



Question and answer

# Mathematics Masterclasses

Stretching the imagination

Edited by

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## 6 Discrete Mathematics and its Application to Ecology

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### 1. Introduction

In this chapter we will illustrate how simple mathematical ideas can be used to understand how a population grows. We first consider the well-known problem which generates the *Fibonacci sequence*. Consider a population of rabbits. Suppose that every pair of rabbits can reproduce only twice, when they are one- and two-months old, and that each time they produce exactly one new pair of rabbits. Assume that all newborn rabbits survive. The problem here is to see if we can predict how many newborn rabbits there will be in a certain generation given an initial newborn rabbit population.

Before beginning, we need to use a convenient notation. Let us define the quantity  $N_m$  to be the number of newborn pairs in generation  $m$ . Suppose that we begin with one newborn pair. Then we say that  $N_0$ , the number of newborn pairs in the zero generation (the Adam and Eve of rabbits), is one. Now, after one month, this pair of rabbits gives birth to one pair of rabbits. Therefore, we have that  $N_1$ , the number of newborn pairs in the first generation, is one. At the end of the second month, Adam and Eve give birth to their second newborn pair and then will no longer give birth to any more rabbits. But, the pair of rabbits in the first generation also give birth to a pair of newborns (Adam and Eve's 'grandbunnies'). Therefore,  $N_2$ , the number of newborn pairs in the second generation, will be  $1 + 1 = 2$ . In the third generation, newborn pairs will arise from those pairs that were newborns in the second generation ( $N_2$ ), and from those newborns in the first generation ( $N_1$ ). Therefore the number of newborns in the third generation,  $N_3$ , will be  $N_2 + N_1 = 2 + 1 = 3$ . The number in the fourth generation,  $N_4$ , will be  $N_3 + N_2 = 3 + 2 = 5$  (see Fig. 1). We can now prove the following theorem.

*Theorem 1 (The Rabbit Problem)*

If

$$N_m = \text{number of newborn pairs in generation } m$$

then

$$N_{m+1} = N_m + N_{m-1}. \quad (1)$$



**Proof**

The number of newborn rabbits in the  $(m+1)$ th generation will come either from one-month old parents who were born in the  $m$ th generation or from two-month old parents who were born in the  $(m-1)$ th generation (see Fig. 1). Hence result.  $\square$

To see how this ties in with the above discussion, let us suppose that  $N_0 = 1$  (this means that we begin with one pair of newborns in the zero generation). Then, we know that  $N_1 = 1$ . Now, if we put  $m = 1$  into equation (1), we have that  $N_2 = N_1 + N_0$ , that is,  $N_2 = 1 + 1 = 2$ , which is the number of newborns in the second generation. Now putting  $m = 2$  into equation (1), we have that  $N_3 = N_2 + N_1 = 2 + 1 = 3$ , the number of newborns in the third generation. For  $m = 3$ , we have  $N_4 = 3 + 2 = 5$ , the number of newborns in the fourth generation. Continuing like this we have that  $N_5 = 5 + 3 = 8$ ,  $N_6 = 8 + 5 = 13$ ,  $N_7 = 13 + 8 = 21$ , etc.

The sequence of numbers 1, 1, 2, 3, 5, 8, 13, 21, ... is known as the *Fibonacci sequence*. Equation (1) is an example of a *recurrence relation* and this type of relation is very common in ecological studies. A mathematical formulation of such a problem is known as a *mathematical model* of the problem. The numbers generated by the Fibonacci sequence are known as the *Fibonacci numbers* and occur widely in nature. For example, the numbers of spirals running in opposite directions on a ripening sunflower or a pine cone are often consecutive Fibonacci numbers.

We now move on to what appears, to begin with, to be a very different problem. We call it the *Beetle Problem*. Suppose that beetles of one generation produce the larvae (immature form of an insect which eventually becomes the insect) of the next generation and then die so that only the larvae survive. Assume that all the larvae survive. The problem here is, can we predict the number of larvae in a certain generation? In this case, we define  $N_m$  to be the number (in some units) of larvae in generation  $m$ . Suppose that the average

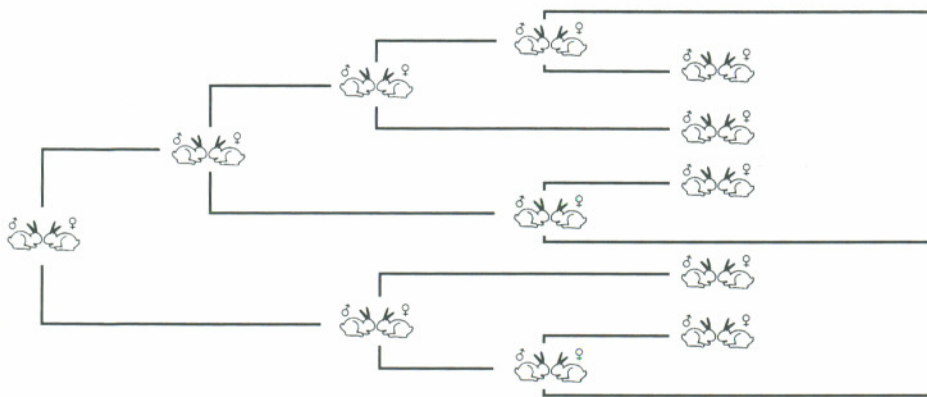


Fig. 1. Proof of Theorem 1 (see text for details)

