Modeling the Growth of Biological Populations

Objectives:
- Create mathematical models of population growth using Excel
- Understand how population parameters such as carrying birth rate, death rate, and carrying capacity influence population growth models

Introduction
As described in lecture, scientists use models to help explain natural phenomena. Scientists can then use simulations based on these models to create predictions that can be tested to evaluate the effectiveness of models. In this lab, you will create a mathematical model to investigate the principles of biological population growth. A biological population can be defined as a group of individuals belonging to the same species and living at about the same place. Because many species reproduce sexually, the definition of a population often includes the requirement that individuals can potentially interbreed. But even in cases where individuals reproduce asexually (e.g. fission), we still use the term ‘population.’ However defined, most populations change in size (numbers of individuals) over time. Understanding this change helps us understand many of the important phenomena in biology, such as: 1) the extinction of species, 2) the invasion of noxious species such as weeds, agricultural pests, and medical pathogens, and 3) the impact of human population on the environment.

Population change is the result of 4 processes: 1) birth, 2) death, 3) immigration and 4) emigration. The latter two processes, immigration and emigration, represent the movement of individuals into and out of a population, respectively. While these are important in some populations, we will ignore them for now and consider a population to change only from birth and death. For example, populations of Darwin’s finches on the Galapagos Islands change mainly due to birth and death, not the immigration of new birds from South America.

To model population growth, we first need to build an equation that represents the population dynamics (i.e. the ways in which populations change). In biological models, \( N \) is used to represent population size (see Table 1). If there are \( N_t \) individuals in the population during time period \( t \) (\( t \) could be a day, a year, a decade, etc.), and each contributes an average of \( b \) offspring to the next generation, then:

\[
\text{the total number of offspring produced in time period } t = bN_t \tag{1}
\]

Some individuals will probably die during the period \( t \). So let \( d \) be the probability of an individual dying in this time period. Then:

\[
\text{the total number of individuals that die in time period } t = dN_t \tag{2}
\]
The number of individuals in the time period after \( t \) (which we will call \( t+1 \)) is equal to the number of individuals present in period \( t \) plus the number of total births and minus the number of total deaths. So the dynamic equation for population change is:

\[
N_{t+1} = N_t + bN_t - dN_t \tag{3}
\]

Equation (3) is a good model for the growth of populations in which births occurs in one particular season (e.g. spring), and adults typically die after the reproductive period. This type of population growth is called **Discrete Growth** and occurs in many insects and annual plants. Many populations, including humans, have a different pattern of growth – instead of individuals reproducing in one season and then dying at the end of the time period, they can reproduce or die during any season. In this case, the pattern of birth and death is *not* discrete, but rather it is Continuous Growth. Continuous population growth is modeled using an equation that is slightly different from equation (3), and we will not deal with it in this laboratory.

### Using Excel to Model Population Growth

Let’s run some simulations of population growth using Excel. The value of this exercise is that we can see the role of **Geometric Population Growth**. In order to perform simulations, we will introduce a symbol that represents the difference between the birth and death rates. The name of this term is the Greek letter, lambda, \( \lambda \).

\[
\lambda = 1 + (b - d) \tag{4}
\]

According to (4), if birth rate minus death is positive, then \( \lambda \) is larger than one. On the other hand, if death rate is larger than birth rate, then \( \lambda \) is less than one. Note that the value of \( \lambda \) cannot be less than 0; can you explain why?

With a little bit of algebra, we can turn equation (3) into the following:

\[
N_{t+1} = \lambda N_t \tag{5}
\]

This is the equation we will use to run our first simulation.

1. Start by opening a new Excel workbook. Immediately save the workbook as “popgrow001”, where the 001 is your section number (ask your TA for your section number). Because we want to investigate how changes in population parameters (birth and death) affect population growth, we need to easily change these parameters. Thus, we will use Excel to Create Names for your variables.
Creating names for your parameters and variables in Excel

2. Go to cell C3, and type the letter ‘b’, for birth rate. All you are doing is providing a label for a cell in which you will later enter the birth rate. Now move to cell C4 and enter a value for the birth rate (type in ‘2’ for this example). Now you need to tell Excel that the parameter, ‘b’ is the name for the value ‘2’. To do this, highlight the two cells (C3 and C4), and go to the menu bar at the top of the spreadsheet and click on ‘Insert’. The drop-down menu will provide a set of options; move to the option ‘Name’. Another set of options appears; click on ‘Create’. After you click ‘Create’, you are given a ‘Checkbox’ listing a set of choices that ask where the ‘Name’ is relative to the value. You will check the option that says ‘top row’ (actually, it is probably already checked for you since Excel tries to anticipate what you want). The reason you choose ‘top row’, is because the name is ‘b’ and it is in the top row, whereas the value, ‘2’ is in the bottom row. You have made it so that instead of having to type the cell reference (C4) whenever you want to use the birth rate in an equation, you can just type “b.” To see the effect of what you have done, click on cell F3 and type ‘= b’, and then hit ‘Enter’. What do you see? Now change the value of ‘b’ to a different number, like 3.

