

# 1 Practical Session 1

1 hour

Use paper, pencil and a ruler to analyze the following, very simple models for population growth (acetates and markers provided where needed),

- The first exercise is aimed at manipulating and graphically representing a discrete-time model, as well as illustrating ideas on limit-cycle and chaotic behaviour. After iterating the model on the graphs, plot the results on acetate using a coloured pen. A brief discussion will follow in which everyone is invited to show their results on a projector.
- In the second exercise we consider a continuous-time version of the above model. The two models are equivalent if only small changes in the population are allowed for (i.e. small values of the constant  $a$  - see below). This model provides an example where an exact (analytical) solution can be obtained in terms of the time variable and the parameters. This solution is explicitly given and you are asked to study its features.

## 1.1 Discrete-time logistic growth.

Consider a population of organisms:

- (a) whose members are identical and share resources identically;
- (b) that is not affected by outside factors;
- (c) in which changes occur only in short and uniformly spaced intervals of time (our unit of time). This is a reasonable assumption, for example, in some insects that have a short period of activity in the summer but are dormant the rest of the year;
- (d) that is large enough to neglect stochastic effects in the changes that occur, i.e. the model is *deterministic*: whenever the population has a given size  $N$  the same amount of change follows.

A possible model giving the population  $N_{t+1}$  at time  $t + 1$  in terms of the population size  $N_t$  at time  $t$  when it last changed, is the following discrete-time equation:

$$N_{t+1} = aN_t \left(1 - \frac{N_t}{K}\right) \quad (1)$$

$$= N_t + (a - 1)N_t - a \frac{N_t^2}{K}, \quad (2)$$

where  $a > 1$  and  $K$  are constant positive numbers, or simply *positive constants*. The growth term  $(a - 1)N_t$  states that each individual produces  $(a - 1)$  offspring per unit time. The control term  $-aN_t/K$  states that the rate of death per individual and per unit of time is proportional to the total number of individuals  $N_t$ : this models competition for resources by bounding population growth.

As the population size must be positive ( $N_{t+1} > 0$ ) this model is only defined for  $0 \leq N_t \leq K$ . Hence  $K$  is termed the *carrying capacity* of the model ecosystem. Without any loss of generality we set  $K = 1$  by rescaling  $N_t/K \rightarrow N_t$  at all times. Now Equation (1) now reads

$$N_{t+1} = aN_t(1 - N_t) . \quad (3)$$

An equilibrium point is reached if there is no further change, i.e.,  $N_{t+1} = N_t \equiv N^*$ . This requires a balance between births and deaths.

- Show that the equilibrium levels are:  $N^* = 0$  and

$$N^* = \frac{a - 1}{a} , \quad (4)$$

with the second solution meaningful only if  $a > 1$  (since  $N^*$  must be positive).

- Given that the function  $x \rightarrow x(1 - x)$  has its maximum at  $x = 1/2$ , show that the maximum value that  $N_{t+1}$  can possibly take (if  $N_t = 1/2$  is reached) is  $N_{max} = a/4$ . This implies, since  $N_{t+1} \leq 1$ , that the model is biologically meaningful only for  $a \leq 4$ . From (4) we then conclude that we are interested in the range

$$1 < a \leq 4 . \quad (5)$$

A property of the equilibrium point  $N^*$  is that, once it is reached the system can not subsequently move away from it (at least for a deterministic model). As the population changes by discrete amounts controlled by  $a$ , for large values of  $a$  the population may never reach  $N^*$  and may thus keep changing forever. In fact, this happens for  $a \geq 3$ .

There are three types of long-term behaviour of the model

- Use the graphs provided to find what the behaviour is in the cases  $a = 2.5, 3.3, 3.52$ , and  $3.9$ .
- (a) Consider the parabolic graph  $(N_{t+1}, N_t)$  in the annexed pages. Start with, say  $X = N_0 = 0.1$ , and draw a vertical line until it crosses the parabola [ $Y = N_{t+1} = aN_t(1 - N_t)$ ]; this gives the point  $(N_0, N_1)$ . Mark this point.
- (b) Draw a horizontal line from  $(N_0, N_1)$  until it meets the straight line [ $N_{t+1} = N_t$ ]. From this point draw a vertical line and obtain  $(N_1, N_2)$ . Mark this point too.
- (c) Simultaneously, project the horizontal lines to mark the points  $(t, N_t)$  on the adjacent graph. This will plot the changes in the population as a series in time, with time  $t$  being the number of iterations. This time series will help you to see whether the behaviour has stabilized or not.
- (d) Repeat a), b) and c) until a pattern of behaviour becomes apparent (typically after a dozen iterations or so).
- Calculate the equilibrium population size  $N^*$  from (4). Does the system reach equilibrium? If not, what is the relation between the long-term behaviour and equilibrium?

The time it takes to reach a steady mode of behaviour varies with  $N_0$  and  $a$ , but if a pattern of behaviour is reached its quantitative features should not depend on  $N_0$ . The convergence time varies with  $a$  and  $N_0$  in a way that is not simple and is apparently erratic. We have carefully chosen the values of  $a$  (for the given  $N_0$ ) so that fairly optimal convergence was obtained for each type of behaviour.

## 1.2 Continuous-time logistic growth.

We now consider a population of simple organisms under the same assumptions as in Example 1, but modify assumption (c): changes (births and deaths) can now occur at any instant in time at given rates per unit time. A simple model describing how the population size  $N(t)$  evolves with time  $t$  is the differential equation

$$\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t)}{K}\right), \quad (6)$$

with  $r$  and  $K$  positive constants. This is a continuous-time version of (1), called the *logistic equation*, whose birth and death terms on the right-hand-side are easily identified. The constant  $K$  has the same meaning as before;  $r$  is the growth rate, and is proportional to the multiplication factor  $a - 1$  in the discrete-time model. Equation (6) has an analytic solution given by

$$N(t) = \frac{K}{1 + [K/N_0 - 1] \exp(-rt)}, \quad (7)$$

where  $N_0$  is the initial population size at  $t = 0$ . (At first sight this expression may look off-putting but, given values of  $K$ ,  $N_0$ ,  $r$  and  $t$ , it can easily be evaluated on a hand calculator, or using a computer package such as Excel.)

