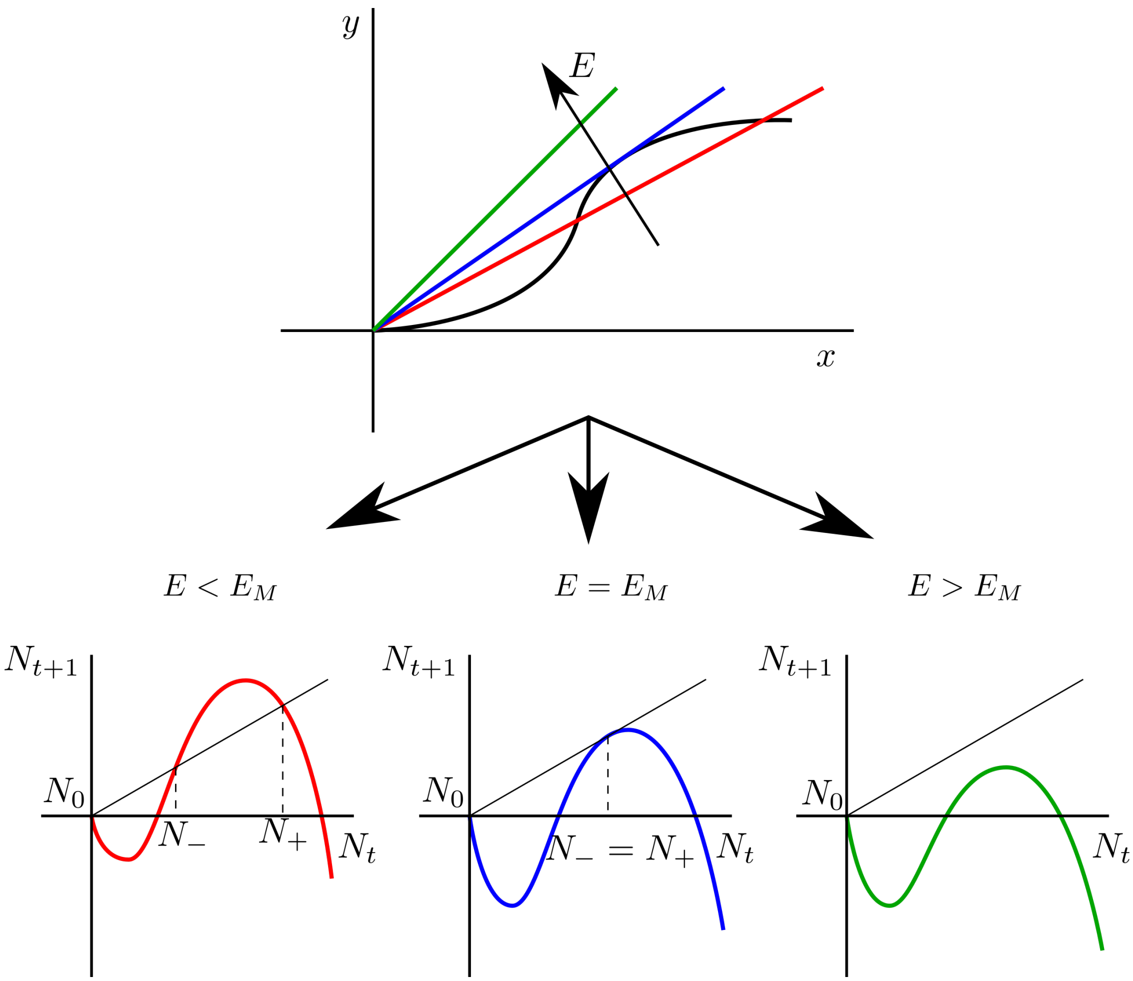


Figure 4: Plotting the two curves from equation (12) and interpreting the two components into (N_t, N_{t+1}) graphs for various values of E.

