1 Population Growth Models

Back to our problem of trying to predict the future.

We start by using the math you already know to study population growth. This field is usually called mathematical biology or mathematical ecology. Our goal is to use knowledge about a species and its environment to give an approximation to the size of the population of that species in the future.

Two ideas for how to do this come to mind. The first is to look at the historical data and see if we can identify trends. This is a great idea, but is often very difficult. Data seldom fits a simple pattern perfectly and we must constantly worry about what trends are "real" in the data, what trends are due to temporary changes in the situation and what trends are created by our human desire to see patterns, even when there are none. We will return to these problems when we discuss probability and statistics.

The second idea is to make a deterministic model of how the population changes using our knowledge of the biology of the species. The model has to be simple enough for us to use and understand, but complete enough to include enough of the major factors governing population to give reasonable predictions.

For now we follow the second idea and construct models based on some (simple) assumptions about biology. Of course, combining both model building and data analysis–using the data to motivate and check the assumptions and using the models to tease out trends in the data–is more powerful than either technique by itself.

Think of this section as practice building models for physical world and seeing what kinds of behavior simple models can predict. The "hidden" agenda is to use some of the functions we have seen in our zoo.

1.1 Exponential Growth Models

As fits our basic outline, we start by making a simple, abstract model of the growth of a population. We are guided by a principle called "Occam's Razor" which states that a model (or explanation) should be the simplest possible model that "works". That is, we do not want to add complication unless we must to match reality.

So, consider a small population of some species let loose in a large area. For example, in October 1859, Thomas Austin released 24 rabbits on his farm in Australia (at least according to Wikipedia). This population eventually grew to over 600 million.

We let t represent time measured in years. If we were considering a population of whales we might measure time in decades while for bacteria, we would measure time in hours or minutes. We let $P(t)$ be the population at time t. Again, we might measure P as number of individuals (for whales), or thousands or millions of individuals (for rabbits or people). We could also let P represent a population density. That is, we could let P be the number of rabbits per square kilometer or square meter. So fractional values of P are allowed.

As the notation suggests, we think of $P(t)$ as a function of t. Our goal is to be able to predict a value of $P(t)$ for any time t. We could just write down a guess for a formula of $P(t)$, but that isn't much more satisfying than just guessing the values of $P(t)$. Instead, let's think a (very) little bit about biology.

What do we know about rabbits? Well, rabbits do what they are famous for and beget more rabbits. The more rabbits you have this year, the more baby rabbits you will have next year. So the (very) basic biology of rabbits tells us not what the population of rabbits is, but rather, how the population changes.

Our models for population size will be based on rules derived from how the population changes. Keeping with Occam's Razor, we start with the simplest aspects of population change and make some explicit assumptions about how they work:

1. The number of births between time t and time $t+1$ is proportional to the size of the population $P(t)$ at time t. That is, there is a constant $b > 0$ such that the number of births between time t and $t+1$ is $b \cdot P(t)$.

2. The number of deaths between time t and time $t+1$ is also proportional to the size of the size of the population $P(t)$ at time t. That is, there is a constant $d > 0$ such that the number of deaths between time t and $t+1$ is $d \cdot P(t)$.

Clearly, these are just the most basic assumptions on how any population might change. There are many factors that effect births and deaths. These include external factors, like the weather, and factors that depend on where the species is on the food chain. However, we start simple and ignore all other mechanisms of that can alter the rate of population change.

Now we must turn these assumptions into statements that we can use to compute future populations. While this makes our discussion look more "mathy"–formulas instead of sentences–we emphasize that all we are doing in this step is translating the sentences above into a form we can use for computation.

Putting our two assumptions together, we can say that the population at time $t+1$ is the population at time t plus the births between t and $t+1$ minus the deaths between t and $t+1$. We can write this on one line as

$$\text{Population at time } t+1 = (\text{population at time } t) + (\text{births } t \text{ to } t+1) - (\text{deaths } t \text{ to } t+1).$$

