UNIVERSITY OF STRATHCLYDE
MATHEMATICS & STATISTICS

MM103 Part II: Applications

1. How many bugs will there be?

Suppose that we know the number of insects of a certain type that live around a pond. The problem is to predict the size of the insect population at the pond in future years.

1.1. First some biology

We shall simplify things as much as possible, just concentrating on the most important features.

Assumptions:

- no insects can enter or leave the region around the pond (the colony is *isolated*);
- the proportion of males to females stays constant, so we can just look at how many female insects there are;
- there is a single breeding season in the summer of each year. Eggs hatch out in early spring, and the insects become adults in the late summer of that year. They then breed, the females lay their eggs and die in the autumn.

1.2. A mathematical description

- Suppose that at the start there are x_0 female insects at the pond, and let x_1, x_2, x_3,..., x_n be the numbers of females at the start of the breeding season after 1, 2, 3,..., n years.

- On average r of the female eggs laid by each female survive to adulthood and breed the following year.
- Because all the adult insects die every year, the number of females alive in one year will be equal to r times the number of females that were alive the previous year.

> if x_n is the number of females in year n, and
> r is the average number of female offspring of each female, then
>
> $$x_{n+1} = r\, x_n \tag{1.1}$$

Equation (1.1) is our first mathematical model. We next need to solve it.

1.3. Solving equation (1.1)

We first assume that r is a constant: i.e. it is the same every year, and doesn't depend on the size of the insect population. We want to 'solve' the equation

$$x_{n+1} = r\, x_n, \quad r = \text{constant}$$

to find x_n in terms of n, r, and the initial population x_0.

Example: if $r = 2$ and $x_0 = 3$ million we calculate

$$\begin{array}{llllllll} n=0: & x_1 & = & r\,x_0 & = & 2\times 3 & = & 6 \text{ million} \\ n=1: & x_2 & = & r\,x_1 & = & 2\times 6 & = & 12 \text{ million} \\ n=2: & x_3 & = & r\,x_2 & = & 2\times 12 & = & 24 \text{ million.} \end{array}$$

We now look for a solution of equation (1.1) which is valid for all r and x_0. Notice that

$$\begin{aligned} x_1 &= r\,x_0 \\ x_2 &= r\,x_1 = r\,(r\,x_0) = r^2\,x_0 \\ x_3 &= r\,x_2 = r\,(r^2\,x_0) = r^3\,x_0. \end{aligned}$$

A sensible guess would be

$$x_m = r^m x_0, \quad \text{for } m = 1, 2, \ldots$$

We can 'prove' that this is in fact a solution by showing that it fits into our equation $x_{n+1} = r\, x_n$.

If $x_m = r^m x_0$, for $m = 1, 2, \ldots$ then for any n we have $x_n = r^n x_0$ and $x_{n+1} = r^{n+1} x_0$. That is

$$x_{n+1} = r\,(r^n x_0) = r\, x_n$$

which is our equation. It also gives the right starting value because $r^0 = 1$.

> The equation $x_{n+1} = r\, x_n$ has the solution $\underline{x_n = r^n x_0}$

This formula means that we can now easily calculate the size of the population predicted by the model, provided that we know r and x_0.

Example: If $x_0 = 1.5$ (million) and $r = 2$, then find x_6.

From the formula:

$$x_6 = r^6 x_0 = 2^6 \times 1.5 = 64 \times 1.5 = 96.$$

What happens to the population size for different values of r?

1. $\boldsymbol{r = 1}$. If $r = 1$ then $r^n = 1$ for any n, and so the population size doesn't change: it is always equal to x_0.

2. $\boldsymbol{r > 1}$. In this case the population size is multiplied by a number bigger than 1 each year, and so the population grows every year.

3. $\boldsymbol{r < 1}$. In this case the population size is multiplied by a number less than 1 every year, and so it shrinks. After long enough it will die out completely.