What happens to the cell F3 where you had entered ‘= b’?

3. (Go ahead and delete the contents of F3; you will not need it any more.)

Now move to cell D3 and type ‘d’, for death rate. Enter a value in D4 for death rate (remember that death rate cannot be greater than 1). Then repeat the process described above for naming the parameter.

4. Next move to cell E3 and type the word ‘lambda’ (the word is easier to enter than the Greek letter). Move to cell E4 and enter the formula to calculate lambda based on equation (4) described above. When you enter the formula for lambda, start with an “=” symbol and follow it with the parameter names, ‘b’ and ‘d’, rather than the actual numbers, or the cell references. After you hit ‘Enter’ you should see that Excel has calculated the lambda value based on your input values of birth and death parameters.

Iterating the Dynamic Equation for Discrete Population Growth

Now, you are ready to write what is known as a ‘recurrence’ formula. This formula will allow you to use Excel to simulate population growth using equation (5).

5. First, let’s make a column representing time periods over which the population grows. Move to cell C9, and type the letter ‘t’, to label a column for the time period. Then move down one cell to C10 and type the number ‘0’ (thus the simulation starts on ‘day’ 0). Hit ‘Enter’, move down to the cell C11 and type 1, and hit ‘Enter’ again (‘day’ 1 comes after day 0). You have just entered two numbers, ‘0’ and ‘1’, representing the first two time periods. This sequence of numbers gives Excel a pattern that it can use to fill in more
numbers. In this case, the pattern is to increase numbers down a column by an increment of ‘1’. Highlight the two cells containing the numbers ‘0’ and ‘1’. Next, use the mouse pointer to ‘grab’ the small square at the bottom right-hand corner of the highlighted boxes, and then pull the mouse down the column to cell C30. Excel will automatically fill in the cells in the column according to the pattern you established by typing ‘0’ and ‘1’. So, you end up with a column numbered successively from 0 to 20.

6. Next, move to cell D9, and type the letter ‘N’, to label a column for the population size. Move down to D10 and enter a number that represents the initial population size at time $t = 0$. For example, enter the number 2; you just have created 2 individuals in your initial population. You will use this number as the first population size in the recurrence relation for geometric population growth.

The population growth equation equals the following:

$$ N_{t+1} = \lambda \times N_t \tag{6} $$

7. We cannot create a name for $N$ as we did with lambda, because $N$ changes over time. But we can still perform the calculation easily. Move to the cell D11, just underneath where you entered the initial population size. You are about to enter a formula, so type ‘=’.

After the ‘equals’ sign type the name ‘lambda’, then type the multiplication sign, ‘*’. After the multiplication sign, enter the cell reference for the cell just above (in this case, it would be D10) in which you had entered the initial population size. Now hit ‘Enter’. In cell D11, you should see a number that represents population size at $t = 1$. Check the math by hand to make sure that the value makes sense.

The population size at time $t = 1$ is lambda multiplied by the population size at time $t = 0$. Likewise, the population size at time $t=2$ is lambda times the population size at time $t = 1$. So, you could move to cell D12 and type ‘= lambda*D11’. But, this would be an inefficient use of time. Instead, just click on the cell D11, and then grab the ‘box’ in the lower right hand corner of the highlighted cell. Then pull the box down one cell to D12 and release it. This copies the equation AND it maintains the appropriate cell reference, so that if you left click on the formula in D12 it should reference the population size in D11. If this works, you can simply copy the recurrence formula all the way down to represent population growth over 20 time intervals. Do this now.

Look at the population sizes. The final ones may seem a little funky; they are probably written in scientific notation. If a number is written like ‘$xE+y$’, it means $x$ times 10 to the $y^{th}$ power. For example, 2.38E+11 is read as 2.38 times 10 to the 11\textsuperscript{th} power, or 238,000,000,000. Scientific notation is just an easy of writing vary large numbers.
**Plotting the results on an arithmetic axis**

Next, we can produce a graph of the results. To do this, highlight the columns that you want to graph (C:9 to D:30), then choose *Insert → Chart* from the top Menu (if using Windows XP). If you are using Windows 2007, click *Insert → Scatter* from the top Menu. The best chart to use in this case is an ‘XY Scatterplot’ – make sure that you choose a ‘sub-type’ that has the data points connected with lines, and then click ‘Finish.’ Your instructor can help you do this (also, you can use the ‘Help’ button). Have your TA check to see if your graph is correct.