number of larvae produced per beetle is 2. Let us assume that in generation 0,  $N_0$  is 1. It is important to note here that setting  $N_1$  to be one does not necessarily mean that in the first generation there is one beetle. This is because we have not specified our units. For example, if the unit was thousands, then  $N_0 = 1$  would mean that there were one thousand beetles in generation 0. Note that  $N_0 = \frac{1}{2}$  would not mean half a beetle, but would mean 500 (one half of a thousand) beetles.

Assuming that  $N_0 = 1$ , we have that  $N_1$ , the number of beetles in the first generation, is  $2 \times 1 = 2$ . The beetles in the second generation arise from the larvae produced by the first generation, so  $N_2$  is  $2 \times N_1 = 4$ . In the same way,  $N_3 = 2 \times 4 = 8$  etc. In fact, we can now prove the following theorem.

**Theorem 2 (The Beetle Problem)**

If

$N_m$  = number of beetles (in some units) in generation  $m$

$r$  = average number of larvae produced per beetle

then

$$N_m = N_0 r^m \quad (2)$$

**Proof**

The generation  $m$  beetles come from the  $(m-1)$ th generation. Now each beetle in the  $(m-1)$ th generation produced  $r$  larvae, so  $N_m = rN_{m-1}$ . Applying the same argument to the  $(m-1)$ th generation, we have  $N_{m-1} = rN_{m-2}$ . So we can write  $N_m = r^2 N_{m-2}$ . If we carry on this reasoning we deduce that  $N_m = N_0 r^m$  (see Fig. 2).  $\square$

For our example,  $r = 2$  and  $N_0 = 1$ . The formula then says that  $N_1 = N_0 \times 2 = 2$ ,  $N_2 = N_0 \times 4 = 4$ ,  $N_3 = N_0 \times 8 = 8$ , etc.

Notice that if we want to calculate the number of beetles in a certain generation, then all we need to know is  $N_0$  and  $r$  and we have immediately that  $N_m = N_0 r^m$ . However, for the rabbit problem, to find  $N_m$ , we need to know  $N_{m-1}$  and  $N_{m-2}$ . But to calculate these values, we need to know  $N_{m-3}$ , etc. Therefore, if  $m$  is very large, then the calculations involved for the beetle problem are easier than those for the rabbit problem. However, in question 6 of Worksheet 1 we will see that there is an easier way to calculate  $N_m$  for the rabbit problem, when  $m$  is large.

- Consider the Fibonacci numbers 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, ...
  - Calculate (to 3 decimal places) the fractions obtained from dividing each number by the previous number, that is,  $\frac{1}{1}, \frac{2}{1}, \frac{3}{2}, \frac{5}{3}, \frac{8}{5}, \frac{13}{8}, \frac{21}{13}, \frac{34}{21}, \frac{55}{34}, \frac{89}{55}, \frac{144}{89}, \frac{233}{144}$ .
  - What do you notice about the values you calculated in (a)?
  - The calculations in (a) and (b) suggest that for two consecutive numbers  $N_{m+1}, N_m$  in the Fibonacci sequence,  $\frac{N_{m+1}}{N_m} \approx r$  for large  $m$ . What is that value of  $r$ ?



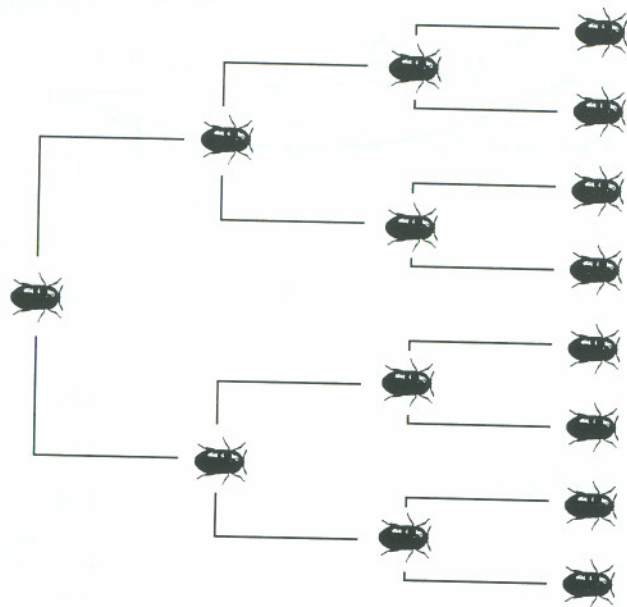


Fig. 2. The Beetle problem for the case  $r = 2$ . Note the differences between this figure and Fig. 1

- (d) Is the Rabbit problem *really* that different from the Beetle problem?
2. From equation (2) calculate  $N_1, N_2, N_3$  and  $N_4$  in the following cases.
- (a)  $N_0 = 2.0, r = 2.0$ .
- (b)  $N_0 = 2.0, r = 0.5$ .
3. From equation (2) what size will  $N_m$  be for  $m$  large in the following cases.
- (a)  $r > 1.0$ .
- (b)  $r = 1.0$ .
- (c)  $r < 1.0$ .
- (d) Do you think that equations (1) and (2) are good mathematical models?