Exercises 1.1

1. What numbers are suitable choices for r, i.e. can r be negative/ a fraction/ an irrational number (like π)?

2. By looking at the model equation show that the starting population x_0 is not important in predicting what will happen to the population size, but that population trends are completely governed by the size of r.

3. Do you think that the model produces physically realistic answers? Why?

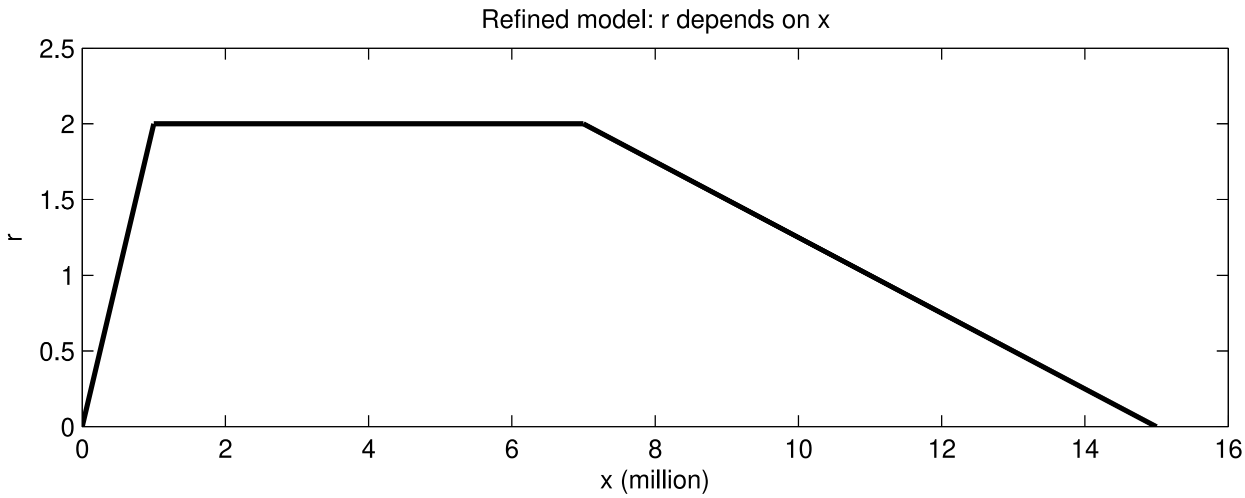
1.4. Refined model: r is not constant

Our first model equation (1.1) relied on the assumption that the average number of surviving female offspring r is the same every year. This is not very realistic, and in general r will depend on a number of things, including the number x of adult females.

- We have seen that if r is constant and less than 1 then the population eventually dies out completely. So if the species is to survive at all there must be some range of values of x for which $r > 1$.
- If the population is very large then we would expect r to be less than 1, as there will be a lot of competition for food and other resources and only those insects which can find enough food will be able to breed successfully.
- We would also expect r to be less than 1 if x is too small, because many females will not be able to find mates.

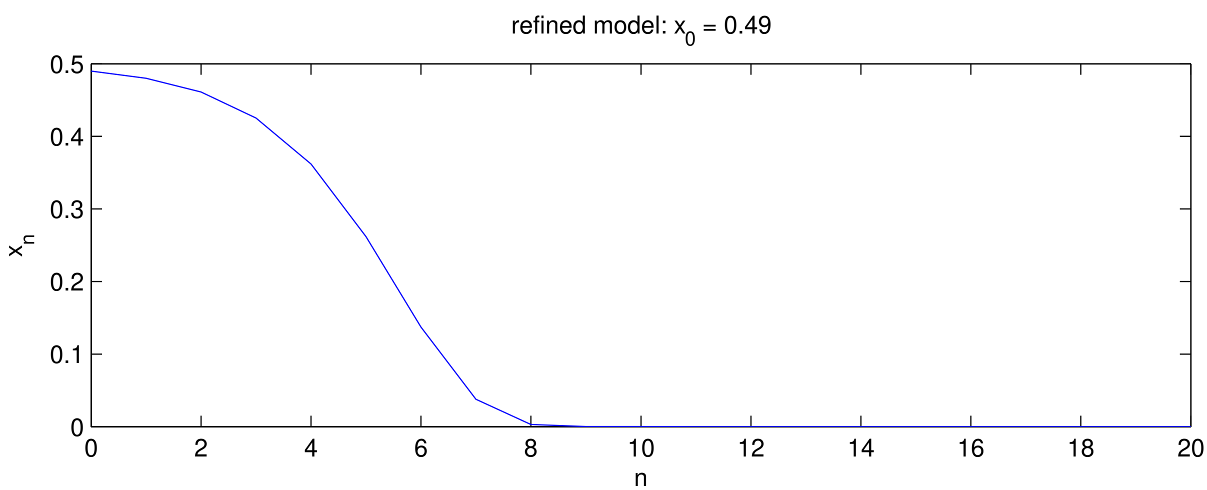
REQUIREMENTS FOR r:
$r > 1$ for some values of x (species survival)
$r < 1$ if x is too big (lack of food etc.)
$r < 1$ if x is too small (few females breed)