- Substitute  $t = 0$  into (7) and check that  $N(0) = N_0$  [hint:  $\exp(0) = 1$ ]. The exact solution allows us to understand the behaviour of the model for all values of  $r$ ,  $K$  and  $N_0$ . (Note that  $K$  is a redundant parameter, as we could set  $K = 1$  by rescaling  $N(t)/K \rightarrow N(t)$  and  $N_0/K \rightarrow N_0$  as before.)
- Find the limit of  $N(t)$  when  $t$  is large [hint:  $\exp -x \rightarrow 0$  as  $x \rightarrow \infty$ ].

Figure 1 below shows the general shape of  $N(t)$  with  $N_0 = 0.01$  and  $K = 1$ , in two cases; (a)  $r = 1$  and (b)  $r = 2$ .

- Identify which graph corresponds to which value of  $r$ .
- Use the graphs to estimate the time for a population of size  $N_0 = 0.01$  to grow 50 fold in both cases (a) and (b). Compare your estimates with the values obtained from the exact solution (7). What is the relation between the two times?
- In Figure 1  $N_0 < K$ . What happens to the population if its initial size is larger than  $K$  [hint: use Equation (6) for the rate of change of the population].

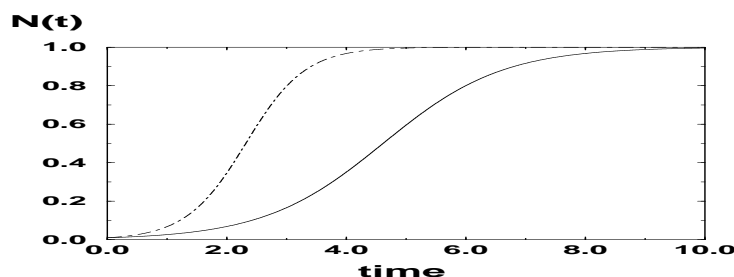


Figure 1: Solution (7) to the logistic equation (6) with  $N_0 = 0.01$ ;  $r = 1, 2$ ;  $K = 1$

## Solutions - Example 1.1

### Equilibrium population levels

- *Stable equilibrium:*  $N_{t+1} = N_t = N^*$

From Equation (1) (from the notes: Practical Session 1) with  $K = 1$  we find

$$\begin{aligned}\Rightarrow N^* &= N^* + (a - 1)N^* - a(N^*)^2 \\ N^* [(a - 1) - aN^*] &= 0\end{aligned}$$

This then tells us that

$$\begin{aligned}N^* &= 0 && \text{if } a \leq 1 \\ N^* &= (a - 1)/a && \text{if } a > 1\end{aligned}$$

- *Maximum of  $N_{t+1}$ :*

Since the maximum value of  $N(1 - N)$  occurs at  $N = 1/2$  then ....

From Equation (3) (from the notes: Practical Session 1) we see

$$\begin{aligned}\max [N_{t+1}] &= a \max [N_t(1 - N_t)] \\ &= a \max [(1/2)(1 - (1/2))] \\ &= a/4\end{aligned}$$

- *Long-term behaviour:*

The results of the iteration for  $N_0 = 0.1$  and the given values of  $a$  are shown in the graphs below.

*The three types of behaviour are:*

- $a = 2.5$  : stable equilibrium
- $a = 3.3$  : limit cycle with period 2
- $a = 3.52$  : limit cycle with period 4
- $a = 3.9$  : chaos - no readily discernible pattern.

- *Equilibrium values:*

The equilibrium population size for  $a > 1$  is  $N^* = (a - 1)/a$ .

Substituting the values 2.5, 3.3, 3.52 and 3.9 for  $a$  gives:

$$N^* = 0.600, 0.697, 0.716, 0.744 .$$

*Relation to equilibrium state:*

- $a = 2.5$  : equilibrium is reached
- $a = 3.3$  : the two values in the limit cycle are either side of  $N^*$
- $a = 3.52$  : the four values in the limit cycle are half one side and half the other side of  $N^*$
- $a = 3.9$  : the values of  $N_t$  appear (almost randomly) distributed on both sides of  $N^*$ .



## Solutions - Example 1.2

- *What is  $N(0)$ ?*

Putting  $t = 0$  in Equation (7) (from the notes: Practical Session 1) gives

$$\begin{aligned} \text{Since } \exp(0) = 1 \quad N(0) &= \frac{K}{1 + [K/N_0 - 1]} \\ &= \frac{K}{K/N_0} \\ &= N_0 \end{aligned}$$

- *Limit when  $t \rightarrow \infty$ :*

$$\begin{aligned} \text{Since } \exp(-\infty) \rightarrow 0 \quad N(t) &\rightarrow \frac{K}{1 + 0} \\ &\rightarrow K \end{aligned}$$

- *Which graph is which?*

The larger the growth rate  $r$  the faster the population grows.

Hence the top graph is the one with  $r = 2$ .

- *Estimate of growth times:*

We want to know the time when the population reaches the size  $N = 50 * 0.01 = 0.5$ .

From the graphs:

$$\text{for } r = 1, \quad t \approx 4.6$$

$$\text{for } r = 2, \quad t \approx 2.3$$

Substituting  $N_0 = 0.01$ ,  $K = 1$  and  $N(t) = 0.5$  in Equation (7) (Practical Session 1):

$$\frac{1}{2} = \frac{1}{1 + [1/0.01 - 1] \exp(-rt)} = \frac{1}{1 + 99 \exp(-rt)}$$

$$\Rightarrow 2 = 1 + 99 \exp(-rt)$$

$$\Rightarrow \exp(rt) = 99$$

$$\Rightarrow rt = \ln(99) \approx 4.595$$

$$\Rightarrow \text{for } r = 1, \quad t \approx 4.595$$

$$\text{for } r = 2, \quad t \approx 4.595/2 \approx 2.298$$

which agrees with the graphical estimates.

N.B. As the exact solution only depends on time  $t$  through the scaled variable  $rt$ , a doubled growth rate gives the same population size in half of the time.

- *What if  $N_0 < K$ ?*

Whenever  $N(t) > K$  then from Equation (6) (Practical Session 1)

$$\frac{dN(t)}{dt} < 0 .$$

This means that  $N$  decreases until  $dN(t)/dt = 0$ , which happens when  $N(t) = K$ . This behaviour is illustrated below.