For the following exercises assume that the recurrence relation has the form

$$N_{m+1} = rN_m(1.0 - N_m). \quad (3)$$

(Note that if  $N_m$  is small, equation (3) looks a bit like equation (2)).

4. Calculate  $N_1, N_2, N_3$  and  $N_4$  in the following cases.
- (a)  $N_0 = 0.6, r = 0.5$ .
- (b)  $N_0 = 0.4, r = 2.0$ .
- (c)  $N_0 = 0.6, r = 2.0$ .
- (d)  $N_0 = 0.5, r = 2.0$ .
- (e) In (b), (c) and (d) what do you think the value of  $N_m$  would be for  $m$  very large?
- (f) Is this a better mathematical model than equations (1) and (2)?

5. Calculate  $N_1, N_2, N_3, N_4$  and  $N_5$  (each to 2 decimal places) for equation (3) in the case where  $r = 3.1, N_0 = 0.70$ . What do you think are the values of  $N_6, N_7, N_8, N_9, \dots$ ?

6. In question 1, we made an approximate calculation for  $r$ . We can make a more exact calculation as follows. Suppose that  $\frac{N_{m+1}}{N_m} = \frac{N_m}{N_{m-1}} = r$ .

(a) From equation (1) show that  $N_{m+1} = \left(1 + \frac{1}{r}\right)N_m$ .

(b) From (a), show that  $1 + \frac{1}{r} = r$ .

(c) From (b), calculate  $r$ .

## 2. The logistic map

In Worksheet 1, question 3, we saw that the models presented in Section 1 have their limitations, and we introduced a new model

$$N_{m+1} = rN_m(1.0 - N_m). \quad (4)$$

This model is called the *logistic model*, or the *logistic map*. Before we analyse this model further we need the following definition.

### Definition

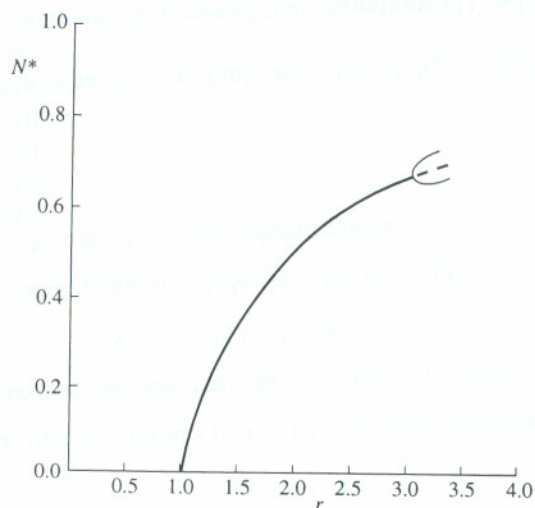
If the successive values calculated from a recurrence relation tend towards some fixed value, we call this value the *steady state value*. It has the property that  $N_{m+1} = N_m = N^*$ , the steady state value, for large  $m$ .

The steady states for equation (4) are given by

$$N^* = 0 \quad \text{or} \quad N^* = \frac{r-1}{r}. \quad (5)$$

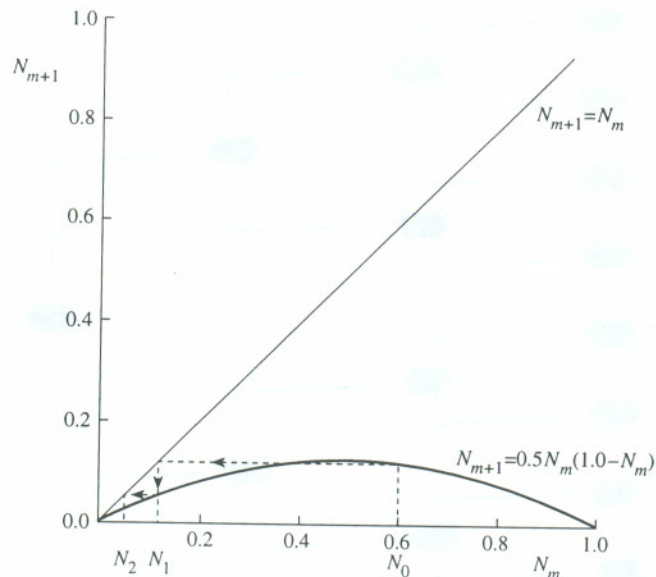
For  $0 < r < 1$  the second steady state does not make sense because it is negative and if we start off with  $0 \leq N_0 \leq 1$  in equation (4) then  $0 \leq N_m \leq 1$  for every  $m$ . So the only sensible solution is the first solution of equation (5) (compare this with Worksheet 1, question 4(a)). For  $1 < r < 3$  the second solution makes sense and it appears from Worksheet 1, question 4(e), that this is the steady state, at least for  $r = 2.0$ . Hence, although there are now two possibilities for the steady state, we have moved off the first solution onto the second. This is called a *bifurcation*. For  $r = 3.1$ , the second solution of equation (5) is still a sensible steady state but Worksheet 1, question 5 suggests that we have a 2-cycle solution. We may summarize these results on the *bifurcation diagram* in Fig. 3. Note that we have been careful not to go too far beyond  $r = 3$  in case there are yet more surprises in store!