The following graph shows a simple model that has all these features. In this, r is constant (equal to 2) when x lies between 1 and 7 million, and decreases to zero if x is less than 1 million or greater than 7 million. If x is bigger than 15 million then r is zero.



Let's test out the behaviour of this new model for different values of x_0.

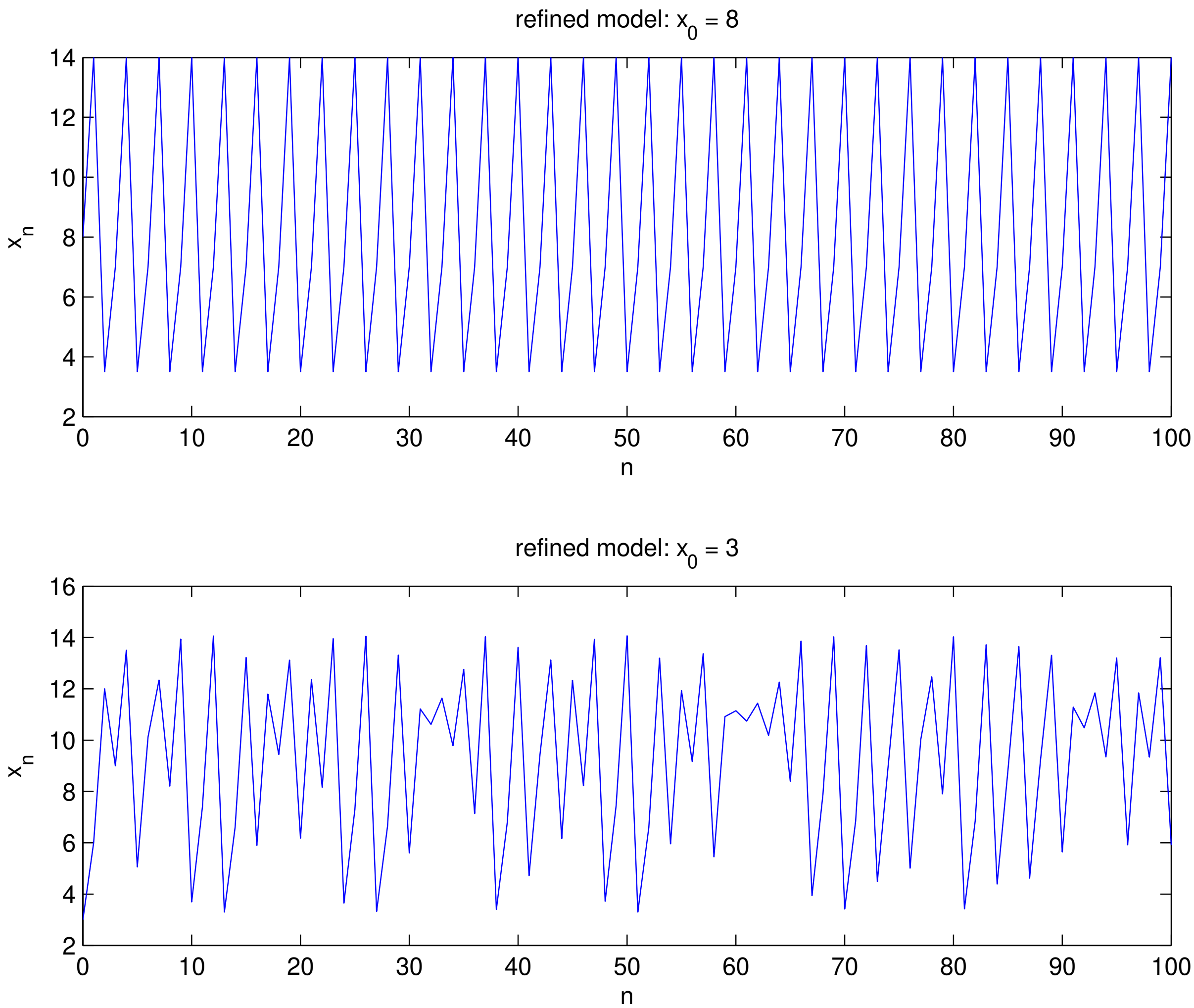
• If $x_0 < 0.5$ then the population dies out quickly:



• If $x_0 = 2^p$ for $p = 0 : 3$ then the population oscillates:

• Most other values of x_0 between 0.5 and 14.86 give more complicated behaviour:

• If $x_0 > 14.87$ then the population dies out:



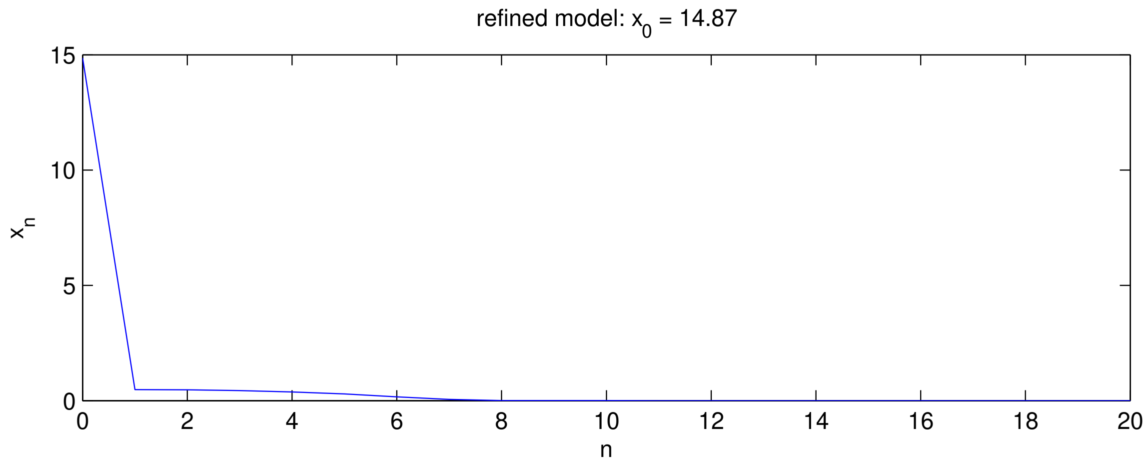
Exercises 1.2

1. Does this model look more or less realistic than the previous one?

2. What other features do you think a good model should take into account?

1.5. Further reading

The book *Mathematical Ideas in Biology* by J. Maynard Smith contains a lot of (more advanced) material on mathematical modelling in biology.