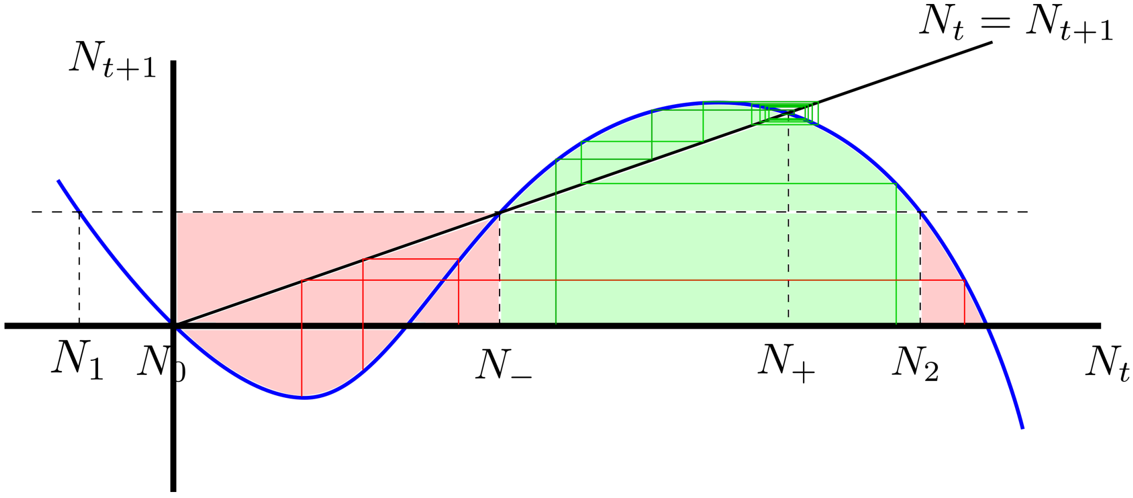


Figure 5: Cobwebbing equation (11) in the case $E < E_M$. The green area and green cobwebs are the realistic region. The red region and red cobwebs go negative and are, thus, unrealistic.

Since we know that N_- is a root we manipulate equation (16) to extract it,

$$\implies 0 = \frac{bN_-^2}{1+N_-^2} - \frac{bN^2}{1+N^2} - E(N_- + N),$$

$$\implies 0 = \frac{b}{\left(1+N_-^2\right)\left(1+N^2\right)}\left(N_-^2\left(1+N^2\right) - N^2\left(1+N_-^2\right)\right) - E(N_- - N),$$

$$\implies 0 = \frac{b}{\left(1+N_-^2\right)\left(1+N^2\right)}\left(N_-^2 - N^2\right) - E(N_- - N),$$

$$\implies 0 = \frac{b(N_- - N)(N_- + N)}{\left(1+N_-^2\right)\left(1+N^2\right)} - E(N_- - N),$$

$$\implies 0 = (N_- - N)\left(\frac{b(N_- + N)}{\left(1+N_-^2\right)\left(1+N^2\right)} - E\right). \tag{17}$$

Equation (17) confirms that N_- is one of the roots. Acknowledging this we can divide through by $(N_- - N)$ and solve the remaining quadratic for the remaining two roots.

$$0 = \frac{b(N_- + N)}{\left(1+N_-^2\right)\left(1+N^2\right)} - E,$$

$$\begin{aligned}\implies 0 =& b(N_- + N) - E\left(1+N_-^2\right)\left(1+N^2\right),\\ =& E\left(1+N_-^2\right)N^2 - bN + E\left(1+N_-^2\right) - bN_-,\\ \implies N_{1,2} =& \frac{b \pm \sqrt{b^2 - 4E(1+N_-^2)\left(E\left(1+N_-^2\right) - bN_-\right)}}{2E(1+N_-^2)}.\end{aligned}$$

Note we do require

$$b^2 - 4E(1+N_-^2)\left(E\left(1+N_-^2\right) - bN_-\right) > 0 \tag{18}$$

for $N_{1,2}$ to exist. However, from Figure 5 we can deduce that whenever N_- exists then so will $N_{1,2}$, thus satisfying $E_M > E$ will also satisfy inequality (18).

3 Cobwebbing in Matlab

The code below simulates the dynamics as presented in question 2. Once again, you can download this code from learning central, or copy and paste it from here.

Simulating discrete dynamics is, in some ways, easier than simulating ODEs. Given a value for N_t and a function f you simply evaluate $f(N_t)$ to calculate N_{t+1}. Thus, most of the cobwebbing code below is for plotting purposes. The actual calculation step occurs in lines 43-46.