We can get an idea of what the solution to equation (4) will look like by using a graphical technique called *cobwebbing*. The technique is illustrated in Fig. 4 and the results represented graphically in Fig. 5.

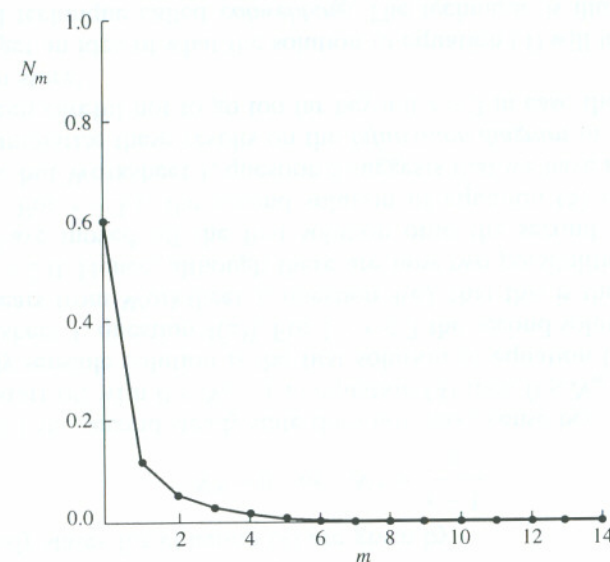


**Fig. 3.** Bifurcation diagram for equation (4) showing how the steady state  $N^*$  varies with  $r$ . The dashed lines are *unstable solutions*

We draw the curve of equation (4) (with  $r = 0.5$ ) and also the straight line  $N_{m+1} = N_m$ . We first find the value 0.6 along the horizontal axis. This is  $N_0$ . Now  $N_1 = 0.5 \times N_0(1 - N_0)$ . But this is exactly the length of the vertical straight line from the point  $N_0$  to the curve. If we then draw from there a line parallel to the horizontal axis, then the distance this line is above the horizontal axis is always

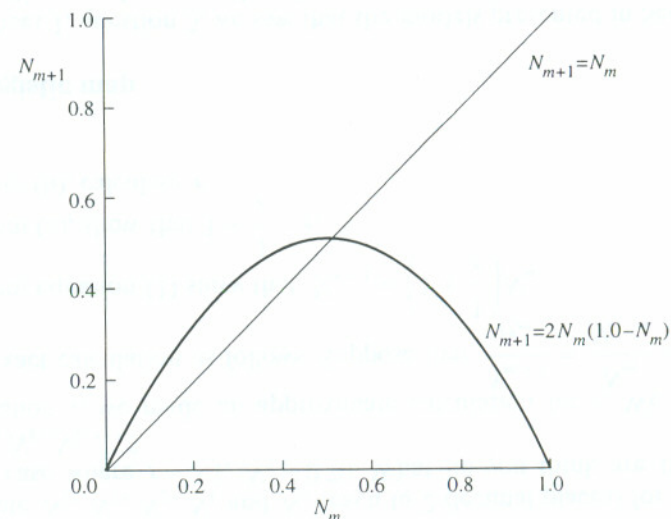


**Fig. 4.** Illustration of the cobwebbing technique for equation (4) with  $N_0 = 0.6$ ,  $r = 0.5$



**Fig. 5.** Graphical representation of the solution obtained by the cobwebbing technique illustrated in Fig. 4 (Compare this solution with that from Worksheet 1, question 4)

$N_1$ . If we drop a perpendicular line onto the horizontal axis from the point where this line intersects the  $N_{m+1} = N_m$  line, we have that the distance from this point to the origin is also  $N_1$ . That is, given  $N_0$ , we have been able to calculate, graphically, the value of  $N_1$ . In a similar way we can now go on to calculate  $N_2, N_3, \dots$ , etc.



**Fig. 6.** Cobweb for Worksheet 2, question 1



## Worksheet 2

1. Use Fig. 6 to cobweb the solution to equation (4) for the case  $N_0 = 0.7$ ,  $r = 2.0$ .
2. Illustrate your results to question 1 graphically. Does this solution cycle or does it go to a steady state?
3. Use your calculator to find  $N_1, N_2, N_3, N_4, N_5, N_6, N_7$ , and  $N_8$  (each to 3 decimal places) for equation (4) in the case  $N_0 = 0.501$ ,  $r = 3.5$ . Draw the cobweb diagram on the following figure (Fig. 7).