2. Fibonacci's rabbits and other equations

Leonardo of Pisa, known as Fibonacci, wrote a book *Liber abaci* in 1202. One problem is the growth of a (biologically unrealistic!) population of rabbits:

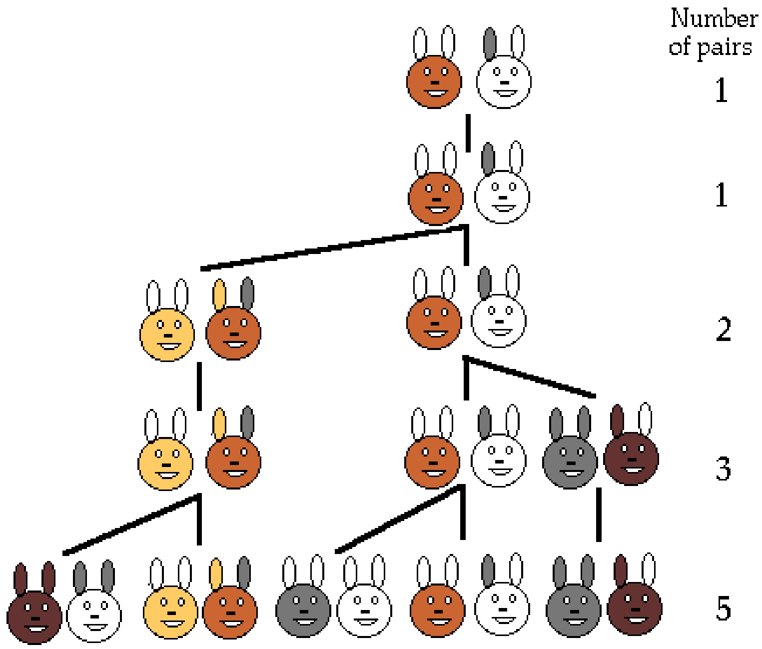
> *A certain man put a pair of rabbits in a place surrounded on all sides by a wall. How many pairs of rabbits can be produced from that pair in a year if it is supposed that every month each pair begets a new pair which from the second month on becomes productive?*

This problem and its underlying mathematical equation are very common in mathematics articles (e.g. Google lists over three million hits for the word "Fibonacci"). A good reference for Fibonacci (the person) is the St Andrews history of mathematics web site `www-history.mcs.st-and.ac.uk/Biographies/Fibonacci.html` and the following description of the problem is adapted from "Fibonacci numbers and nature" at `www.maths.surrey.ac.uk/hosted-sites/R.Knott/Fibonacci/fibnat.html` .

What equation governs the number of pairs?

- At time zero, there is one pair of rabbits.
- At the end of the first month the original pair of rabbits mate, but there is still one only 1 pair.
- At the end of the second month the female produces a new pair, so now there are 2 pairs of rabbits in the field.

- At the end of the third month, the original female produces a second pair, making 3 pairs in all in the field.
- At the end of the fourth month, the original female has produced yet another new pair, and the female born two months ago produces her first pair, making 5 pairs in total.



- At the end of the nth month, the number of new pairs of rabbits is equal to the number of pairs in month $n-2$, and the total number of pairs is this plus the number of rabbits alive in month $n-1$. So, if x_n is the number of pairs at the end of month n and $n \geq 2$, then $x_n = x_{n-1} + x_{n-2}$.

It is easier if we look at the equation for x_{n+2} rather than x_n, and this is:

$$x_{n+2} = x_{n+1} + x_n \,, \tag{2.1}$$

where we also know that $x_0 = 1$. In this notation, Fibonacci's original question was: what is x_{12}?

Observation: We don't have enough information to find x_{12}!

In fact, we don't even have enough information to find x_2: if we substitute $n = 0$ into (2.1), then this gives $x_2 = x_1 + x_0 = x_1 + 1$ because $x_0 = 1$. So we cannot find x_2 (or any x_n with $n > 2$) without also specifying x_1.

Why is this? We only needed to specify x_0 in order to solve equation (1.1), $x_{n+1} = r\,x_n$, in the previous section. This is because (1.1) only involves the population size x at two time levels (x_{n+1} is given in terms of **one** past value), but equation (2.1) involves the population size at three time levels (x_{n+2} is given in terms of **two** past values). So for (2.1) we need to specify the first **two** values, i.e. x_0 and x_1, and we saw earlier that both of these are equal to 1.