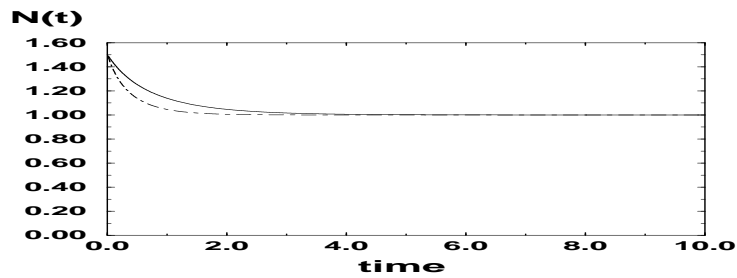


Figure 2: Solution (7) (Practical Session 1) to the logistic equation with  $N_0 = 1.5$ ;  $r = 1, 2$ ;  $K = 1$





## 2 Practical Session 2

1 hour 30 minutes

### 2.1 Predator-prey model

Let us assume that we have a population  $F$  whose intrinsic growth rate is described by the continuous-time logistic of Example 1.2. However, to make the model slightly more realistic, we introduce a second population  $P$  which preys on our original population. Each member of  $P$  consumes members of  $F$  at a certain rate so that the rate of change in  $F$  is now given by

$$\frac{dF}{dt} = rF \left(1 - \frac{F}{K}\right) - IP ,$$

where  $I$  is the feeding or *uptake rate* per predator, and as before  $r$  is the growth rate, and  $K$  the carrying capacity for the prey population.

This uptake rate is normally considered to be a simple function of the prey population density:

$$I = \frac{I_{\max}F}{F + F_0} ,$$

where  $I_{\max}$  and  $F_0$  are constants.

You should be able to sketch  $I$  as a function of  $F$  and illustrate how varying the two constants affects the graph.

We will assume that the predator population can change as follows. We will assume that the reproductive rate of an individual is proportional to its prey intake rate but that death rate is constant. The rate of change in the predator population is then

$$\frac{dP}{dt} = \epsilon IP - \mu P ,$$

where  $\epsilon$  and  $\mu$  are constants.

If you substitute zero for both  $F$  and  $P$  in the equations above, you should see that both rates of change are zero. Thus,  $(F = 0, P = 0)$  is a simple equilibrium state of the system. Also check that there is another trivial equilibrium when the predator population is zero and the food population is at its carrying capacity. In addition to these two, there is a third and more interesting equilibrium where both populations are non-zero. By setting the two differential equations to zero and using simple algebra, you should be able to form expressions for the equilibrium populations in terms of the 6 constant parameters ( $K, r, I_{\max}, F_0, \epsilon$  and  $\mu$ ). You should also be able to form two conditions for both these equilibrium populations to be strictly positive (assuming that all the parameters are positive). Try to understand the physical meaning of each condition, and from that understanding, speculate as to which of the two trivial steady states this system will return to if either one of the conditions is not met.

Suppose that  $F$  represents a crop and  $P$  a pest. A farmer wishing to increase crop yield could either add fertilizer to increase the crop growth rate  $r$  or could increase the acreage, thereby increasing the carrying capacity  $K$ . You should see from your steady state values that somewhat counter-intuitively neither of these actions changes the steady state crop population level. This effect is known as the *paradox of enrichment*.

Although we can obtain the steady state values of the system analytically, we cannot write down analytic solutions for  $P(t)$  and  $F(t)$  (contrast this with Example 1.2). In order to investigate the non-equilibrium behaviour of the model we must evaluate our model equations numerically. A program has been written to this: open a new window onto the software section of the course website. From there launch the **Deterministic Predator Prey model**. A new browser window will appear with a form showing the following values

$$\begin{array}{llll}
 I_{max} & = & 10 & & F_0 & = & 1 & & \text{Maximum Time} & = & 100 \\
 \mu & = & 4.0 & & \epsilon & = & 0.5 & & \text{Number of observations} & = & 1000 \\
 r & = & 10 & & K & = & 8 & & & & 
 \end{array}$$

taken by the model parameters. You will modify these later, but can reset to these values at any time by clicking on the *Defaults* button. For now just click on the *Run Model* button at the bottom of the page. After a few moments the window will refresh and display the output of the model run.

The display shows the solution of the differential equations which are obtained by numerical integration using the RK-4 method discussed in the notes. The results are provided in two formats. Initially you see a timeseries plot of the predator and prey populations. You should see that both equations settle down to equilibrium values. Check these against your analytic values. Since the two populations are attracted to the steady state: we say that the equilibrium is stable.

The second format provided is a phase plot (or phase portrait) where the predator population size is plotted against that of the prey. **Before** you click on the *Phaseplot* tab think about what this plot should look like. Make sure you understand how the phase plot relates to the earlier time plot (note: toggle between the timeseries and phase plots using the tabs under the graphs).

Investigate the effect of increasing the carrying capacity  $K$  on the trajectories of the two populations. To achieve this do several calculations each time increasing  $K$  by a small amount (0.25, say). Using time plots you should observe that, as  $K$  increases, the transient state (that is, before the solution settles to equilibrium) lasts for longer and longer. Eventually the system never settles down, but continues to oscillate around the steady state. The steady state is now said to be unstable.

As you go along observe the effect this has on the phase plots, and make sure that you can see the link with the time plots.

Once you have obtained a value of  $K$  for which the equilibrium is unstable, continue to increase  $K$  slowly and investigate the effect this has on the amplitude and frequency of the oscillations.

## Introducing stochasticity

The stochastic version of this predator prey model is defined by the events and rates shown below. Note that the rates are *lifted* straight from the deterministic model.

Description	Event	Rate
Birth of prey	$F \rightarrow F + 1$	$rF(1 - F/K)$
Death of prey	$F \rightarrow F - 1$	$IP$
Birth of predators	$P \rightarrow P + 1$	$\epsilon IP$
Death of predators	$P \rightarrow P - 1$	$\mu P$

Run the **Stochastic predator-prey model**. What do you find? Can you fix it?