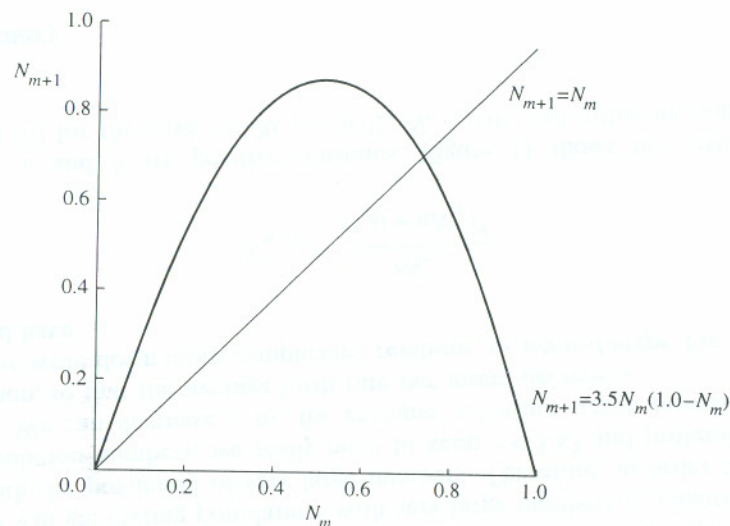


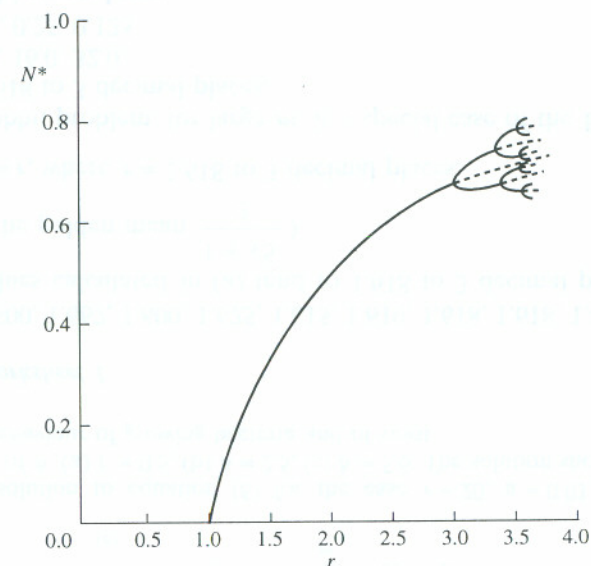
Fig. 7. Cobweb for Worksheet 2, question 3

4. Illustrate your results to question 3 graphically.
5. From equation (4), what is the equation for  $N_{m+2}$  in terms of  $N_m$ ? What are the steady states of this equation?

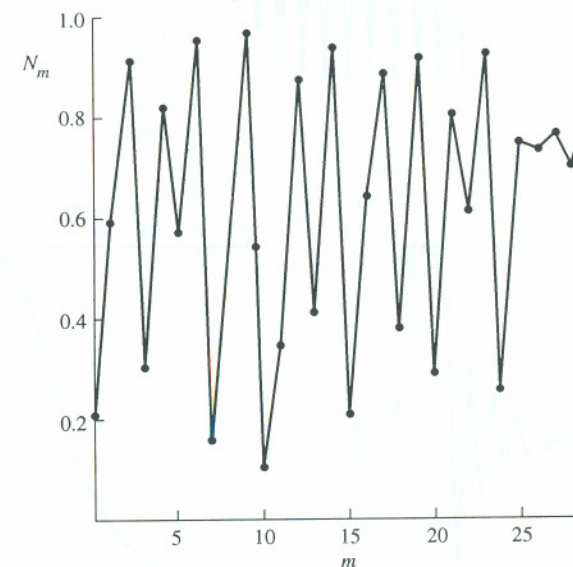
## 3. Chaos

From Worksheet 2, question 3, we saw that if  $r = 3.5$ , then equation (4) has a 4-cycle solution. As  $r$  increases further, we get an 8-cycle solution and then a 16-cycle solution, etc. We can represent these results (Fig. 8) on the bifurcation diagram we began to draw in Fig. 3.

If we increase  $r$  beyond a critical value  $r_c \approx 3.83$  we lose the periodic structure of the solution. Figure 9 illustrates the case when  $r = 3.9$ . In this case the solution does not have a periodic structure. It is said to be *chaotic*. If we were to change the value of  $N_0$  slightly we would get a completely different looking solution. Another chapter in this book, 'A Little Bit of Chaos', introduces you to other aspects of chaos.

Fig. 8. The completed bifurcation diagram illustrating, schematically, the *cascade of period doubling bifurcations*

Equation (4) is a good model for insect growth—many insect populations either reach a steady state or oscillate in a 2-cycle (see Fig. 10).

