Introduction to functions and models: EXPONENTS, *e* AND EXPONENTIAL MODELS

1. Introduction and a simple model of growth (easy)

In many popular accounts of population change, the word 'exponential' is used to describe something that is increasing very rapidly. However, the term has a very much more exact meaning, and it also applies to situations other than populations. Furthermore, not all populations grow exponentially.

Under ideal conditions, the number of new organisms appearing in a population is related to the current population. Take a very simple example, where a single bacterium is capable of dividing once per day. On the second day, there are two bacteria, and on the third day each of these divides, giving four bacteria. On day four, each of the four bacteria has divided to give eight, on day five there will be 16, on day six there will be 32 and on day seven 64.

The rate of increase remains the same, in that the population doubles each day. However, the total number of bacteria added to the population each day changes with time, because this is determined by the current population. Written as a word equation, the population of our imaginary bacteria on a given day can be described as a function of the previous day's population:

$$\text{Population (today)} = 2 \times \text{Population (yesterday)}$$

or tomorrow's population can be predicted if you know today's population:

$$\text{Population (tomorrow)} = 2 \times \text{Population (today)}$$

This is a very simple model which is more properly described as a geometric series (as compared to an arithmetic series, which is additive). The model makes the very important assumption that all bacteria survive indefinitely, and furthermore that the population grows by undertaking one division each day. Obviously, in real life cell divisions will be taking place at different times, so that the population will change smoothly rather than in a series of steps.

2. Real-world growth models – why geometric series don't work (easy)

If we have a large population of bacteria which are dividing at an average rate of once per day, we would expect the population to double each day as described in the introduction. This time, we will start with 100 bacteria, and the population change can be represented in a table like this:

Time (days)	Starting population	New bacteria produced
0	100	0
1	100	100
2	200	200
3	400	400
4	800	800

However, in a large population individual bacteria can divide at any time. What happens if we use the geometric series to calculate the population size every 12 hours (half of the doubling time)? We would expect that half of the bacteria would have divided in that interval:

Time (days)	Starting population	New bacteria produced
0	100	0
0.5	100	50
1	150	75
1.5	225	113
2	338	169
2.5	508	254
3	762	381
3.5	1143	572
4	1715	857

In this second calculation, the growth rate is still the same (once per day) but we have evaluated the series at 12 h (0.5 day) intervals and the population appears to grow faster. This is because the bacteria added at each interval contribute to the 'current' population that will divide in the next interval.

So which model is correct? The answer, sadly, is neither! The bacteria are the same, each one dividing once per day. But the population calculations are dependent on the time interval used. If we calculate the geometric series using different time intervals, we see that we approach a stable value for population growth as the interval gets smaller and smaller. This can be seen if we use the population after one day as a benchmark:

Time interval for calculation (days)	Number of bacteria after one day
1	200
0.5	225
0.25	254
0.1	260
0.05	266
0.02	269
0.01	271
0.005	271

Decreasing the time interval in a geometric series like this does two things – it adds new bacteria to the population more quickly (increasing the current population) but also decreases the population increase at each time-step (because the time interval decreases). So we expect that as we shorten the time interval more and more, the population growth curve will gradually settle down to the same value.

It is easy to evaluate the geometric series in a spreadsheet, but it becomes tedious to calculate populations over long periods of time with very short time intervals. More importantly, the growth rate over very short intervals is not a simple fraction of the average growth rate. Instead of the simple geometric series, we need a population growth model that can be evaluated for any time and is independent of time interval.

3. An exponential model for population growth (intermediate)

We introduced the geometric series in a 'word equation' like

Population (tomorrow) = Daily rate of increase × Population (today)

We have then shown that we can decrease the time interval over which we evaluate the series, and gradually approached a population growth curve that does not change significantly for further decrease in interval. We can write a new word equation for this curve, which involves an exponent:

Population (tomorrow) = Population (today) × exponent (growth constant × time difference)

This gives us a way to measure the population change reliably at any time, or for any time difference. Written in a mathematical format:

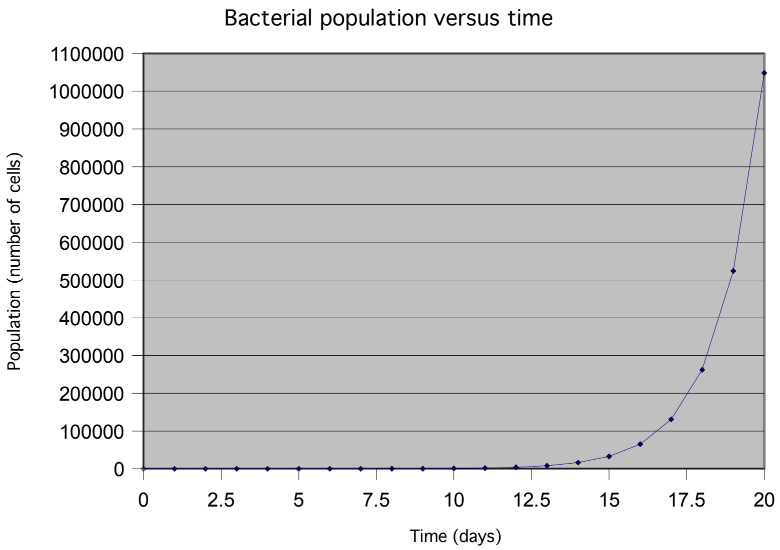
$$P_t = P_0 . \exp(k.t)$$

The values in this equation are:

P_0 is the initial population, and P_t is the population at time **t**

The expression $\exp(k.t)$ is termed the 'exponent' of the time (**t**) multiplied by a growth constant (k), which has the units of time^{-1} (that is, 'per unit time').

This can be set up using a spreadsheet, and a plot of an exponential growth model looks like this:



4. Exponential functions from the ground up (advanced – you can skip to section 5 if you wish)

Mathematically we start with the growth of the population (P) over time (**t**) such that:

$$dP/dt = kP$$

Over a time interval, denoted by δt ('delta-t'), the mathematical solution to this equation is:

$$P_{(t+\delta t)} = P_t . \exp(k.\delta t)$$

where P_t and $P_{(t+\delta t)}$ are the population sizes at times **t** and $(t + \delta t)$ respectively.

This is an ***exponential function***, hence the name ***exponential growth***. The expression:

$$\exp(k.\delta t) \text{ is another way of writing } e^{(k.\delta t)}$$

[Technical note: e is called Euler's number or Napier's constant and is one of the most important numbers in mathematics. The other important numbers are 1, 0, the imaginary value i and π. e is a constant, with a value of 2.71828 18284 59045 23536... In mathematical terms e is the unique real number so that the derivative of the function $f(x) = e^x$ at the point where $x = 0$ is equal to 1. The function e^x is called the exponential function and the inverse of this number is the natural or Naperian logarithm. Find out more at:

http://en.wikipedia.org/wiki/E_%28mathematical_constant%29
http://betterexplained.com/articles/an-intuitive-guide-to-exponential-functions-e/]

5. Doubling time for populations (intermediate)

We started this document by looking at a geometric series as a simple model for population growth. However, we showed that this is not a robust model, as it does not allow us to make valid calculations for intermediate time-steps. From there, we moved to an exponential model of the form:

$$P_t = P_0 . \exp(k.t)$$

Where:

P_0 is the initial population, and P_t is the population at time t

The expression $\exp(k.t)$ is termed the 'exponent' of the time (t) multiplied by a growth constant (k), which has the units of time^{-1} (that is, 'per unit time').

A more general version of this equation is:

$$P_{t2} = P_{t1} . \exp(k.[t2-t1])$$

where P_{t1} and P_{t2} are the population sizes at times $t1$ and $t2$ respectively, and $[t2-t1]$ is the time interval separating these two observations.

For the initial example with the geometric series, we looked at a population whose population doubled each day. In this case, the period of one day is termed the ***doubling time***. So how is the value of the growth constant, k, related to doubling time?

If we look at the population size at two times that are separated by the doubling time, t_D, we can rewrite the last equation:

$$t2-t1 = t_D$$

$$P_{t2} = P_{t1} . \exp(k.t_D)$$

We also know that the population will have doubled over this period (by definition), so that:

$$P_{t2} = 2.P_{t1}$$

So the growth equation can be rewritten in terms of P_{t1} only, and then re-arranged to give a relationship between k and t_D:

$$2.P_{t1} = P_{t1}.\ \exp(k.t_D)$$

$$\exp(k.t_D) = 2.P_{t1}/P_{t1} = 2$$

$$k.t_D = \ln(2)$$

The symbol '**ln**' indicates the natural logarithm (that is the logarithm expressed to the base ***e***). So it is now possible to calculate the value of ***k*** for a given doubling time, or the doubling time if you know ***k***:

$$k = \ln(2)/\ t_D$$

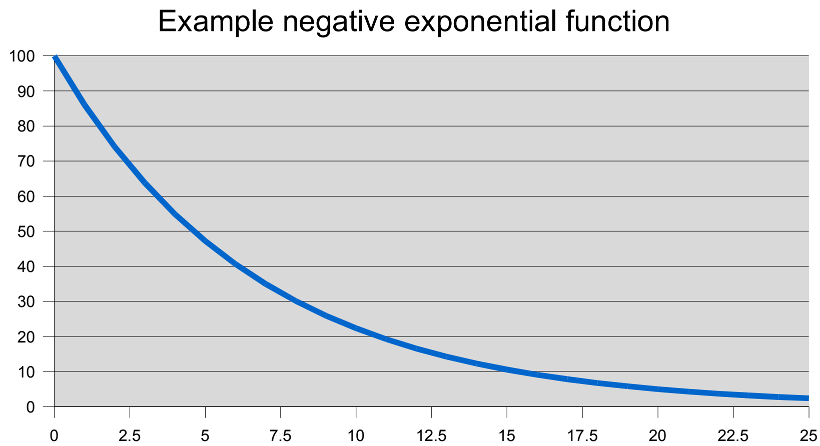
$$t_D = \ln(2)/k$$

In the case of a doubling time of one day, the value of ***k*** is 0.693147 d^{-1}, whilst for doubling times of two and five days the values are 0.346573 d^{-1} and 0.138629 d^{-1} respectively. Note that the constant is written with units 'per day' – it would have a different value if we had used hours as units but kept the doubling time as one day (ie 24 h).

6. Negative exponents (intermediate)

If you plot an exponential growth curve, it is clear that the slope (gradient) of the curve increases as the independent variable (for instance time) increases. The rate at which the slope changes is determined by the constant, denoted ***k*** in previous sections.

If ***k*** is negative, the dependent variable decreases as the independent variable increases. Instead of increasing, the slope of a negative exponential curve decreases as the independent variable increases, so that the curve appears gradually to level out. An example is shown here:



An example of exponential decrease (or decay) is the absorption of light by a medium such as water. Imagine that each photon has a defined chance of being absorbed as it traverses a metre of water. If this chance is 5% (1 in 20), 95% of the photons will pass through a metre of water. Over the next metre, 5% of the ***remaining*** photons will be absorbed, leaving 90.3% of the photons to enter the third metre layer. As the number of photons decreases, the number absorbed over each successive metre also decreases.

We can write a relationship between light level and depth as an exponential function:

$$E_z = E_0 . \exp(-K_D . z)$$

where E_0 and E_z are the light intensity at the surface and a depth of z metres, respectively, and K_D is the absorption coefficient (more properly the 'diffuse attenuation coefficient', in units of depth^{-1}).

An important quantity in the functioning of aquatic ecosystems is the depth to which sufficient light penetrates to allow photosynthetic growth to take place. Although many different factors influence the minimum amount of light plants need for photosynthesis, a good rule of thumb at least for the open ocean is that photosynthetic growth is possible down to 1% of the light incident at the surface. If we term this depth $z_{1\%}$ and call the 1% light level $E_{1\%}$, we can rewrite the equation:

$$E_{1\%} = E_0 . \exp(-K_D . z_{1\%})$$

We can rewrite $E_{1\%}$ in terms of E_0, and then put this value into the equation and re-arrange this to give an equation relating depth and K_D:

$$E_{1\%} = 0.01 . E_0$$

$$0.01 . E_0 = E_0 . \exp(-K_D . z_{1\%})$$

$$\exp(-K_D . z_{1\%}) = 0.01 . E_0 / E_0 = 0.01$$

$$-K_D . z_{1\%} = \ln(0.01)$$

The symbol '**ln**' indicates the natural logarithm (that is the logarithm expressed to the base e). So it is now possible to calculate the value of K_D for a known 1% 'light depth', or the 1% depth if you know K_D:

$$K_D = -\ln(0.01)/z_{1\%}$$

$$z_{1\%} = -\ln(0.01)/K_D$$

[Technical note: the logarithm of a number less than one has a negative sign. K_D is conventionally written as a positive number, so the minus sign in the exponent provides an answer in 'positive' metres.]

For a 1% light depth of 50 m, the value of K_D is 0.092103 m^{-1}, whereas for a 1% light depth of 20 m K_D is 0.230258 m^{-1} (note the units of 'per metre'). The diffuse attenuation coefficient increases as water becomes more turbid (ie absorbs more light), corresponding to a shallower 1% light depth. In the initial discussion of light penetration, we suggested that photons had a 5% chance of being absorbed within one metre. Thus K_D is 0.05, and the 1% light level occurs at a depth of 92 m – the sort of value that is only found in very clear water such as the middle of deep ocean areas.

You can use the same basic equation to work out the proportion of surface light that reaches a given depth, z^* if you know the value of K_D:

$$E_{z^*} = E_0 . \exp(-K_D . z^*)$$

$$E_{z^*} / E_0 = \exp(-K_D . z^*)$$

Where the expression E_{z^*}/E_0 is the proportion of surface light at a depth of z^*. If you wanted to express this as a percentage, you would need to multiply the result by 100.