As you will have noticed it is extremely difficult to prevent extinction of the predator population? Typically the predators become extinct whilst prey numbers rise to the carrying capacity. This instability is a well known problem with models of predator-prey and host-parasite interactions. Since biological predator-prey populations are able to maintain themselves we must ask what is wrong with our model? Introducing a spatial element to the model, with movement of both predators and prey, not only adds realism but also stabilises the dynamics. The idea is that prey can find refuge in areas where predator numbers are low, and predators can move to regions with sufficient prey. addition real predator prey systems are

Launch the **Stochastic and spatial predator-prey model**. In this model the animals exist on a set of connected patches. The dynamics within each patch are controlled by the nonspatial stochastic model discussed above, whilst the spatial aspects are controlled by five parameters ( $Mr$ ,  $Mc$ ,  $\lambda$ ,  $\lambda_{prey}$ ,  $s$ ). The number of rows ( $Mr$ ) and columns ( $Mc$ ) define the size ( $N=Mc*Mr$ ) and shape of the lattice. The dispersal of predators is controlled by the movement rate  $\lambda$  and the parameter  $s$  which determines the size of the neighbourhood the animal may move to. For  $s = 0$  movement is uniform across the entire lattice whilst  $s > 0$  gives a probability of movement between two patches which decays with the distance between them.  $s \geq 10$  corresponds to nearest neighbour movement only. The dispersal of prey is also controlled by  $s$  and the movement rate  $\lambda_{prey}$ . The propensity of animals to move to a new patch increases with  $\lambda$  and  $\lambda_{prey}$ .

Experiment with different movement rates. Can you stabilise the predator population? Start with the default  $5 \times 5$  lattice. Increase the movement rates of the predator and prey (e.g.  $\lambda = 0, \lambda_{prey} = 0$  (nonspatial);  $\lambda = 10, \lambda_{prey} = 1$ ;  $\lambda = 100, \lambda_{prey} = 10$   $\lambda = 10, \lambda_{prey} = 100$ ; now change the random number seed to 9999!). Although movement does allow the predator population to persist for longer extinction still occurs in a relatively short time. Try increasing the size of the lattice to  $10 \times 10$  and try the following movement rates:  $\lambda = 10, \lambda_{prey} = 1$   $\lambda = 1, \lambda_{prey} = 10$ ;  $\lambda = 10, \lambda_{prey} = 10$ . Have a look at the histograms of the population sizes as you do this. Now, paying attention to the phase plots, try the following sequence:  $\lambda = 1, \lambda_{prey} = 1$   $\lambda = 10, \lambda_{prey} = 1$ ;  $\lambda = 100, \lambda_{prey} = 100$ . What do you notice?

What do you think are the significance of these results to conservation biology and habitat fragmentation?

## 2.2 Childhood Illnesses

Childhood illnesses are one of the classic applications of mathematical modelling. The collation of case reporting by public health bodies provides particularly rich, even uniquely detailed data of an ecological system. Much progress has been made in the last ten years in understanding the persistence of diseases such as measles. In this section we will look at two recent debates from this field; the first is the role of chaos in biological systems; and the second relates to persistence of childhood disease in cities. As we shall see these issues are related.

One hotly debated subject in mathematical biology is that mathematical models suggest that chaos should be a common occurrence. However, few (if any) biological time series have been shown to exhibit chaos. Time series of the numbers of reported cases of childhood illnesses (e.g. measles, chicken-pox etc.) in cities are considered by some to exhibit signs of chaos.

The most popular model of childhood diseases is the SEIR model presented below. People are considered to be born into a class labeled susceptible (S). On contact with a person who has the disease and is infectious (I) the susceptible moves into a category which contains the those who have the disease but are not yet infectious (E). After a short number of days the

person then leaves this exposed category (E) and becomes infectious (I). After another short period the person recovers and moves to the category (R) where they remain until death. The population as a whole is assumed to be constant (N), with births matching deaths. This system is described by the following equations:

$$\begin{aligned}\frac{dS}{dt} &= mN - mS - bSI \\ \frac{dE}{dt} &= bSI - mE - aE \\ \frac{dI}{dt} &= aE - mI - gI \\ \frac{dR}{dt} &= gI - mR\end{aligned}$$

$$S + E + I + R = N$$

Make sure that you understand the structure of the model and the significance of each of the constants. You should be able to solve these equations for the non-trivial steady state and find the minimum value of the total population for which the disease persists. Discuss how the current slowdown in birth rates and increased lifespan, seen in the developed world, affects this value.

## Sensitivity Analysis

Current thinking suggests that the contact rate parameter ( $b$ ) should not be a constant but should vary with time, since children are more at risk in winter when they are at school than in summer when they are not. One (crude) way to represent this is given below:

$$b = b_0(1 + b_1 \cos(2\pi t)) ,$$

where  $t$  is the time in years.

The best fit values of these parameters to a measles data set are:

$$\begin{aligned}m &= 0.02 , \\ g &= 55.0 , \\ a &= 50.0 , \\ b_0 &= 0.001 \\ b_1 &= 0.28 .\end{aligned}$$

However, here we will investigate the effect of varying the parameter  $b_1$  between 0 and 0.3 on the dynamics of the disease in a population of 1,000,000 using the **Deterministic Seir model**. The default values are those shown above, but start with  $b_1 = 0.0$  and increase this value slowly.

The graphs *Timeseries* and *Histogram* show the numbers of infectives, whilst *Phaseplot* shows the numbers of people in the categories I and E. You should observe that the system becomes chaotic at high values of  $b_1$ . Have a look at the phase plot in this case; the resultant pattern is a so-called *strange attractor*. As the system evolves in time the trajectory in phase-space (i.e. the values of  $I$  and  $E$ ) move around this strange attractor in a rather complicated way. This is in contrast to the simple motion around limit cycle attractors which we found in the predator-prey model (and for low values of  $b_1$  in the SEIR model).

## Introducing stochasticity

The stochastic version of the SEIR model follows as before from the explicitly defined rates and implicitly assumed events in the deterministic model. These are shown below.

Description	Event	Rate
Birth of susceptibles	$S \rightarrow S + 1$	$m(S + E + I + R)$
Death of susceptibles	$S \rightarrow S - 1$	$mS$
Infection	$S \rightarrow S - 1 \ \& \ E \rightarrow E + 1$	$bSI$
Death in exposed class	$E \rightarrow E - 1$	$mE$
End of latent stage	$E \rightarrow E - 1 \ \& \ I \rightarrow I + 1$	$aE$
Death in infective class	$I \rightarrow I - 1$	$mI$
End of infectious stage	$I \rightarrow I - 1 \ \& \ R \rightarrow R + 1$	$gI$
Death from recovered class	$R \rightarrow R - 1$	$mR$

Run the **Stochastic SEIR model**. What do you find?