Fig. 9. The solution to equation (4) for the case  $r = 3.9$ ,  $N_0 = 0.2$ . Note that for some generations the population gets very large then crashes back in the following generation

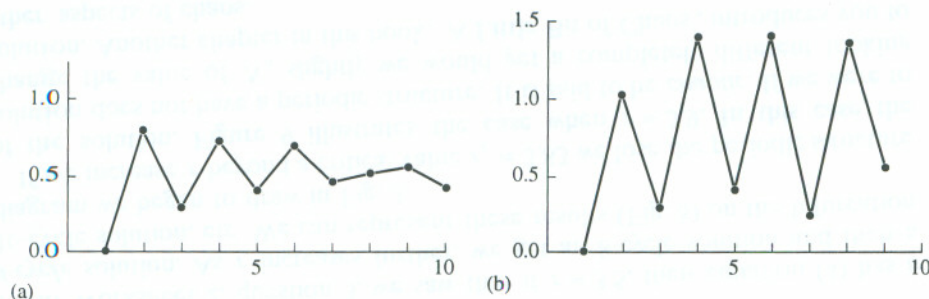


Fig. 10. Examples of population growth of two types of beetles. The vertical axis is the number of beetles (thousands), the horizontal axis is the generation number. (Redrawn from Hassel (1976))

Note that for  $r > 4$  the model predicts negative populations and thus is not realistic in this case. You may want to do a few iterations or draw some cobweb maps to see why (hint: start off with  $r = 4.1$ ,  $N_0 = 0.5$ ).

The analysis of the model equation (4) suggests that if we let  $r$  get too large then we will get cycling populations with very large numbers or chaotic populations with the possibility of very large numbers. Therefore, in order to control the population numbers, we really need to keep  $r < 3.83$  and preferably much smaller. We can decrease  $r$  by, for example, releasing sterile insects into the population, so that the average birth rate per insect decreases.

We can write down more complicated relations, or *iterated maps*. For example, we could have

$$N_{m+1} = \frac{rN_m}{(1.0 + aN_m)^b} \quad (6)$$

where  $r$ ,  $a$  and  $b$  are positive constants. Figure 11 shows the results from equation (6) for the case  $r = 20$ ,  $a = 0.01$ ,  $N_0 = 0.01$  and different values of  $b$ .

#### 4. Summary

In this chapter we have illustrated how mathematical models can be used to study population growth. The analysis of these models determines if the assumptions we made in forming the model are sensible. If not, we have to reformulate the model. This helps us to understand more deeply the processes of population growth that we are trying to model and also predicts how the population will react if we carry out certain experiments. The role of a predictive mathematical model is very important. For example, it can aid our understanding of how certain diseases spread within a population and help us to choose the best control strategy. Mathematical models are important not only in ecology, but also in the fields of biology, physics, chemistry and medicine.

