GENERATIONS: LINKING CONTINUOUS AND DISCRETE POPULATION GROWTH

Populations grow because individuals multiply and die. For most populations this happens all the time and therefore we typically consider population growth as a continuous process: the human population changes in size because of births and deaths. Bacteria on petri dish or in a flask multiply continuously. In mathematical language we can describe this with a differential equation model for continuous growth:

$$\frac{\mathrm{d}n}{\mathrm{d}t} = b\,n(t) - m\,n(t) = (b-m)\,n(t), \tag{1}$$

where $n(t)$ is the size of the population at time t, b is the *per capita* growth rate and m is the *per capita* mortality rate and $b-m$ is the net growth rate. The solution to this simple model is the function for exponential growth $n(t) = n(0)e^{(b-m)t}$. The population will grow if $b-d > 0$, that is, when the net growth rate is positive. If the mortality rate exceeds the birth rate the net growth rate is negative and the population will, over time, decrease in size.

Another way to describe population growth is through discrete time steps. For instance, if bacteria multiply once every hour, the progeny of this bacterium is $2, 4, 8, 16\ldots$ bacteria etc. If all bacteria would divide synchronously[1] we can describe the growth of the population with a difference equation model:

$$N_{i+1} = RN_i, \tag{2}$$

where N_i is the size of the population after i generations, and R is the multiplicative factor of growth, or multiplier for short. For our bacteria we would set $R = 2$. The solution to this model is $N_i = N_0R^i$: the population increases in size if $R > 1$ and decreases otherwise.

In describing population growth we often use these descriptions almost interchangeably, as if they are the same. But are they the same and can we somehow rewrite one model into the other and in that way make a link between the continuous and discrete time models? And how do the conditions for population growth relate, what $b-d > 0$ to $R > 1$?

A mathematician's answer to this question would be to turn the discrete time model into continuous time by taking ever smaller time steps. In the end (*i.e.* in the limit of the length of the time step tending to zero), the discrete difference equation time model will turn into continuous differential equation model. This works, and this works well, and it is how we numerically calculate approximate solutions to differential equations like (1) in a mathematically sound way. But in doing so, we have lost the biological interpretation of the model parameters: the inherently discrete birth and death events of individuals have been turned into something in which with every little time increment a bit of net offspring is squeezed out like toothpaste out of a tube.

So rather than following the mathematician's logic and turn a discrete difference equation model into a continuous differential equation, we will go the other way. We will turn the continuous time model into a discrete time one and preserve the biological interpretation of the continuous time model which specifies birth and

---

[1] They don't! By following individual cells it is possible to measure the time between actual divisions. There is considerable variation in the time between bacterial divisions Elfwing A, et al. (2004).

death processes. For this we will rewrite the continuous growth model in terms of generations.

A generation expansion. A generation is another word for a birth cohort: it is a group of individuals that are all born from the parents in the previous cohort. This recursive way of defining a generation makes clear that to know what a generation is we need to know what a birth and what a death is. And because we define a generation in relation to the previous generation, we also need to define a zeroth generation.

For our continuous time model (1) we will define the zeroth generation as all individuals that are present at time $t = 0$, at which time we have $n(0)$ individuals. Only individuals that are present when we start the clock at time zero are allocated to the zeroth generation, and this generation therefore will only get smaller over time, as individuals die. Let the number of individuals in the zeroth generation at time t be given by $n_0(t)$: this changes over time as:

$$\frac{\mathrm{d}n_0}{\mathrm{d}t} = -m\, n_0(t), \tag{3}$$

and with $n_0(0) = n(0)$. We can easily solve this differential equation to give $n_0(t) = n(0)e^{-mt}$. The size of this generation is obviously $m(0)$; all the individuals that we allocated to it when we started the clock. But another way to measure the size of the population is by counting all the deaths that occur. The size of the first generation there for also can be written as $\int_0^\infty m\, n_0(t)\,\mathrm{d}t$. It is easily checked that indeed $m \int_0^\infty n_0(t)\,\mathrm{d}t = n(0)$

The first generation are all individuals born from the zeroth generation. This generation has zero individuals when we start the clock, but will accumulate individuals as time goes on. And as time goes on further, these individuals will die. Let the number of individuals in the zeroth generation at time t be given by $n_1(t)$. The first generation changes over time as:

$$\frac{\mathrm{d}n_1}{\mathrm{d}t} = b\, n_0(t) - m\, n_1(t), \tag{4}$$

and with $n_1(0) = n(0)$. In a similar manner we can define the second, third fourth etc. generations. They change as

$$\begin{aligned}
\frac{\mathrm{d}n_2}{\mathrm{d}t} &= b\, n_1(t) - m\, n_2(t) \\
\frac{\mathrm{d}n_3}{\mathrm{d}t} &= b\, n_2(t) - m\, n_3(t) \\
\frac{\mathrm{d}n_4}{\mathrm{d}t} &= b\, n_3(t) - m\, n_4(t) \\
&\vdots
\end{aligned}$$

In general, we can write for $i > 0$:

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = b\, n_{i-1}(t) - m\, n_i(t) \tag{5}$$

and with $n_i(0) = 0$ for all $i > 0$.