Infact the infection can be made to persist, but only for population sizes of around 10 million and above. This is generally considered to be too large to be realistic, and it is widely accepted that the only way to stabilise the dynamics for realistically sized cities is to add a *background* infection rate:

Description	Event	Rate
Background infection	$S \rightarrow S - 1 \ \& \ E \rightarrow E + 1$	$\nu S$

This acknowledges the fact that cities are not isolated but that people move between them and other urban and rural areas. A realistic background rate of infection for a city with population of a million is considered to be  $\nu = 0.0001$ . Try this. Look at the difference between the stochastic and deterministic dynamics. Do you notice anything strange about the deterministic dynamics?

Take a look at the *Fadeout fraction* shown below the figures on the output screen. This is the fraction of observed times when the disease was not present. Whilst the disease now persists (infact it couldn't do anything else as we have a regular importation of cases) the fadeout fraction is much higher than observed in a range of data from North American and British cities and from small island data. One way to reduce the fadeout is to increase the background infection to unrealistically high levels - try it. However, this is unsatisfactory and it is now generally accepted that the best way of reconciling models and data is to (yes you've guessed it!) introduce a spatial element into the model structure.

## Adding spatial structure

A standard way of introducing spatial structure into models of childhood epidemics is to divide the population into a set of districts and then assume that infection within districts has a contact rate  $b$  (overall rate  $bSI$ ) as above, but that contacts between districts are reduced by a mixing parameter  $\lambda$  (rate  $\lambda bSI$ ). Thus  $\lambda = 1$  corresponds to the nonspatial model whilst  $\lambda < 1$  introduces spatial heterogeneity. This model has been implemented as the **Spatial and stochastic SEIR model**. Try  $\lambda = 1$  and various levels of heterogeneity. What impact does this have on the *Fadeout fraction*?

Although we have defined our *spatial* structure in terms of districts, it can also be thought of in terms of *social* structure. In other words defining the contact structure between social groups. The overlap between the two is perhaps most easily understood if you assume that people who live in the same district send their children to the local school. However, if people send their

kids to a more remote school they may in effect be in closest contact with people in another district.

## Modelling Experiments

Improved medical treatment could be represented in the model in one of three ways:

- (i) reduced infectiousness (reducing  $b_0$  try a 10,20 and 30% reductions)
- (ii) reduced latency period (increasing  $a$ )
- (iii) reduced infectious period (increasing  $g$ )

Assuming that  $b_1 = 0.28$ ,  $\nu = 0.0001$  and  $\lambda = 0.001$  investigate the effect of these on the dynamics of the population.

## Addendum

The current state of the art in terms of modelling measles dynamics is a little more complex than the SEIR model considered here. The Realistic Age Structured (RAS) model divides the population into age classes and then each age class into S,E,I and R compartments. The time varying nature of the contact rate  $b$  is still crucial although a more realistic model is often used which assumes one level on school days and a lower level during school holidays. In the RAS model the infection can only be made to persist by adding a background rate of infection, but again for realistic levels of  $\nu$  the fadeout fraction is found to be greater than observed. Adding spatial heterogeneity reduces fadeout to realistic levels. The critical population size is defined to be the smallest population for which the fadeout fraction becomes zero. In the case of measles data this is seen to be around 250,000 – 500,000 and this is correctly predicted by the spatially heterogeneous RAS model. (A good review article is the chapter by Ferguson, May and Anderson in Tilman and Kareiva, 1997))

## Solutions - Example 2.1

### Form of the uptake rate

For the uptake rate

$$I(F) = \frac{I_{\max}F}{F + F_0},$$

of prey by the predators it is straightforward to see that

$$\begin{aligned} I(F = 0) &= 0, \\ I(F = \infty) &= I_{\max}, \\ I(F = F_0) &= \frac{1}{2}I_{\max}. \end{aligned}$$

Thus  $F_0$  is the value of  $F$  for which  $I(F)$  attains half its maximum value ( $I_{\max}$ ): increasing  $F_0$  slows down the increase of  $I$  with  $F$ , as is shown below.

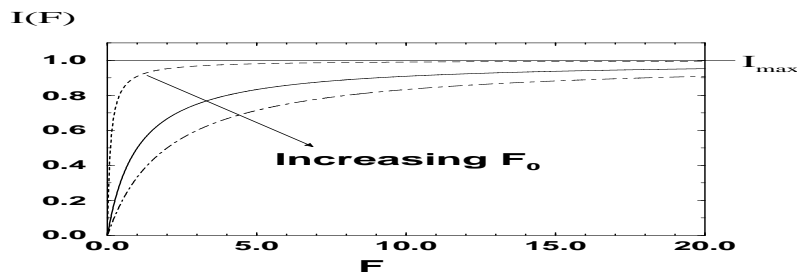


Figure 3: Uptake rate with  $I_{\max} = 1$  and  $F_0 = 0.1, 1.0, 2.0$

### The three equilibria

Recall that our predator-prey model is described by the following equations,

$$\begin{aligned} \frac{dF}{dt} &= rF \left(1 - \frac{F}{K}\right) - IP, \\ \frac{dP}{dt} &= \epsilon IP - \mu P, \end{aligned}$$

and the steady states occur when

$$\frac{dF}{dt} = \frac{dP}{dt} = 0.$$

There are three such fixed points of the system dynamics:

(a) Both populations extinct ( $F = 0, P = 0$ ):

$$\begin{aligned}\frac{dF}{dt} &= r \times 0 \times \left(1 - \frac{0}{K}\right) - I \times 0 = 0, \\ \frac{dP}{dt} &= \epsilon I \times 0 - \mu \times 0 = 0.\end{aligned}$$

(b) Predators extinct, prey at carrying capacity ( $F = K, P = 0$ ):

$$\begin{aligned}\frac{dF}{dt} &= rK \left(1 - \frac{K}{K}\right) - I \times 0 = 0, \\ \frac{dP}{dt} &= \epsilon I \times 0 - \mu \times 0 = 0.\end{aligned}$$