Have a go at altering the parameters b and E in lines 9-10. Equally, change the initial conditions in lines 36-38 to see where you will end up.

If you are really feeling adventurous, alter the code to work with the discrete logistic equation and simulate chaos!

```
%% Ensure we start from a blank slate
clear all
close all
clc

%% Initialise variables
fs=15; % Set fontsize

b=4;
E=0.8;

Np=(b+sqrt(b^2-4*(1+E)^2))/(2*(1+E)); %N+ from question 2.
Nn=(b-sqrt(b^2-4*(1+E)^2))/(2*(1+E)); %N- from question 2.
N1=(b-sqrt(b^2-4*E*(1+Nn^2)*(E*(1+Nn^2)-b*Nn)))/(2*E*(1+Nn^2)); %N1 from question 2.
N2=(b+sqrt(b^2-4*E*(1+Nn^2)*(E*(1+Nn^2)-b*Nn)))/(2*E*(1+Nn^2)); %N2 from question 2.

%% Set up the basic plotting space
N=linspace(-1,8);

hold on
plot(N,N,'k') % Plot N(t)=N(t+1)
```

```
plot(N,b*N.^2./(1+N.^2)-E*N,'b') % Plot N(t+1)=f(N(t))
plot(N,Nn*ones(1,length(N)),'--k','linewidth',1) % Plot N(t+1)=N-
plot([N1 N1],[0 Nn],'--k','linewidth',1) % Plot N(t)=N1
plot([Nn Nn],[0 Nn],'--k','linewidth',1) % Plot N(t)=N-
plot([N2 N2],[0 Nn],'--k','linewidth',1) % Plot N(t)=N2
axis([0 5 0 2])
xlabel('$N_t$')
ylabel('$N_{t+1}$')

%% Calculate the cobweb diagram
% The Cobweb(x1,x2,x3,x4) function has 4 arguments x1-x4.
% x1 is the initial point from which the cobweb starts.
% x2 and x3 are the parameters b and E, respectively.
% x4 is the colour of the cobweb.
Cobweb(3,b,E,'b')
Cobweb(0.5,b,E,'r')
Cobweb(4.5,b,E,'r')
set(gca,'fontsize',fs) % Set fontsize.

function Cobweb(N0,b,E,c)
% The following for loop computes the first 100 iteration values.
Nt(1)=N0;
for i=1:100
    Nt(i+1)=b*Nt(i)^2/(1+Nt(i)^2)-E*Nt(i);
end


% The following code plots the cobweb.
plot([Nt(1) Nt(1)],[0 Nt(2)],c,'linewidth',1)
for i=1:100-2
    plot([Nt(i) Nt(i+1)],[Nt(i+1) Nt(i+1)],c,'linewidth',1)
    plot([Nt(i+1) Nt(i+1)],[Nt(i+1) Nt(i+2)],c,'linewidth',1)
end
end
```

Exam Revision

4 A different infection model

An animal population is prone to a fatal disease. There is a limited vaccine that creates immunity in the susceptible population but has no effect on infected animals. The higher the number of infected animals observed, the more vigorously vaccinations are administered.

Let I denote the number of infected animals, S the number of susceptible animals, V the number of vaccinated animals and R the number of dead animals. An ordinary differential equation description of these interactions can be written

$$\frac{\mathrm{d}S}{\mathrm{d}T} = -\beta SI - pSI, \tag{19}$$

$$\frac{\mathrm{d}I}{\mathrm{d}T} = \beta SI - aI, \tag{20}$$

$$\frac{\mathrm{d}R}{\mathrm{d}T} = aI, \tag{21}$$

$$\frac{\mathrm{d}V}{\mathrm{d}T} = pSI. \tag{22}$$

1. Explain the biological interpretation of each of the terms in the model.

2. Non-dimensionalise the model to give

$$\frac{\mathrm{d}s}{\mathrm{d}t} = -si(1+\eta), \tag{23}$$

$$\frac{\mathrm{d}i}{\mathrm{d}t} = i(s-1), \tag{24}$$

$$\frac{\mathrm{d}r}{\mathrm{d}t} = i, \tag{25}$$

$$\frac{\mathrm{d}v}{\mathrm{d}t} = \eta si. \tag{26}$$

where s, i, r, v and t are the non-dimensional variables corresponding to the upper-case dimensional variables. The parameter $\eta > 0$ should be given in terms of a, β and p.