Note that if you sum up all the generations we get the total population back ($\sum_{i=0}^{\infty} n_i(t) = n(t)$), and the change of in the number of individuals of all generations added together is the differential equation (1):

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \frac{\mathrm{d}\sum_{i=0}^{\infty} n_i(t)}{\mathrm{d}t} = b \sum_{i=0}^{\infty} n_i(t) - m \sum_{i=0}^{\infty} n_i(t) = (b-m)\, n(t). \tag{6}$$

This is called a generation expansion: we have rewritten the population growth as a sum of successive generations.

The generation expansion keeps track of the different generations as they develop over time. Because the individuals in each generation live for a certain time (here, the average life time is $1/m$) and newborns are produced over the life time of the generation, the successive generations spread out over time. This happens in most populations. You probably have seen it in your own family: the difference in age between the youngest and oldest cousins in your family is probably larger than the age difference between your uncles and aunts.

The multiplicative factor. We can now write an exponentially growing population as a sum of generations. To find out how the population grows we will consider the size of the successive generations. As we noted before, we can measure the total size of the generation be following it until the last individual dies and totting up all the deaths until all individuals of that generation have passed away. We will denote the total size of a generation as N_i. In mathematical language, the totak size of generation i is given by

$$N_i = m \int_0^{\infty} n_i(t)\, \mathrm{d}t$$

. we had already worked out that $N_0 = n(0)$. But can what is the size of the generations after the zeroth generation?

Now here comes the clever bit: because the exponential growth model is the solution of a linear differential equation with constant parameters, we can find out that what that is really easily. It goes like this: if we integrate eqn (5) on both sides from 0 to t we get

$$n_i(t) - n_i(0) = b \int_0^t n_{i-1}(t)\, \mathrm{d}t - m \int_0^t n_i(t)\, \mathrm{d}t.$$

If we now wait long enough until all individuals in generation i have passed away–or in mathematical terms, take the limit of t tending to infinity–we find (and remember that $n_i(0) = 0$):

$$0 = b \int_0^{\infty} n_{i-1}(t)\, \mathrm{d}t - m \int_0^{\infty} n_i(t)\, \mathrm{d}t = \tfrac{b}{m} N_{i-1} - N_i.$$

In taking this limit we have discovered how the size of a generation depends on the size of the previous generation. If we rewrite this a little it takes the form:

$$N_{i+1} = \tfrac{b}{m} N_i. \tag{7}$$

Compare eqn (7) to the difference model (2). Apart from the value of the multiplier, they are the same! But (7) we have derived through a generation expansion from the continuous time differential equation (1). In doing so we have found the biological link between birth and death rates b and m and the multiplier:

$$R = \frac{b}{m}.$$

Let's look closer at this expression for the multiplier. At is the birth rate, b, multiplied by $1/m$, which is the average time until death in this model. And as we have (implicitly) assumed that individuals can give birth continuously throughout their lifetime, b/m is the total average number of offspring produced per individual. This interpretation links the net growth rate $b-m$ to the multiplier R: if individuals produce more than one individual over their lifetime the net growth rate is positive, and if it is less than one the net growth rate is negative. So if the population described by the differential equation growth, so will the population described by the corresponding discrete time model for the generations

But other than this connection it is important to realise that the two models give by eqns (1) and (2) are rather different, even when they describe the same population. The continuous time model (1) describes the population in $n(t)$: the actual number of individuals present at time t. The discrete time model (2) describes the population in N_i: the total number of individuals that will make of generation i. And we lose the description in actual time, all we know is that after we have scrutinised all the death records once all the individuals in a generation have passed away how big that generation was. The average time between generations in this model is $1/m$ so i gives some indication of time, but the two are very different. Therefore, although the two models describe the same population, they cannot be used interchangeably.

Other uses of multiplicative factor. The reason the discrete time model is used so often that in practical terms it is much easier to use: a model with discrete steps is much easier to implement in a computer. Probably the biggest advantage of the discrete model for the generations is that the interpretation of the multiplier is much simpler. Here, we figured out that the multiplier is simply the average number of individuals.

In other fields the same reasoning is used to great effect, and you almost certainly will encounter the same multiplicative factor for the generations that we have derived here under other names. In genetics and evolutionary theory this is how fitness is defined: the average number of offspring of individuals with a certain genetic make up. And in epidemiology the multiplier is known as the reproduction number: the average number of new infections that in individual infected with a certain infectious agent makes.

The same logic can be applied to much more complex reasonings. For instance, we can structure the population so that the linear differential equation turns into a system of ordinary differential equations. You can work out the population growth using the theory of Leslie matrices, and in an epidemiological context, calculate the reproduction number using a next generation matrix approach.