(c) Stable point where both predator and prey co-exist ( $F = F^*, P = P^*$ ):

Take  $\frac{dP}{dt} = 0$ , this leads to

$$\begin{aligned}\Rightarrow \epsilon IP - \mu P &= 0 \\ \Rightarrow \epsilon IP &= \mu P \\ \Rightarrow \epsilon I &= \mu \\ \Rightarrow I &= \frac{\mu}{\epsilon} & (*) \\ \Rightarrow \frac{I_{\max} F}{F + F_0} &= \frac{\mu}{\epsilon} \\ \Rightarrow I_{\max} F &= \frac{\mu}{\epsilon} F + \frac{\mu}{\epsilon} F_0 \\ \Rightarrow F \left[ I_{\max} - \frac{\mu}{\epsilon} \right] &= \frac{\mu}{\epsilon} F_0 \\ \Rightarrow F &= \frac{\frac{\mu}{\epsilon} F_0}{\left[ I_{\max} - \frac{\mu}{\epsilon} \right]} \\ \Rightarrow F = F^* &= \frac{\mu F_0}{\epsilon I_{\max} - \mu} & (8)\end{aligned}$$

Taking  $\frac{dF}{dt} = 0$  leads to

$$\begin{aligned}\Rightarrow rF \left(1 - \frac{F}{K}\right) - IP &= 0 \\ \Rightarrow IP &= rF \left(1 - \frac{F}{K}\right) \\ \Rightarrow P &= \frac{rF}{I} \left(1 - \frac{F}{K}\right) \\ \Rightarrow P = P^* &= \frac{\epsilon r F^*}{\mu} \left(1 - \frac{F^*}{K}\right), & (9)\end{aligned}$$

where in the last line we used the fact that at equilibrium  $I = \mu/\epsilon$  (see (\*)).

*Positivity of equilibrium (c)*

From (8) for  $F^*$  to be positive we require

$$\epsilon I_{\max} - \mu > 0 \tag{A}$$



To see the physical meaning of this recall that

$$\frac{dP}{dt} = (\epsilon I - \mu)P,$$

Thus, condition (A) says that the predator population must grow ( $dP/dt > 0$ ) when they are feeding at the maximum uptake rate  $I_{\max}$ . If the predator population does not grow even when feeding at this maximal rate then there is no stable state where both populations co-exist: the predators die out and the prey reach the carrying capacity  $K$  (i.e. system returns to steady state (b)).

From (9) for  $P^*$  to be positive we require

$$1 - \frac{F^*}{K} > 0$$

Thus we require the predator population level to be below the carrying capacity, namely  $F^* < K$

$$\begin{aligned} \Rightarrow \frac{\mu F_0}{\epsilon I_{\max}} &< K \\ \Rightarrow \mu F_0 &< \epsilon I_{\max} K - \mu K \\ \Rightarrow \mu(F_0 + K) &< \epsilon I_{\max} K \\ \Rightarrow \mu &< \frac{\epsilon I_{\max} K}{(F_0 + K)}. \end{aligned} \tag{B}$$

This condition is similar to condition (A) but more strict. This is because whilst the maximum value of the uptake  $I$  is  $I_{\max}$ , in this system the maximum *attainable* uptake is limited to

$$\frac{I_{\max} K}{(F_0 + K)},$$

since the prey population level may not exceed the carrying capacity  $K$ . If the predator death rate  $\mu$  is too high and condition (B) not met then the predators will become extinct and the prey population will reach the carrying capacity.

*The paradox of enrichment:* Note from (8) that the equilibrium value of  $F$  does not depend on either  $r$  or  $K$ , but is set purely by the predator.

You should find that the equilibrium (c) (where both species co-exist) becomes unstable around  $K = 9.0$ . As the carrying capacity  $K$  increases further the amplitude of the oscillations increases, but their frequency decreases.

*Phase space plots:*

Stable equilibrium  $\Rightarrow$  trajectory settles to a single point.

Unstable equilibrium  $\Rightarrow$  trajectory eventually moves around a closed loop.

## Solutions - Example 2.2

### Meaning of parameters

$m$  - birth *and* death rate

all individuals born into susceptible category at total rate  $mN$

individuals die from each category at *per capita* rates:  $mS$ ,  $mE$ ,  $mI$ ,  $mE$ .

$b$  - contact rate

per capita rate at which susceptibles become exposed (E) *per infected individual*  
i.e., total rate of infection:  $bSI$

$a$  - rate at which exposed individuals (E) become infected (I)

i.e., total rate:  $aE$

$g$  - rate at which infected individuals (I) recover (R)

i.e., total rate:  $gI$

## Equilibrium values

At equilibrium the model in example 4 satisfies the following equations

$$\begin{aligned}\frac{dS}{dt} &= mN - mS - bSI = 0 \\ \frac{dE}{dt} &= bSI - mE - aE = 0 \\ \frac{dI}{dt} &= aE - mI - gI = 0 \\ \frac{dR}{dt} &= gI - mR = 0 .\end{aligned}$$

In reverse order, the last three of these lead to

$$\begin{aligned}R &= \frac{g}{m}I , \\ E &= \frac{(m+g)}{a}I , \text{ and} \\ S &= \frac{(m+a)E}{bI} = \frac{(m+a)(m+g)}{ab} ,\end{aligned}$$

respectively, which are all positive so long as  $I > 0$ . Since the total population is constant we also obtain  $S + E + I + R = N$

$$\begin{aligned}\Rightarrow & \frac{(m+a)(m+g)}{ab} + I + \frac{(m+g)}{a}I + \frac{g}{m}I = N \\ \Rightarrow & I = \frac{N - \frac{(m+a)(m+g)}{ab}}{1 + \frac{m+g}{a} + \frac{g}{m}} .\end{aligned}$$

Thus, if  $I$  is to be positive we require

$$N > \frac{(m+a)(m+g)}{ab} .$$

For the parameter values given ( $m = 0.02$ ,  $a = 50$ ,  $g = 55$  and  $b = b_0 = 50$ ) this means the population must be larger than 55,042.