Suppose that the initial conditions are

$$s(0) = s_0, i(0) = i_0, r(0) = 0, v(0) = 0,$$

where $s_0, i_0 > 0$ and assume that $i \to 0$ as $t \to \infty$.

3. Show
$$s + i + r + v = \text{constant}, \tag{27}$$
where the constant should be defined.

4. What does equation (27) mean? Is this physically correct?

5. Define $r_\infty = \lim_{t\to\infty} r(t)$ and $s_\infty = \lim_{t\to\infty} s(t)$. What do r_∞ and s_∞ represent?

6. By considering $\mathrm{d}i/\,\mathrm{d}s$ and $\mathrm{d}v/\,\mathrm{d}s$ show that
$$r_\infty = \frac{1}{1+\eta} \ln\left(\frac{s_0}{s_\infty}\right). \tag{28}$$

4.1 Answers

1. Susceptibles become infected at a rate proportional to their interaction rate with infectives with rate constant β. Susceptibles are vaccinated at a rate proportional to their interaction rate with infectives with rate constant p. Infectives die at a rate proportional to their population size, with rate constant a.

2. For each variable sub in the form $P = [P]p$, where P is the dimensional variable, p is the non-dimensional variable and $[P]$ is the dimensional scale.
$$\frac{[S]}{[T]}\frac{\mathrm{d}s}{\mathrm{d}t} = -\beta[S][I]si\left(1 + \frac{p}{\beta}\right), \tag{29}$$
$$\frac{[I]}{[T]}\frac{\mathrm{d}i}{\mathrm{d}t} = [I][S]i\beta\left(s - \frac{a}{\beta[S]}\right), \tag{30}$$
$$\frac{[R]}{[T]}\frac{\mathrm{d}r}{\mathrm{d}t} = a[I]i, \tag{31}$$
$$\frac{[V]}{[T]}\frac{\mathrm{d}v}{\mathrm{d}t} = p[S][I]si. \tag{32}$$
Comparing equations (29)-(32) with equations (23)-(26) we see that
$$\frac{1}{[T]} = \beta[I], \quad \eta = \frac{p}{\beta}, \quad \frac{1}{[T]} = \beta[S], \quad \frac{a}{\beta[S]} = 1, \quad \frac{[R]}{[T]} = a[I], \quad \frac{p[S][I][T]}{[V]} = \eta. \tag{33}$$
So,
$$[S] = \frac{a}{\beta} = [I] = [R] = [V], \quad [T] = \frac{1}{a}, \quad \eta = \frac{p}{\beta}. \tag{34}$$

3. Adding equations (29)-(32) together the right-hand side disappears. Integrating with respect to time gives equation (27). Since the constant holds for all time it is true initially, thus
$$s(t) + i(t) + r(t) + v(t) = s_0 + i_0 \tag{35}$$
for all $t \geq 0$.

4. The entire population is conserved, thus, an individual can only transition between one of four states: susceptible, infected, removed (dead), vaccinated. Note this means that there is no birth, nor death from other causes. Of course this is not physically correct, but we are assuming that the disease occurs over a short enough time scale that births and deaths via other sources do not influence the result greatly.

5. r_∞ is the (non-dimensionalised) population that has died from the virus. s_∞ is the (non-dimensionalised) population that is susceptible after the infection has disappeared.