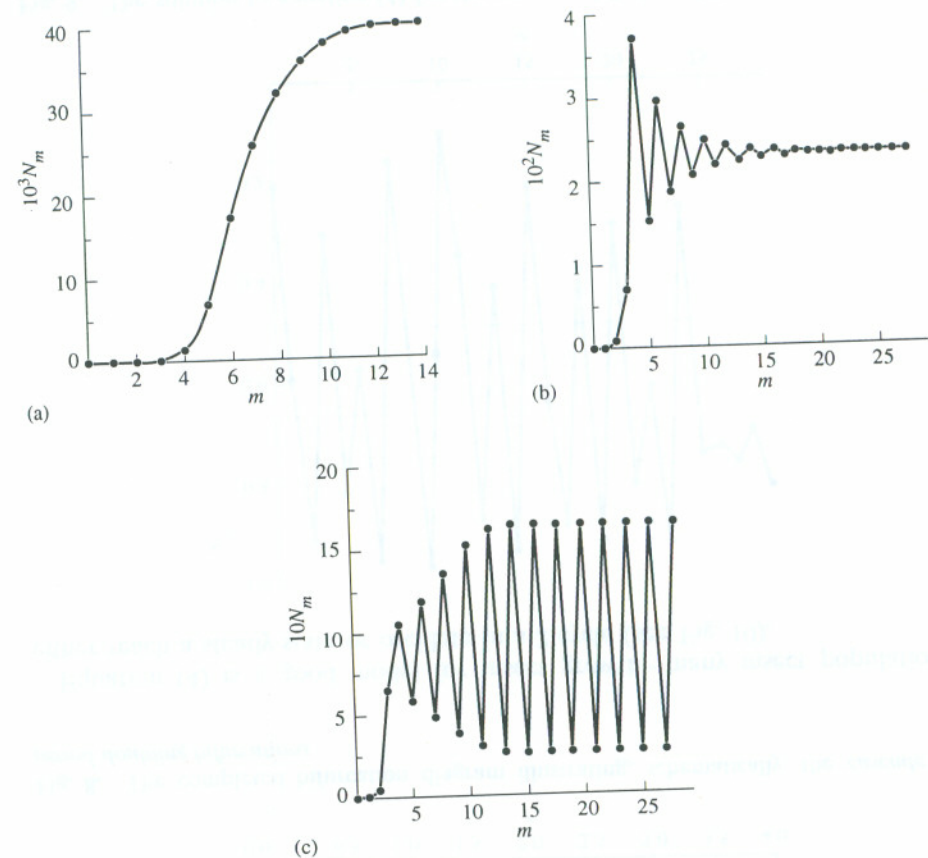


Fig. 11. The solution to equation (6) for the case  $r = 20$ ,  $a = 0.01$ ,  $N_0 = 0.01$  and different values of  $b$ : (a)  $b = 0.5$ , (b)  $b = 2.5$ , (c)  $b = 5.0$ . The solution shown in (a) is very similar to the behaviour of growing bacteria and of yeast

#### Solutions to Worksheet 1

- 1, 2, 1.500, 1.667, 1.600, 1.625, 1.615, 1.619, 1.618, 1.618, 1.618, 1.618.
  - The values calculated in (a) tend to 1.618 to 3 decimal places. (In fact, this is the golden mean  $\frac{1 + \sqrt{5}}{2}$ ).
  - $\frac{N_{m+1}}{N_m} \approx r$ , where  $r \approx 1.618$  to 3 decimal places.
  - The Rabbit problem, for large  $m$ , is a special case of the Beetle problem with  $r = 1.618$  to 3 decimal places.
- 4.0, 8.0, 16.0, 32.0.
  - 1.0, 0.5, 0.25, 0.125.
- $N_m$  will be very large.
  - $N_m = N_0$ .



- (c)  $N_m$  will be very small.  
 (d) Equation (1) predicts that the population of rabbits will grow forever; equation (2) predicts that the population of beetles will either grow and grow (if  $r > 1.0$ ), or die down to zero (if  $r < 1.0$ ) or stay at its initial value (if  $r = 1.0$ ). Neither of these models is very good because populations do not behave in this way. For example, death has been ignored.
4. (a) 0.120, 0.053, 0.025, 0.012 to 3 decimal places.  
 (b) 0.480, 0.499, 0.500, 0.500 to 3 decimal places.  
 (c) 0.480, 0.499, 0.500, 0.500 to 3 decimal places.  
 (d) 0.500, 0.500, 0.500, 0.500.  
 (e)  $N_m$  tends to 0.5 for large  $m$ .  
 (f) This seems a better model because for certain  $r$ -values the population reaches a steady value.
5. 0.65, 0.71, 0.65, 0.71, 0.65, 0.71, 0.65, 0.71, ...
6. (a) From the assumption,  $N_{m-1} = N_m/r$ , therefore equation (1) becomes  $N_{m+1} = N_m + N_m/r$ .  
 (b) From (a), we have  $N_{m+1} = (1 + 1/r)N_m$ . The assumption says that  $N_{m+1} = rN_m$ . Therefore  $1 + 1/r = r$ .  
 (c) From (b),  $r^2 - r - 1 = 0$ . Therefore  $2r = 1 \pm \sqrt{5}$ . The negative solution does not make sense because  $r$  is assumed positive, therefore  $r = (1 + \sqrt{5})/2$ .

### Solutions to Worksheet 2

1.

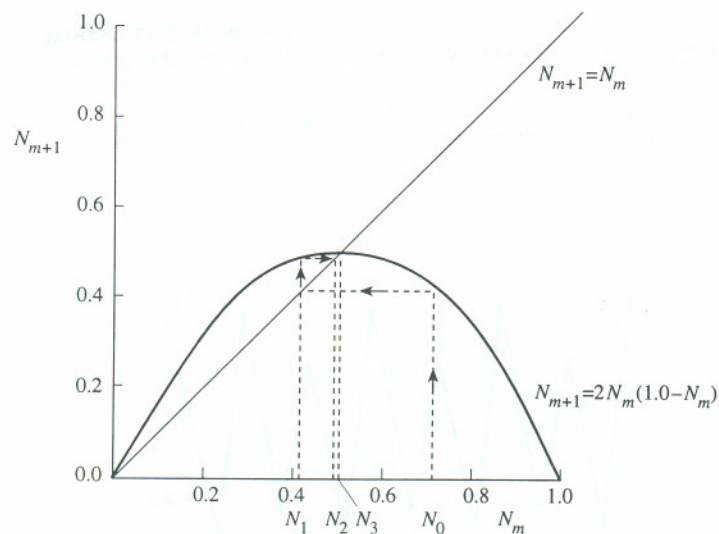


Fig. 12 Cobweb diagram for Worksheet 2, question 1

2.

