Introduction to functions and models: LOGISTIC GROWTH MODELS

1. Introduction (easy)

The growth of organisms in a favourable environment is typically modeled by a simple exponential function, in which the population size increases at an ever-increasing rate. This is because the models, at their most simple, assume a fixed net 'birth' rate per individual. This means that as the number of individuals increases, so does the number of individuals added to the population (see the resource on exponential models). This description of population change pre-supposes that resources for growth are always adequate, even in the face of an ever-increasing population.

In the real world, resources become limiting for growth, so that the rate of population growth declines as population size increases. There are several numerical models that simulate this behaviour, and here we will explore a model termed 'logistic' growth.

2. The logistic growth model explored (intermediate)

In order to model a population growing in an environment where resource availability limits population growth, the model needs to have a variable growth rate, that decreases as the population size increases towards a notional maximum, often termed **carrying capacity** in population ecology.

For population ecologists, the most common type of model derives from a series of equations ascribed to two researchers. The Lotka-Volterra equations include an expression for population change where the key parameters are a growth term (broadly the balance between fecundity and mortality) and a maximum population size (carrying capacity). The relationship is normally expressed as a differential equation:

$$dN/dt = rN \,.\, (1 - N/K)$$

In this equation, the expression dN/dt represents the rate of change of number of organisms, N, with time, t, and r is a growth term (units time^{-1}) and K is the carrying capacity (same units as N). It is clear that for small values of N, N/K is very small so that $(1-N/K)$ is approximately equal to one, and the equation is effectively:

$$dN/dt = rN$$

As N increases, $(1-N/K)$ becomes smaller, effectively reducing the value of r. This is termed **density-dependence**, and is an example of negative feedback because the larger the population, the lower the growth rate.

This equation can be re-written in a form that can be evaluated for any value of N at two times t and $(t+1)$, giving the equation:

$$N_{(t+1)} = (N_t . R)/(1 + aN_t)$$

Notice that this equation contains new parameters R and a. These are related to r and K by:

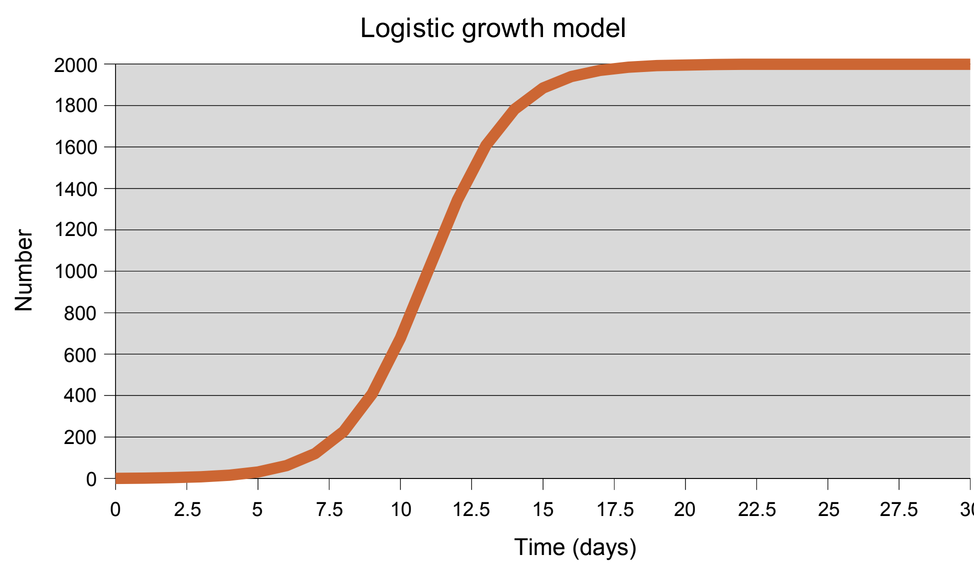
$$R = 1/(\text{fecundity . mortality}) = \exp(r)$$

and

$$a = (R - 1)/K$$

3. What the model looks like (simple)

A plot of the logistic growth curve looks like this:



Notice that the population starts with one individual, and eventually reaches an equilibrium value, in this case about 2000 individuals (the value of K set for this example). The rate at which the slope of the curve **increases** initially is mirrored by the rate at which the slope **decreases** as the population approaches the carrying capacity. The greatest value of the slope of the curve occurs just after ten days in this example, when the population is exactly half of the carrying capacity ($0.5K$).

In this example, the value of r has been set so that initially the population doubles once per day. If r had been larger, the population would have increased more rapidly initially, and would have reached a level equal to $0.5K$ earlier. It would then have seen a faster decline in growth rate close to carrying capacity, which would also be earlier than in this example. The curve would look just like this illustration, but compressed horizontally. Conversely, a low value of r would make things happen more slowly, if K were left unchanged. The curve would appear to be stretched out horizontally.

We can explore the effects of changing ***r*** *by looking at the time taken to reach a population of 0.5**K**:*

K (number - constant)	2000	2000	2000	2000
R (see section 2)	1.5	2	3	4
r *(d^{-1})*	*0.4055*	*0.6931*	*1.0986*	*1.3863*
Time to achieve 0.5***K*** *(d)*	c. 18.5	c. 10.5	c. 7	c. 5.5

The shaded column uses the same parameter values as the example illustrated in this section.