6. Using equation (27) we know that

$$s_\infty + r_\infty + v_\infty = s_0 + i_0. \tag{36}$$

Further

$$\frac{\mathrm{d}i}{\mathrm{d}s} = -\frac{i(s-1)}{si(1+\eta)} \text{ and } \frac{\mathrm{d}v}{\mathrm{d}s} = -\frac{\eta is}{si(1+\eta)}.$$

So,

$$\int_{i_0}^{0} 1+\eta \,\mathrm{d}i = \int_{s_0}^{s_\infty} \frac{1}{s} - 1 \,\mathrm{d}s \text{ and } \int_{0}^{v_\infty} \mathrm{d}v = \int_{s_0}^{s_\infty} -\frac{\eta}{1+\eta} \,\mathrm{d}s,$$

resulting in

$$-(1+\eta)i_0 = \ln\left(\frac{s_\infty}{s_0}\right) - (s_\infty - s_0) \text{ and } v_\infty = \frac{\eta}{1+\eta}(s_0 - s_\infty). \tag{37}$$

Substituting i_0 and v_∞ from equations (37) into equation (36) then gives

$$\begin{aligned}
r_\infty =& s_0 - s_\infty - \frac{s_0 - s_\infty}{1+\eta} - \frac{1}{1+\eta}\ln\left(\frac{s_\infty}{s_0}\right) - \frac{\eta}{1+\eta}(s_0 - s_\infty), \\
=&(s_0 - s_\infty)\left(1 - \frac{1}{1+\eta} - \frac{\eta}{1+\eta}\right) - \frac{1}{1+\eta}\ln\left(\frac{s_\infty}{s_0}\right), \\
=&\frac{1}{1+\eta}\ln\left(\frac{s_0}{s_\infty}\right).
\end{aligned} \tag{38}$$

5 Discrete Ricker model

Suppose that the evolution of a population can be described by a discrete-time Ricker model of the form

$$N_{t+1} = N_t \exp\left(r\left(1 - \frac{N_t}{K}\right)\right) = f(N_t), \tag{39}$$

where $r, K > 0$ are constants.

1. Describe the biological interpretation of the model.
2. Determine any non-negative steady states and their linear stability.

Let us now fix $K = 1$.

3. Construct a cobweb map for the model when $0 < r < 2$ and discuss the global qualitative behaviour of the solutions.
4. Using Figure 6, or otherwise, specify the steady states and their stability in the three cases of the discrete Ricker model when $r = 1$, 2.1 and 3.

5.1 Answers

1. It is a reproduction model with rate r and carrying capacity K.
2. Solving

$$N = N\exp\left(r\left(1 - \frac{N}{K}\right)\right), \tag{40}$$

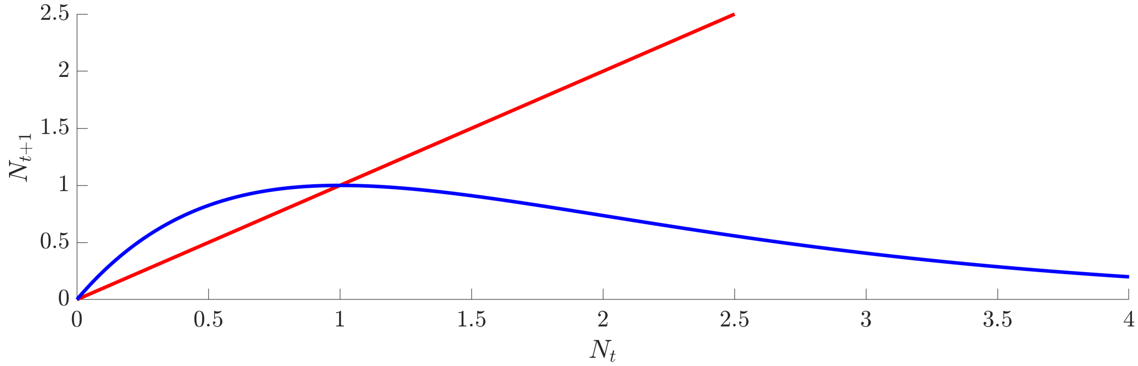
gives $N = 0, K$. The stability of the steady states are derived from considering the size of $f'(N)$ at the steady states,

$$\begin{aligned}
f'(N) &= \frac{\mathrm{d}}{\mathrm{d}N}\left(N\exp\left(r\left(1 - \frac{N}{K}\right)\right)\right), &(41)\\
&= \exp\left(r\left(1 - \frac{N}{K}\right)\right)\left(1 - \frac{Nr}{K}\right). &(42)
\end{aligned}$$