Now our assumptions say that the births time t to $t+1$ are given by $bP(t)$ while the deaths are given by $dP(t)$. Hence, we can shorten the sentence above with notation, writing

$$P(t+1) = P(t) + bP(t) - dP(t).$$

This completes our translation of the assumptions into a formula (and it really is only a translation). We can now use the algebra you learned long ago to simplify things even more. By factoring out $P(t)$ on the right, we get

$$P(t+1) = (1 + b - d)P(t).$$

We can consolidate a bit more by letting

$$k = 1 + b - d$$

and calling k the "growth rate constant". Our model can now be written in the very efficient form

$$P(t+1) = kP(t).$$

If there are more births than deaths ($b > d$), then $k > 1$ and the population at time $t+1$ is larger than the population at time t. If we know the population at time $t = 0$, then at time $t = 1$ we have

$$P(1) = kP(0)$$

and at time $t = 2$ we have

$$P(2) = kP(1) = k(kP(0)) = k^2P(0)$$

and at time $t = 3$ we have

$$P(3) = kP(2) = k(k^2P(0)) = k^3P(0).$$

You can see the pattern developing here. The proof (by induction) shows the general case by noting that if $P(N-1) = k^{N-1}P(0)$, then

$$P(N) = kP(N-1) = k(k^{N-1}P(0)) = k^NP(0)$$

and we have a formula for the population for all future times $N-$ provided we know the population at time zero.

This type of model is called an "exponential growth" population model because the population $P(N)$ is an exponential function. For example, if $P(0) = 24$ and $k = 2$, that is, the population starts at 24 at time $t = 0$ and the population doubles each year, then

$$P(34) = 2^{34} \cdot 24 = 412,316,860,416$$

or the original population of 24 will grow to over 400 billion in only 34 years. This is remarkably fast growth (see Fig. 1).

Note that exponential growth occurs even when k is just slightly greater than one. For example, if $k = 1.01$ and $P(0) = 0.3$ then (see Fig 2)

$$P(N) = 1.01^N(0.3).$$

In order to use this model to predict future populations, we need two things. First, we need the initial population $P(0)$. This can actually be the population at any time since we get to decide when $t = 0$, that is, we decide when to start the clock. We also need the value of k.

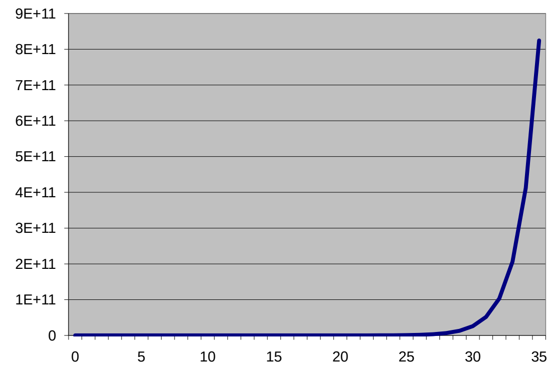

Figure 1: Exponential growth with $k = 2$, $P(0) = 24$

1.1.1 Predicting world population

Suppose we want to predict the world population, say starting in the year 1000 and going into the future, that is, we let $t = 0$ be the year 1000 and we are interested in $P(t)$ for $t \geq 1001$. Since there are a lot of people, we use units of one billion people. So saying $P(0) = 0.3$ means that in the year 1000 there were about $300,000,000$ people.

Now, what value of k do we pick? We see right away possible problems using the exponential growth model. Average life spans and birth rates have changed a great deal over the past 1000 years, so choosing just one value of k is a huge simplification. Noting that much of the increase in life span has happened in the last 100 years, we make a guess (and its just that) of a life span of 50 years, so guess a death rate of $1/50 = 0.02$ percent of the population per year.

Birth rate is harder to estimate and has fluctuated due to advances in health care and social norms. Half the population is women and each woman spends half to one third of her life in child bearing years. We make an estimate of about 1/10 of the women in child bearing years have a child in a given year (this is the biggest guess), then an estimate for birth rate of $(1/2) \cdot (1/2) \cdot 1/10 = 1/40 = 0.025$.

Hence, we estimate our growth rate constant as

$$k = 1 + \frac{1}{40} - \frac{1}{50} = 1 + 0.025 - 0.02 = 1.005.$$

So we get a population growth prediction in year N of

$$P(N) = 1.005^N \cdot 0.3.$$

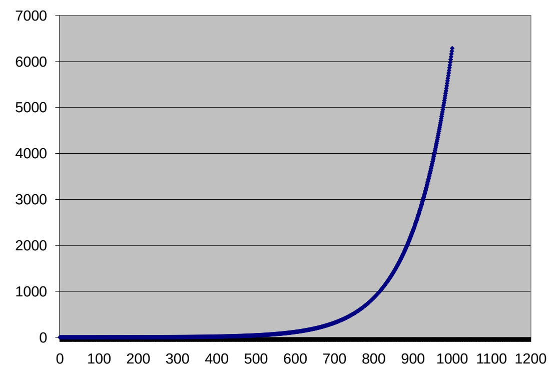

Figure 2: Exponential growth with $k = 1.01$, $P(0) = 0.3$

This gives the graph below and the prediction that the population in the year 2010 ($t = 1010$) should be about 41 billion.