### Demographic change

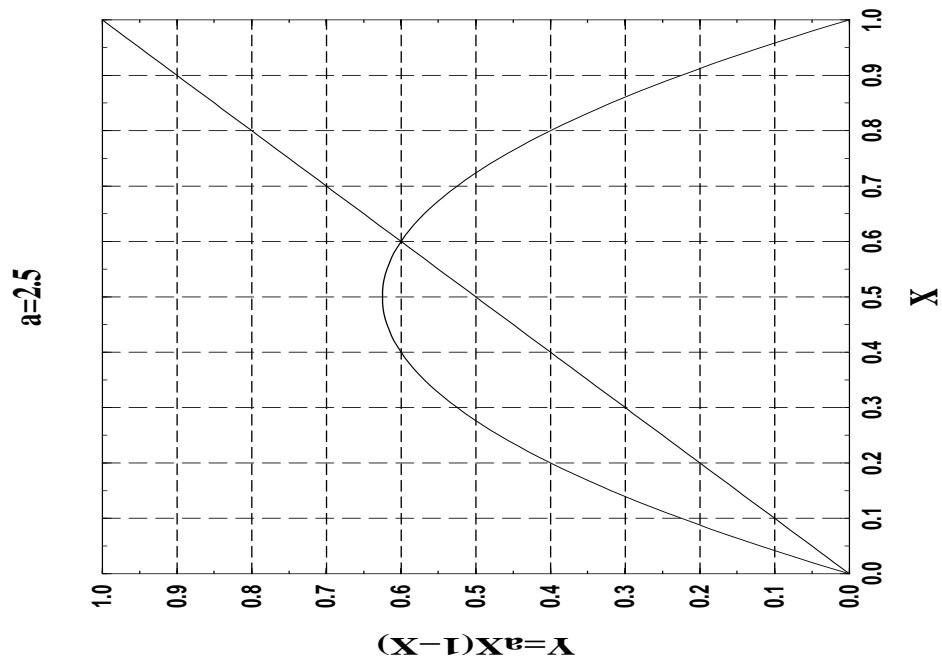
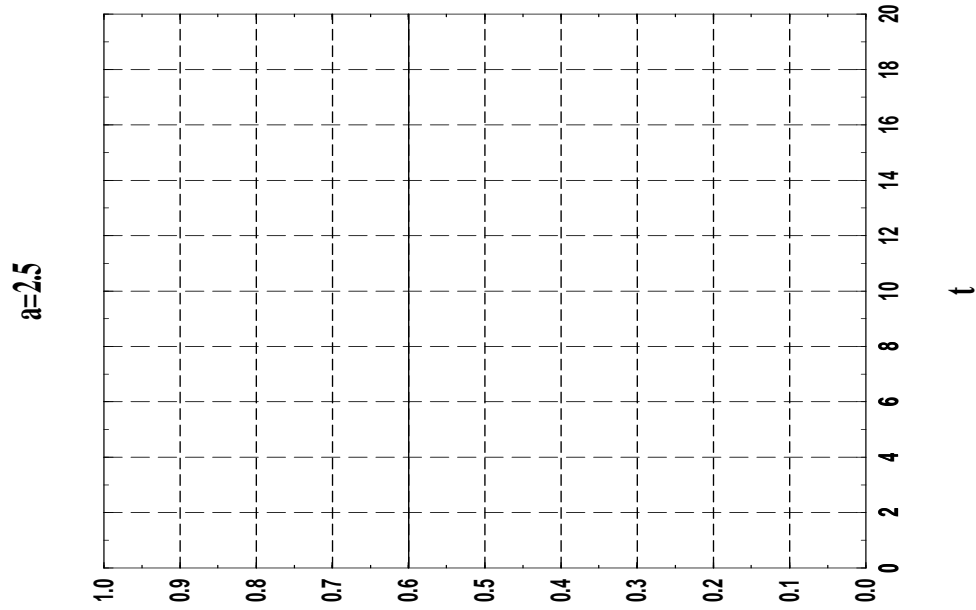
The reduction in birth rates and the lengthening of lifespan both reduce the parameter  $m$ . Suppose we reduce  $m$  by a factor of 100, the critical value

$$N > \frac{(m+a)(m+g)}{ab} = 55,000 ,$$

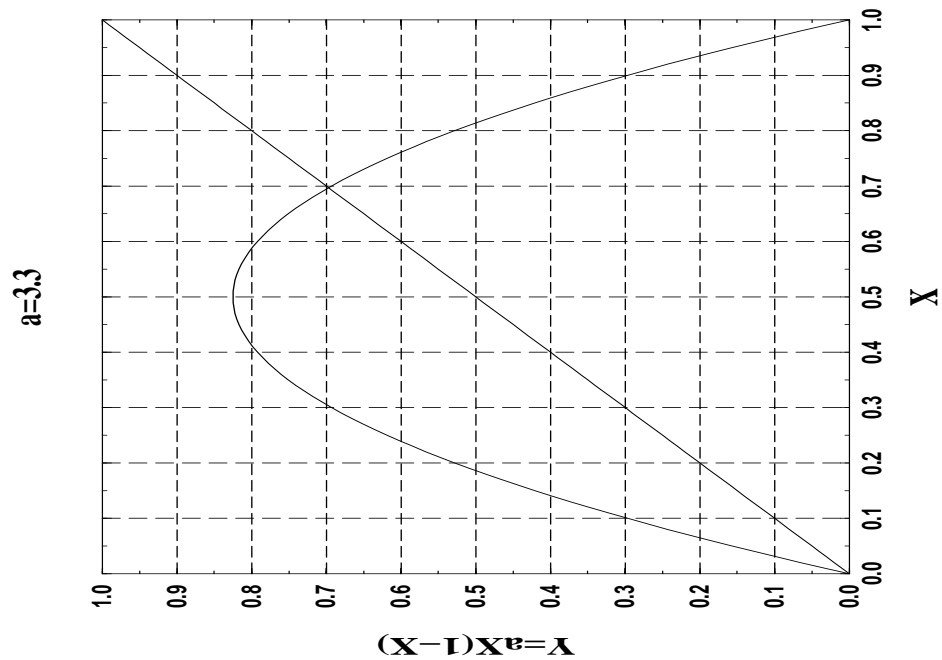
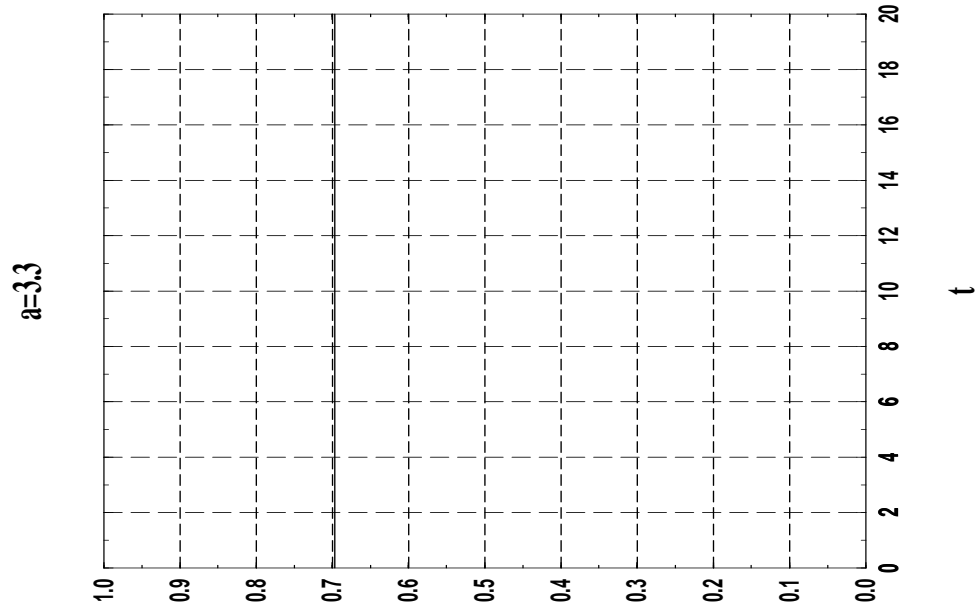
is virtually unchanged. Thus, demographic change does reduce the size of the population necessary to allow long term persistence of the disease, but the effect is marginal.