Similarly, we can examine the effects of changing ***K*** whilst keeping ***r*** constant. Altering carrying capacity affects the speed at which the population stabilizes – for a given value of ***r***, low ***K*** means that the population stabilizes early whilst high ***K*** means that it takes a longer time to equilibrate. However, the effects of quite large changes in ***K*** are less marked, especially when ***r*** is high as in the illustrated example:

K (number)	*500*	*1000*	*2000*	*5000*
R (see section 2)	2	2	2	2
r *(d^{-1} - constant)*	0.6931	0.6931	0.6931	0.6931
Time to achieve 0.5***K*** *(d)*	c. 9	c. 10	c. 10.5	c. 12.5

4. The significance of *r* and *K* (advanced)

As can be seen above, the two parameters of the Lotka-Volterra model determine how the population growth is controlled. The growth term, ***r***, is typically the excess of fecundity (reproductive output) over mortality over the lifetime of an individual. High values of ***r*** imply high initial growth rate and, consequently, a rapid change in population growth rate as the carrying capacity is approached. Organisms with high values of ***r*** are successful in the initial colonization of a habitat, because the achieve their optimum population rapidly.

The value of ***K*** represents the number of organisms that a habitat can sustain. In established habitats, where the rate of population growth (characterised by high ***r***) is less important, success is measured by carrying capacity, that is high value of ***K***. These are very simplistic distinctions, but they have been used to contrast the ecological strategies of **responsive species** in dynamic habitats ('r-strategists') and **dominant species** in established habitats ('K-strategists').

5. An alternative logistic model (advanced)

In considering exponential growth by microorganisms reproducing by binary division, we introduced the equation:

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

Where:

P_{start} 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}.

As already established, this model predicts population change that accelerates as more individuals enter the population and in turn produce more successor organisms. The reality for most environments is obviously that resources will be used up as the population increases, in turn limiting growth of both individual organisms and the population as a whole. Other controls, such as density-dependent mortality due to predation, may also operate. As a result, the absolute rate of population increase does not continue to increase, but rather declines towards zero as the population approaches a maximum value, akin to the carrying capacity, K, in the model derived from the Lotka-Volterra equations (see section 2).

Here, we use a formula that is related directly to the exponential growth model at the start of this section. It is based on a starting population, an equilibrium population and a growth constant:

$$P_t = P_{equil}/(P_{start} + [(P_{equil} - P_{start}).\exp(1\text{-}kt)])$$

In this model:

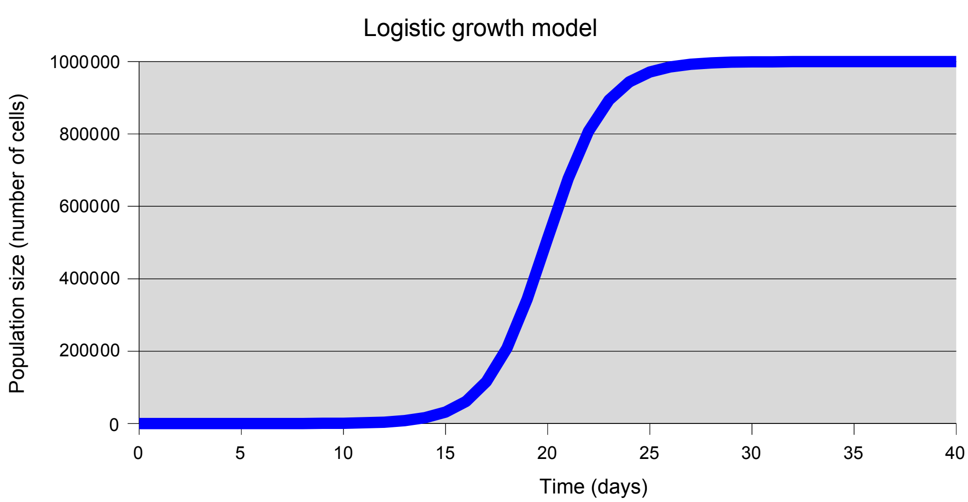
P_t is the population size at time t

P_{start} is the starting population size

P_{equil} is the equilibrium population size (equivalent to K – the carrying capacity - in the Lotka-Volterra equation)

k is a growth constant, which is has the same relation to doubling time as the growth constant in an exponential growth model ($k = \ln(2)/doubling\ time$)

The model is similar in form to that derived from the Lotka-Volterra equations, and looks like this:



We can compare the population growth predicted by the logistic model with that resulting from exponential growth with the same values of P_{start} and $\mathbf{k}$ (ie doubling time).

It is clear that for very low population size (that is, within the first few days of population increase), the two models predict identical numbers. Gradually, however, the numbers predicted by the logistic model fall below those from the exponential model. When the population is about 10% of carrying capacity, the value predicted by the logistic model is about 90% of that predicted for purely exponential growth, whilst at 50% of carrying capacity the ratio is 50%, and at 90% of the carrying capacity it is only 10% of the exponentially-increasing population.