Luckily, this is larger than the actual population of about 6 billion. Our estimate of k must be too high. If we take $k = 1.003$ then the model predicts a population in 2010 of about 5.8 billion, which is a lot more reasonable.

1.2 Criticism of the Exponential Growth Model

As noted above, the use of a constant growth rate constant k is the most serious assumption in this model. For human populations improvements in public health, wars, changes in social attitudes can make a large difference in k.

This does not mean that the exponential growth model is useless–it just means that we have to be careful where and how we use it. For the example above, it tells us that for most of the last thousand years, the growth rate constant must have been very small. We are forced to re-examine our assumptions about birth and death rates. A small population in a large environment under fairly constant conditions will probably follow an exponential growth model fairly accurately, at least until the population becomes too large.

The moral is: There is no magic answer and no substitute for careful thought when building and evaluating models.

1.3 Another View of the Exponential Growth model

Before looking at more generally applicable population models, we need to use what we know about functions to get a different view of the exponential growth model.

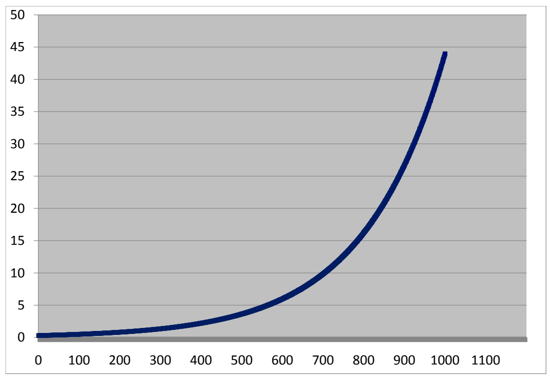

Figure 3: Exponential growth with $k = 1.005$, $P(0) = 0.3$

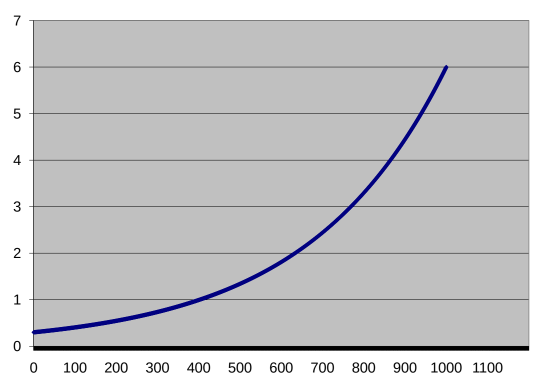

Figure 4: Exponential growth with $k = 1.003$, $P(0) = 0.3$

So far we have only drawn graphs of the population $P(t)$ as a function of time t. That is, t is on the horizontal axis and $P(t)$ is on the vertical axis. A completely different way to visualize this same model is to draw the graph of the relation ship between the population at time t and the population at time $t+1$. If t is in years, then we use the population this year, $P_{\text{this year}}$, along the horizontal axis and the population next year, $P_{\text{next year}}$, along the vertical axis. Our model states that

$$P_{\text{next year}} = k \cdot P_{\text{this year}}$$

This is the equation of a line through the origin with slope k (see Fig.5).

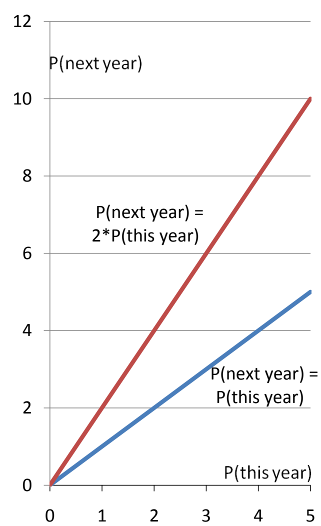

Figure 5: Graph of the exponential growth model with $P_{\text{This year}}$ on the horizontal axis and $P_{\text{next year}}$ on the vertical axis. Here $k = 2$.