Definition. The Fibonacci sequence is

$$x_{n+2} = x_{n+1} + x_n \quad \text{for } n \geq 0,$$

with $x_0 = 1$ and $x_1 = 1$.

We can now calculate x_{12}.

- Set $n = 0$ in (2.1) and use $x_0 = 1$ and $x_1 = 1$ to get $x_2 = 1 + 1 = 2$.
- Set $n = 1$ in (2.1) to get $x_3 = x_2 + x_1 = 2 + 1 = 3$.
- Set $n = 2$ in (2.1) to get $x_4 = x_3 + x_2 = 3 + 2 = 5$.
- ...
- Set $n = 10$ in (2.1) to get $x_{12} = x_{11} + x_{10} = 144 + 89 = 233$.

The sequence x_n for $n = 0{:}12$ is 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233 – notice that each entry is the sum of the previous two. Although we have managed to find x_{12} by direct calculation, it is a fairly tedious way to do it, and would not be a very practical way to find x_{100}, say. Fortunately there is a much better way to solve equations like (2.1), and we shall look at the solution in general before going back to (2.1).

2.1. Solving 3-step difference equations

Equations like (1.1) and (2.1) in which the unknown x is labelled by an integer are called **difference equations**.

Both (1.1) and (2.1) are **linear** equations, because a constant multiple of a solution is also a solution, and the sum of any two solutions is also a solution.

Example 2.1

1. Suppose that the sequence y_n solves (2.1). Show that $c\,y_n$ is also a solution for any constant c.
2. Suppose that the sequences y_n and z_n both solve (2.1). Show that $u_n = y_n + z_n$ is also a solution.

We want to solve equations of the form $a\,x_{n+2} + b\,x_{n+1} + c\,x_n = 0$ (where a, b and c are constants), and we motivate the method by going back to (1.1).

Equation (1.1) is $x_{n+1} = r\,x_n$, and we originally solved it by constructing the solution. We could instead have looked for a solution of the form $x_n = A\,\lambda^n$ by substituting this into (1.1) and looking for a value of λ that "works".

If $x_n = A\,\lambda^n$ for any n, then $x_{n+1} = A\,\lambda^{n+1}$ and (1.1) gives

$$A\,\lambda^{n+1} = r\,A\,\lambda^n$$

and cancelling out A and λ^n from both sides gives $\lambda = r$, so the **general solution (GS)** of (1.1) is $x_n = A\,r^n$, where A is a constant. (It satisfies the equation (1.1) for any value of A.)

The **particular solution (PS)** is the solution of (1.1) that has a particular value when $n = 0$. For example, if we know that $x_0 = 2.3$, then substituting $n = 0$ in the GS gives

$$2.3 = x_0 = A\,r^0 = A\,1 = A\,,$$

so the particular solution in this case is $x_n = 2.3\,r^n$.

We do very much the same thing for a 3-step equation like (2.1), first substituting in $x_n = A\,\lambda^n$ and looking for values of λ that "work", to find the GS. We see below that λ for a 3-step equation is the root of a quadratic equation, and so there are typically two different values of λ that work, and the GS involves both of them, each multiplied by a constant.

We first illustrate the method for an equation for which the calculations are a bit easier than for the Fibonacci equation (2.1).

Consider the 3-step equation

$$x_{n+2} - x_{n+1} - 6\,x_n = 0 \tag{2.2}$$

with

$$x_0 = 3 \quad \text{and} \quad x_1 = -1\,. \tag{2.3}$$

We first find the general solution (GS) of (2.2) and then find the particular solution (PS) which also satisfies (2.3).