Congratulations, you have just done your first scientific simulation! Lookout for the balloons dropping from the ceiling! You have just plotted exponential growth on an ‘arithmetic’ axis, and you have obtained an **exponential growth curve**. *Can you explain why the curve is not a straight line?*

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**Plotting population growth on a logarithmic axis**

The graph of exponential population growth curves upward sharply; however, the **per capita population growth rate** does not change. If we are interested in factors that affect per capita growth rate, a **logarithmic axis** will show changes in per capita growth. The logarithm of a number, X, is the power that you raise a base number to in order to get X. For example, if the base is 10, then the log of 100 (base 10) is 2, because you raise 10 to the power 2 to get 100. The most useful base is the number denoted by $e$, 2.71718..., where $e$ goes on forever after the decimal point. This type of logarithm is called the **natural log**, and it is often denoted as $\ln$. You do not need to worry about entering $e$ in the spreadsheet, or solving for the power that gives you the logarithm of a number. In Excel all you have to do to find the **natural log** of a number X, is to enter the equation, =$\ln(X)$, in the worksheet.

8. Label cell E9 ‘$\ln N$’, next to your column of population sizes. Then in E10 enter the formula that calculates the natural log of the initial population size at time 0. Highlight that cell and copy this formula down the column until you have the natural log of all populations. Check to make sure the reference population in column D is updated. Now graph the natural log of population size against time.

What does this plot look like? *Can you explain why the graph has this particular shape?*

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Graphs with logarithmic axes are useful because they **only make a straight line if the per capita effects are constant** (i.e. the per capita population growth rate does not change). If the line is not straight, then you know some factor is influencing the per capita growth rate.
Limits to Population Growth

In the previous simulation, populations grew without an upper limit to their population size. In reality, populations are always limited by a finite level of resources. In other words, resources such as food or nesting sites are used up by individuals in the population. This limits the population growth rate, eventually placing an upper limit on the number of individuals capable of surviving in the environment. We can model this limit using a carrying capacity, which is the largest number of individuals that the environment can support.

One way to represent the effect of carrying capacity is with the following equation:

\[ N_{t+1} = N_t + (\lambda - 1)*N_t*((1 - (N_t/K)) \]

Here \( K \) is the carrying capacity. First, notice that if \( K \) is much larger than \( N_t \), then the ratio of \( N_t/K \) is approximately zero. If you actually try setting this to zero you can (if you do some algebra) rearrange the terms so that the equation looks similar to the recurrence equation without limitation (6).

9. Try entering the recurrence relation for population growth with a carrying capacity in your Excel spreadsheet. To keep the previous work you did, create new column for the size of a population that grows to a carrying capacity; enter a value of 2 for the initial populations size (\( N_t \)). Create another named variable, \( K \), for the carrying capacity of the population. Simulate 20 generations using equation (7). Note that you should use the original value of lambda for this new simulation, so your results are directly comparable to your results from simulating exponential population growth. Produce a graph of these results with the population size log-transformed. What do these graphs look like? Why? Did your population survive?

Models of discrete population growth with a carrying capacity can yield a wide variety of strange dynamic behaviors, including something called ‘chaos’. Chaos has been the subject of intense ecological research as well as popular press in recent years (it was even referred to in Jurassic Park). Now you will enter different values for the birth and death rates to see what dynamic behaviors you generate in the population model. For example, some parameter values for birth and death will allow the population to grow gradually to the carrying capacity, while others will cause oscillations, in which the population sizes ‘bounces’ up and down between two population sizes. Try to generate other dynamic behaviors, including chaos, which is a very irregular pattern of population size.
10. Produce graphs which exhibit chaos, stable limit cycles, and damped oscillations by tweaking your birth and death rate parameters as shown in the figures below. For each type, you should create new variables (e.g., bchaos, lambdadamped) so that your earlier graphs are not lost. Produce a graph with a logarithmic axis for each type. Here are some examples:

Table 1. Variables used to model population growth.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>population size</td>
</tr>
<tr>
<td>t</td>
<td>time period</td>
</tr>
<tr>
<td>b</td>
<td>population birth rate</td>
</tr>
<tr>
<td>d</td>
<td>population death rate</td>
</tr>
<tr>
<td>λ</td>
<td>difference in population birth and death rates</td>
</tr>
<tr>
<td>K</td>
<td>population carrying capacity</td>
</tr>
</tbody>
</table>