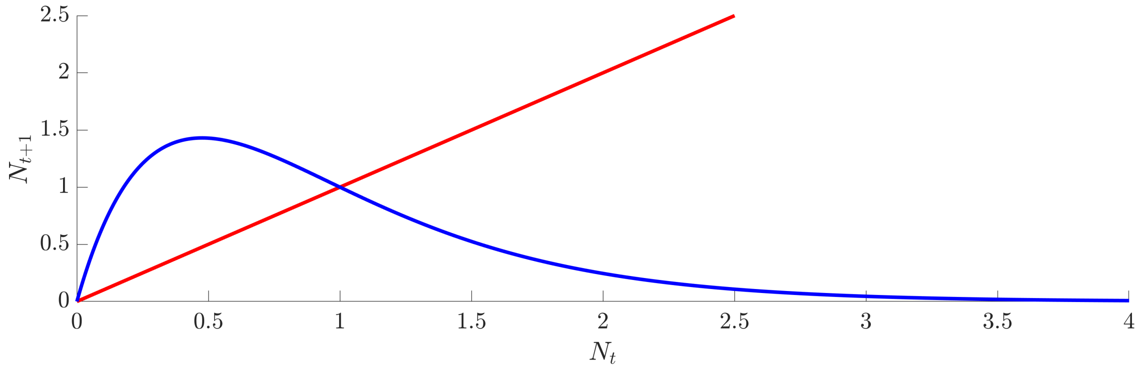
Thus, $f'(0) = \exp(r) > 1$ for all $r > 0$, hence 0 is always unstable. Further,

$$f'(K) = 1 - r. \tag{43}$$

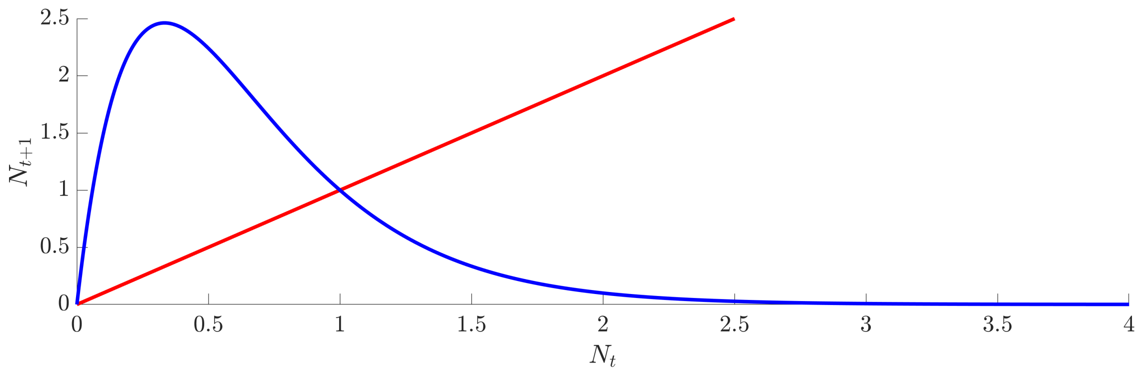
Thus, $N = K$ is stable for $0 < r < 2$ and unstable for $r > 2$.