Although these results are correct for the deterministic model their value is questionable in light of the behaviour of the stochastic model.

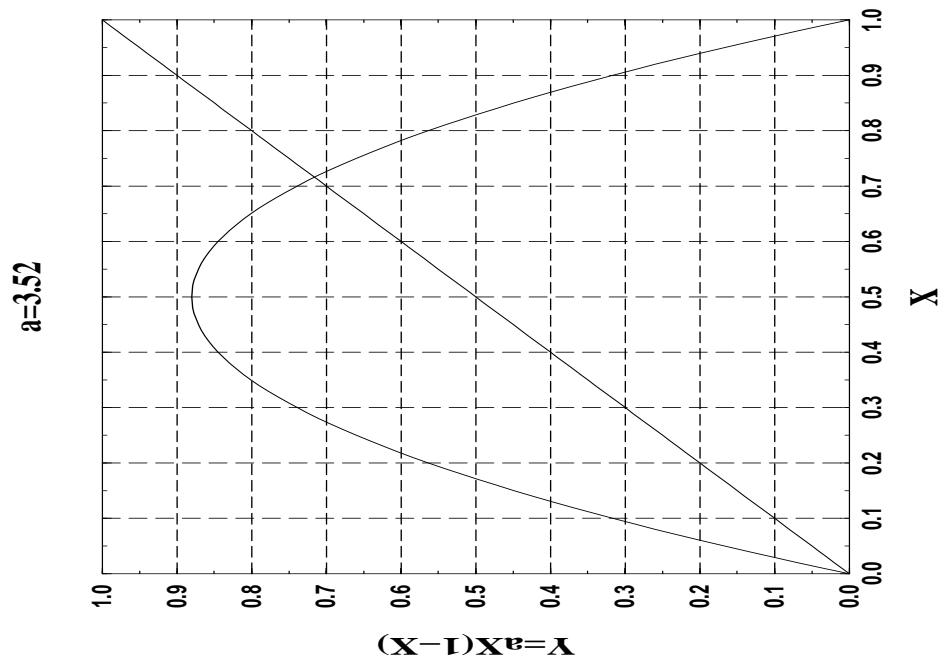
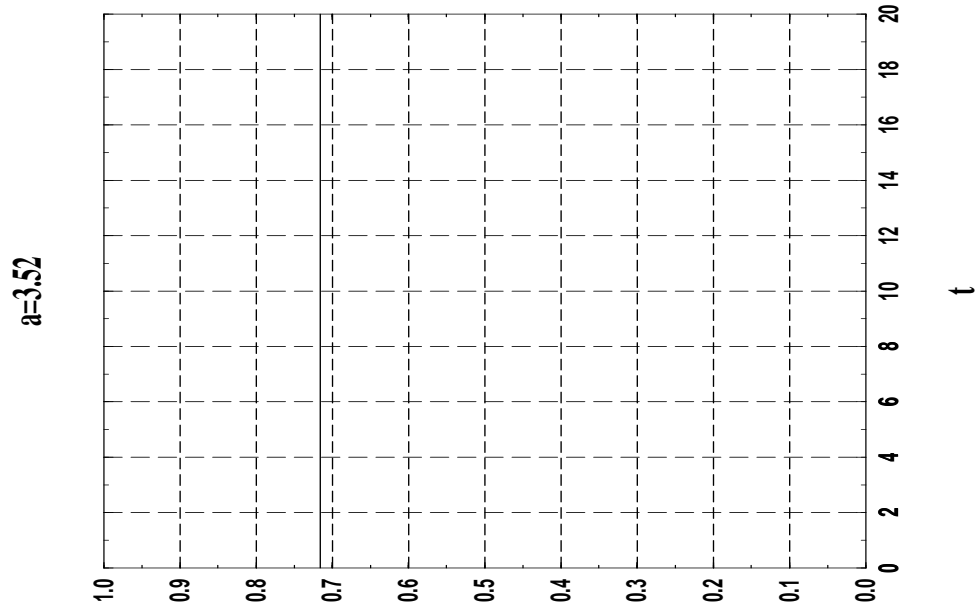
1. Logistic map  $Y = aX(1 - X)$  (bottom) and time-series graph (top).



2. Logistic map  $Y = aX(1 - X)$  (bottom) and time-series graph (top).



3. Logistic map  $Y = aX(1 - X)$  (bottom) and time-series graph (top).



4. Logistic map  $Y = aX(1 - X)$  (bottom) and time-series graph (top).