While this is just basic graphing of functions, we are actually doing something pretty sophisticated. We now have two ways to graph or picture the same model–the "time series" where we graph $P(t)$ versus time t, and the graph of the model equation graphing $P_{\text{next year}}$ against $P_{\text{this year}}$. Each of these graphs can be used to tell us something about what the model predicts.

For example, the graph of $P_{\text{this year}}$ vs $P_{\text{next year}}$ immediately tells us the the population next year will be greater than the population this year except when the population is zero. This is because the line giving $P_{\text{next year}}$ as a function of $P_{\text{this year}}$ is above the diagonal where $P_{\text{next year}} = P_{\text{this year}}$. Moreover, as the population this year gets larger, the increase to the population next year gets larger.

Which of these two graphical representations of the model we use depends what we want to learn about what the model predicts. It is like looking at the body of an elephant or the DNA of an elephant. They give similar information, but in a very different forms. If we want to see what the model predicts for the population far in the future for a particular initial population $P(0)$, then we look at the graph with time t on the horizontal axis and $P(t)$ on the vertical axis. If we want to visualized the model directly, seeing how different populations change in a year, then we look at the graph with the population this year on the horizontal axis and the population next year on the vertical axis, which allows us to predict one year in the future for any P value. Being able to move between these two pictures is a very useful skill which we study next.

2 Exponential Growth and Harvesting

The case of rabbits in Australia is one of the best known and one of the most dramatic cases of exponential growth of an introduced invasive species. Sadly, it is not the only case–other examples include cane toads in Australia, Kudzu in the southern U.S., and zebra muscles in the midwestern U.S. (and recently in western Massachusetts).

What seems a harmless, or even beneficial species from another area of the world, can become a pest or weed very quickly when there are no natural controls on its population growth. An example in the news lately is the Asian or silver carp which was imported to the U.S. to clean commercial fish farm tanks. After their escape during a flood to the lower Mississippi, the carp spread north and now been caught in Lake Michigan. These carp eat plankton voraciously cutting off the food chain for native species. They also have the annoying habit of jumping out of the water when disturbed by boats. (You can find videos of this on youtube–search jumping asian carp. A more thoughtful video on this invasive species is at `http://www.youtube.com/watch?v=oii4U3cQx_E`) Expect to hear a lot more about these fish as they spread through the great lakes.

Of course, not all invasive species are dangerous pests–many of the foods we enjoy and grow have been imported from other parts of the world. Some ecologists have argued recently that a fanatical attack on every introduced species is not justified. This brings up a difficult question of what really is “natural” and how should we best preserve nature (or is our habit of moving plants and animals around really part of nature?)

On the other hand, some introduced species really are annoying or dangerous (e.g., think of West Nile virus). Once a species is recognized as a pest, attempts are made to control its growth. Typically, these include attempts to “harvest” the species, that is, remove as many as possible from the environment.

2.1 One More Feature of Exponential Growth

Before moving on to more complicated population models, let's return for a moment to our original model of rabbits and make one more important observation about this model.

For $k = 2$ (doubling of the population each year) and $P(0) = 24$, we saw that after 34 years,

$$P(34) = 2^{34} \cdot 24 = 412,316,860,416.$$

But what if the initial count had been off by just one rabbit? What if $P(0) = 25$ instead of 24? Then

$$P(34) = 2^{34} * 25 = 429,496,729,600,$$

which is a difference of $429,496,729,600 - 412,316,860,416 = 17,179,869,184$ or over 17 billion rabbits. That is a lot of rabbits!

The fact that a tiny error in $P(0)$ makes a huge difference in the prediction after a few years is troubling. The birth or death of one extra rabbit can, after a few years, make a huge difference in the precise quantitative prediction of the model. We say that an initial "error" between $P(0) = 24$ and $P(0) = 25$ can grow exponentially, just like the population.

This does not mean the exponential model is useless We say the exponential model predicts a population explosion. If there are hundreds of billions of rabbits around, an extra 17 billion plus or minus is not too big a concern. We will see later that this expnonetial growth of error can have huge consequences for other models and is the basis for "chaos theory".