Method:

- First set $x_n = A\,\lambda^n$ in (2.2), $x_{n+2} - x_{n+1} - 6\,x_n = 0$:

$$A\,\lambda^{n+2} - A\,\lambda^{n+1} - 6\,A\,\lambda^n = 0\,.$$

- Divide this equation through by A and λ^n to get:

$$\lambda^2 - \lambda - 6 = 0\,.$$

- Solve the above equation for λ. It is a quadratic equation and has **two** roots:

$$\lambda_1 = 3 \quad \text{and} \quad \lambda_2 = -2\,.$$

- The **general solution** of (2.2) is

$$x_n = A\,\lambda_1^n + B\,\lambda_2^n = A\,3^n + B\,(-2)^n\,, \tag{2.4}$$

  where A and B are constants.

- The final stage is to use the values $x_0 = 3$ and $x_1 = -1$ given in (2.3) to find A and B to obtain the particular solution.

  Set $n = 0$ in (2.4) to get $3 = A\,(3)^0 + B\,(-2)^0 = A + B\,.$

  Set $n = 1$ in (2.4) to get $-1 = A\,(3)^1 + B\,(-2)^1 = 3\,A - 2\,B\,.$

  The solution to the pair of simultaneous equations

$$\begin{aligned} A + B &= 3 \\ 3\,A - 2\,B &= -1 \end{aligned}$$

  is $A = 1$ and $B = 2$. Hence the PS of (2.2)–(2.3) is

$$x_n = 3^n + 2\,(-2)^n\,.$$

Note that $x_n \to \infty$ as $n \to \infty$ because the dominant term in the solution is 3^n.

Quadratic roots formula: Recall that the two roots of the quadratic equation $a\,\lambda^2 + b\,\lambda + c = 0$ are

$$\lambda_{\pm} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}\,.$$

Example 2.2

1. Find the general solution of $3\,x_{n+2} - 7\,x_{n+1} + 2\,x_n = 0$. Find the particular solution when:
   (a) $x_0 = -2$ and $x_1 = 1$;
   (b) $x_0 = 3/5$ and $x_1 = 1/5$.
2. Find the general solution of $9\,x_{n+2} - x_n = 0$.

How do these solutions behave for large n?

2.2. Solving the Fibonacci equation (2.1)

We now apply the above method to solve the Fibonacci problem. We first find the GS of (2.1) in terms of two constants. The PS is the solution for which $x_0 = 1$ and $x_1 = 1$.

Solution:

- First set $x_n = A\,\lambda^n$ in (2.1), $x_{n+2} = x_{n+1} + x_n$:

$$A\,\lambda^{n+2} = A\,\lambda^{n+1} + A\,\lambda^n\,.$$

- Divide this equation through by A and λ^n to get:

$$\lambda^2 - \lambda - 1 = 0\,.$$

- Solve the above equation for λ to obtain the two roots:

$$\lambda_{\pm} = \frac{1 \pm \sqrt{5}}{2}$$

- The **general solution** of (2.1) is

$$x_n = A\,\lambda_+^n + B\,\lambda_-^n\,, \tag{2.5}$$

  where A and B are constants.

- The final stage is to use the values $x_0 = 1$ and $x_1 = 1$ to find A and B to obtain the particular solution.

  Set $n = 0$ in (2.5) to get $1 = x_0 = A\,\lambda_+^0 + B\,\lambda_-^0 = A + B\,.$

  Set $n = 1$ in (2.5) to get $1 = x_1 = A\,\lambda_+^1 + B\,\lambda_-^1 = A\,\lambda_+ + B\,\lambda_-\,.$

  That is, A and B solve the pair of simultaneous equations:

$$\begin{aligned} A + B &= 1 \\ A\,\lambda_+ + B\,\lambda_- &= 1 \end{aligned}$$

  The solution is $A = (5 + \sqrt{5})/10$ and $B = (5 - \sqrt{5})/10\,.$

This calculation shows that the **particular solution** of (2.1) (i.e. the solution x_n of the equation which also satisfies $x_0 = 1$ and $x_1 = 1$) is

$$x_n = \left(\frac{5 + \sqrt{5}}{10}\right)\lambda_+^n + \left(\frac{5 - \sqrt{5}}{10}\right)\lambda_-^n\,,$$

where $\lambda_\pm = \left(1 \pm \sqrt{5}\right)/2$.