(a) $r = 1$



(b) $r = 2.1$



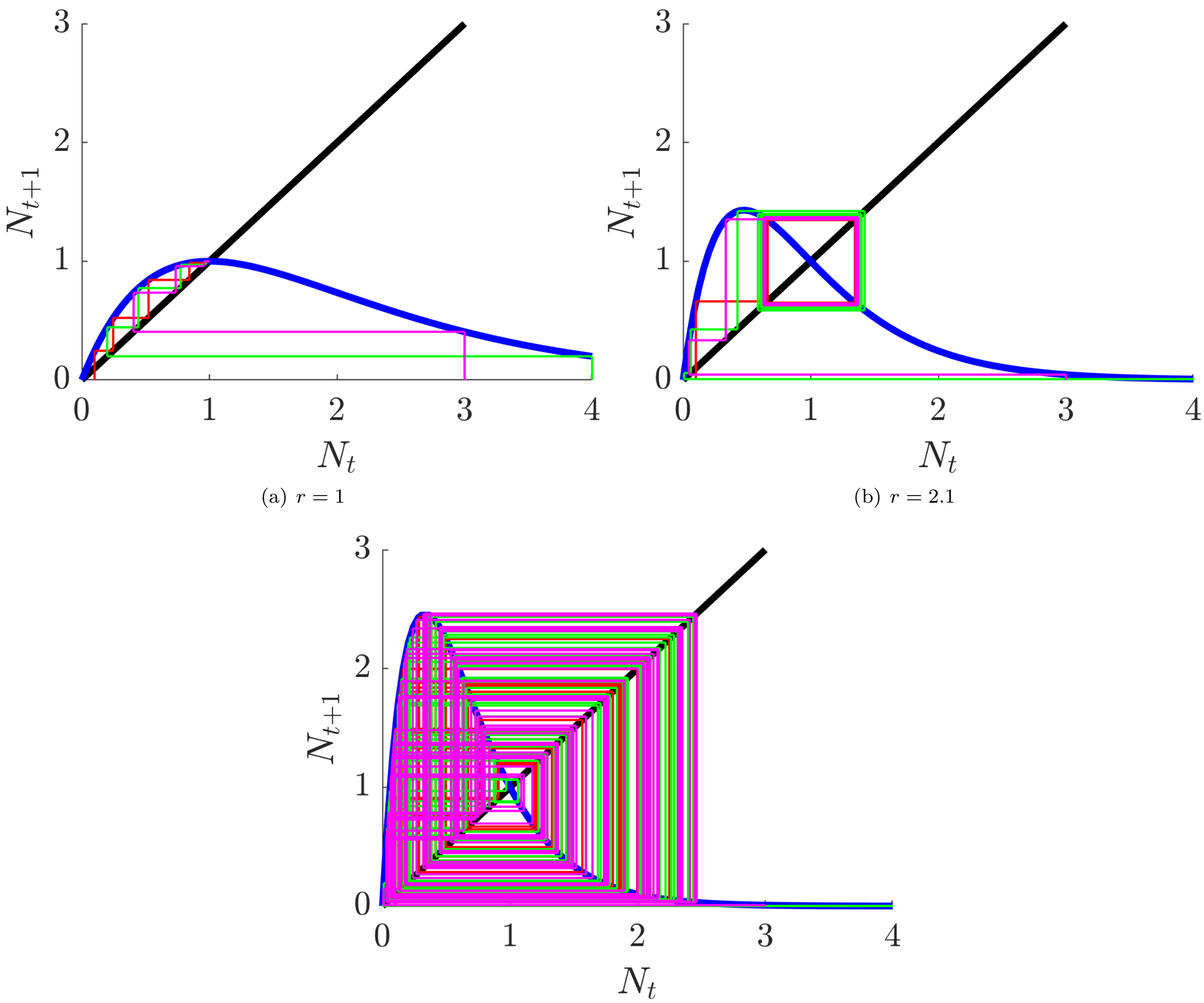
(c) $r = 3$

Figure 6: Plot of the discrete Ricker model for different values of r (specified beneath each figure). In all case $K = 1$.

3. See the answer to $r = 1$ below. Note the point of this question was that you should try and sketch the curve yourself, before copying the printed versions.

4. Firstly, we note that the steady is independent of r, so, when $K = 1$, the steady states are always $N = 0$ and 1.

    - When $r < 2$ the analysis and the cobweb both suggest that $N = 0$ is unstable and $N = 1$ is globally stable.
    - When $r > 2$ the analysis suggest that $N = 1$ is unstable but we do not know what happens then. From the cobweb we see that when $r = 2.1$ the trajectories tend to a period 2 oscillatory state.
    - When $r = 3$ the cobweb suggests a chaotic trajectory.



(a) $r = 1$

(b) $r = 2.1$

(c) $r = 3$

Figure 7: Cobwebbed solutions of the discrete Ricker model for different values of r (specified beneath each figure). In all case $K = 1$. The red, green and magenta lines show trajectories with different starting points. Red starts at $N_0 = 0.1$, green starts at $N_0 = 3$ and magenta starts at $N_0 = 4$.