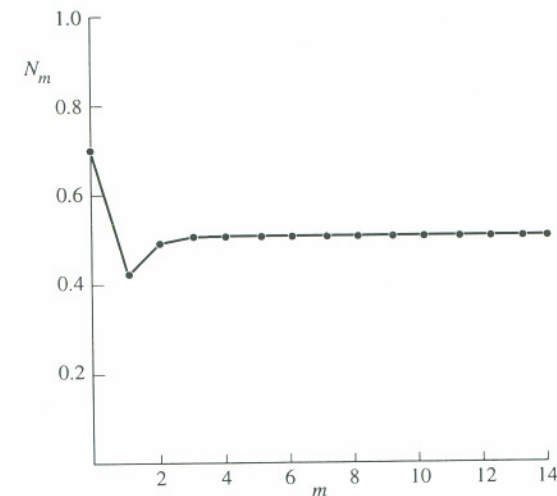


Fig. 13 Graphical representation of the solution obtained by the cobwebbing technique for Worksheet 2, question 1. The solution goes to a steady state

3. 0.875, 0.383, 0.827, 0.501, 0.875, 0.383, 0.827, 0.501

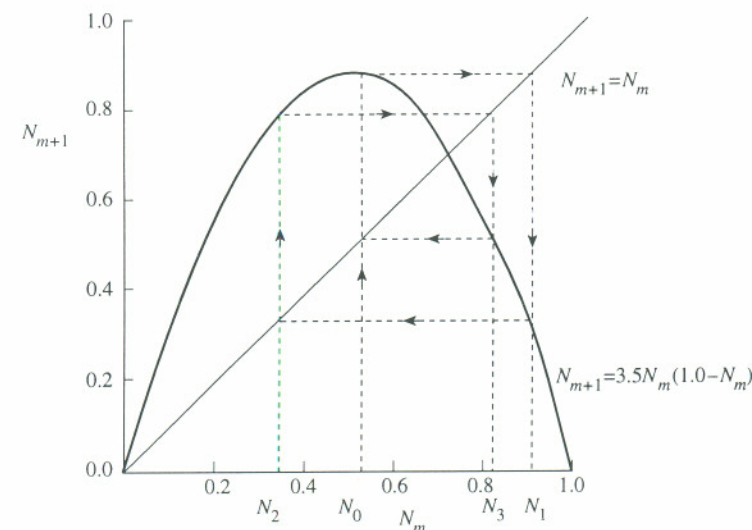
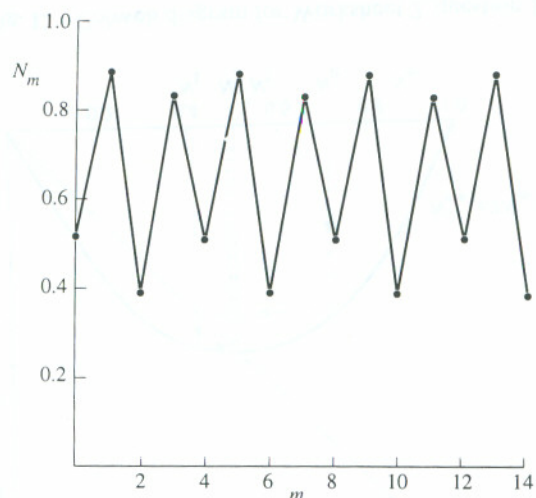


Fig. 14 Cobweb diagram for Worksheet 2, question 3

4.



**Fig 15** Graphical representation of the solution obtained by the cobwebbing technique for Worksheet 2, question 3

5. From equation (4) we can write  $N_{m+2} = rN_{m+1}(1.0 - N_{m+1})$ . Using equation (3) again, we have  $N_{m+1} = rN_m(1.0 - N_m)$ , so we can write

$$N_{m+2} = r^2 N_m (1.0 - N_m) (1.0 - rN_m (1.0 - N_m)). \quad (7)$$

The steady states of equation (7) are given by  $N_{m+2} = N_m = N^*$ . Thus we have

$$N^* = r^2 N^* (1.0 - N^*) (1.0 - rN^* (1.0 - N^*)) \quad (8)$$

which has solution  $N^* = 0$  or

$$(N^*)^3 - 2(N^*)^2 + \left(1 + \frac{1}{r}\right)N^* + \frac{1}{r^3} - \frac{1}{r} = 0. \quad (9)$$

We know that  $1 - \frac{1}{r}$  is also a steady state so we can factor this out from equation (9) to get

$$\left(N^* - 1 + \frac{1}{r}\right) \left((N^*)^2 - \left(1 + \frac{1}{r}\right)N^* + \frac{1}{r} + \frac{1}{r^2}\right) = 0. \quad (10)$$

Thus the two further solutions are given by the roots of  $((N^*)^2 - (1 + 1/r)N^* + 1/r - 1/r^3) = 0$ , that is,  $2N^* = 1 + 1/r \pm [(1 + 1/r)^2 - (4/r)(1 + 1/r)]^{1/2}$ . This may be written as  $2N^* = 1 + (1/r) \pm (1/r)[(r-1)^2 - 4]^{1/2}$ . Note that this solution will make sense only if  $r > 3$ , so we have a 2-cycle solution possible if  $r > 3$ .

## References

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