Verification:

We use this formula to compute x_n for $n = 0 : 20$. The results are output below.

n	x
0	1
1	1
2	2
3	3
4	5
5	8
6	13
7	21
8	34
9	55
10	89
11	144
12	233
13	377
14	610
15	987
16	1597
17	2584
18	4181
19	6765
20	10946

Observations

1. The formula looks to be giving the correct answers.
2. The multipliers in equation (2.1) and the two starting conditions x_0 and x_1 are all integers (they're actually all equal to 1), and yet the formula involves $\sqrt{5}$! This is a good illustration that you often need much more sophisticated mathematics to solve a problem than to state it. (Fermat's Last Theorem is an even more striking example of this.)

3. We have $\lambda_+ = \left(1+\sqrt{5}\right)/2 \approx 1.6180$ and $\lambda_- = \left(1-\sqrt{5}\right)/2 \approx -0.6180$. For large n, λ_+^n will grow unbounded, while λ_-^n will go to zero, so the ratio x_{n+1}/x_n will be close to λ_+ when n is large. E.g. to 16 decimal places:
$$\frac{x_{20}}{x_{19}} = \frac{10946}{6765} = 1.618033998521803\,, \qquad \lambda_+ = 1.618033988749895\,.$$

2.3. Solving 3-step difference equations with repeated roots

One case we have not yet considered is what happens when there is only one solution λ of the quadratic equation (i.e. the quadratic has repeated roots).

Example: Find the general solution of $x_{n+2} - 4\,x_{n+1} + 4\,x_n = 0$. Find the particular solution when $x_0 = -1$ and $x_1 = 6$.

Proceeding as before, we look for a GS of the form $x_n = A\,\lambda^n$. After cancellation this gives
$$\lambda^2 - 4\,\lambda + 4 = 0\,,$$
and the solution is $\lambda_\pm = 2$, (the quadratic has two equal roots). In this case we cannot write the GS (which must involve two distinct constants) as $x_n = A\,2^n + B\,2^n$, because this can be rewritten as $C\,2^n$ for $C = A + B$, and so it really only involves one constant. Instead the GS is $x_n = A\,2^n + n\,B\,2^n$ – i.e. one of the terms must be multiplied by n. (Exercise: show that this solves the equation.)

For the PS, setting $n = 0$ gives $A = -1$, and $n = 1$ gives $B = 4$, so the PS is $x_n = (4\,n - 1)\,2^n$.

In theory any linear difference equation in which the terms x_m are just multiplied by constants can be solved by first looking for a solution of the form $x_n = A\,\lambda^n$, but if the equation involves x_n and x_{n+p} for $p > 2$, then λ will satisfy a cubic or higher polynomial, and it might not be possible to calculate it exactly.

Exercises 2

1. Find the general solution of $x_{n+1} = 4\,x_n$.
2. Find the general solution of $2\,x_{n+1} + x_n = 0$. Find the particular solution when $x_0 = 3$.
3. Find the particular solution of $2\,x_{n+1} = x_n$ which satisfies $x_0 = -6$.
4. Find the general solution of $x_{n+2} - 3\,x_{n+1} + 2\,x_n = 0$.
5. Find the general solution of $8\,x_{n+2} - 6\,x_{n+1} + x_n = 0$. Find the particular solution when $x_0 = 2$ and $x_1 = 3/4$.
6. Find the particular solution of $x_{n+2} - x_n = 0$ for which $x_0 = 5$ and $x_1 = 1$.
7. Find the general solution of $4\,x_{n+2} - 4\,x_{n+1} + x_n = 0$.
8. Find the general solution of $x_{n+2} - 2\,x_{n+1} + x_n = 0$. Find the particular solution when $x_0 = -2$ and $x_1 = 3$.
9. Find the general solution of $x_{n+3} - 2\,x_{n+2} - x_{n+1} + 2\,x_n = 0$.

In each case describe how the solution x_n behaves when n is large.