2.2 Model of Exponential Growth with Harvesting

As our next model, we adjust the exponential growth model to add the effect of harvesting. This is an interesting and important topic both for controlling invasive species and for managing useful wild populations, but we also have a hidden agenda. At the end of the last section we saw that there are two ways to "picture" the exponential growth model. That is, there are two different graphs that we can draw that contain all the information about the model. They are the graph of the population as a function of time and the graph of the population next year as a function of the population this year. In this section we study how these two views of a model are related and how we can use both pictures to make predictions about the future from the model.

We start with the same notation and assumptions we had in the last section. That is, t is time (which, for convenience, we say is measured in years), $P(t)$ is the population at time t measured in some convenient units. For the exponential model, we assume that the population only changes because of births and deaths and that the number of each of these is proportional to the total size of the population. Our fundamental equation is

$$P(t + 1) = kP(t)$$

or

$$P_{\text{next year}} = kP_{\text{this year}}$$

where k is the growth rate constant. As long as $k > 1$, and the initial population $P(0)$ is bigger than zero, the population will grow exponentially,

$$P(N) = k^N P(0).$$

We picture this below for $k = 1.5$. Fig. 6 is the graph of the population next year as a function of the population this year. Fig. 7 is a typical graph of the growth of a particular population where $P(0)$ is chosen to be 0.3 (so here we are measuring P in thousands or millions of individuals or by density, individuals per square kilometer, so that decimal numbers for population make sense). Note that to produce Fig. 7 we need to specify both k and $P(0)$– this graph changes if $P(0)$ is adjusted.

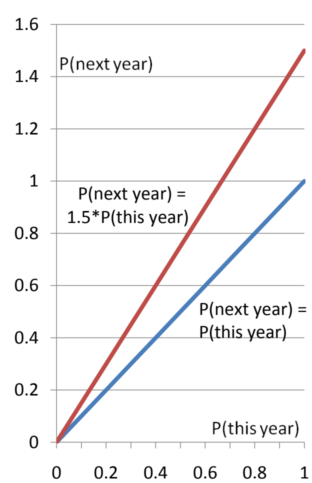

Figure 6: Graph of the exponential growth model with $P_{\text{This year}}$ on the horizontal axis and $P_{\text{next year}}$ on the vertical axis. Here $k = 1.5$.

Now we add the effect "harvesting" to the exponential model. By harvesting we mean the removal of members of the population. The simplest way to manage a useful population is to give out a certain predetermined number of licenses (hunting licenses or catch limits for fishing or permits for logging, etc.) When trying to eliminate a pest or weed population, as many individuals as possible are removed and the limiting factor is the amount of money

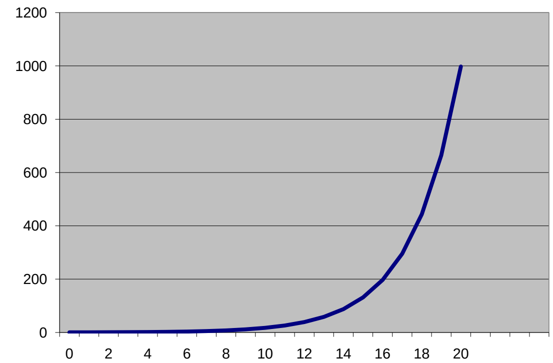

Figure 7: Graph of the exponential growth model with time t on the horizontal axis and population $P(t)$ on the vertical axis. Here $k = 1.5$ and the initial population is $P(0) = 0.3$.

available. In either case, we assume that the number of individuals removed each year is a constant which we call H. Also, for simplicity, we assume H remains constant from year to year.

Our new model can now be written

$$P_{\text{next year}} = kP_{\text{this year}} - H.$$

We are assuming that the harvesting does not effect the growth rate constant k (individuals of the species reproduce just as effectively as before), so the only change in the new population model is the $-H$ term. To see how this changes things, let's pick particular numbers. Say $k = 1.5$ as above and let's take $H = 0.2$ and graph the population next year as a function of the population this year (see Fig. 8).

Note that the only difference between Fig.8 and Fig. 6 for the exponential model, is that the line is pushed down. The "vertical intercept" is now at -0.2, while the slope k, the same as above.

2.3 What Does This Model Predict?

Taking $k = 1.5$ and $H = 0.2$, we compare the predictions of the exponential growth model,

$$P_{\text{next year}} = 1.5P_{\text{this year}}$$

to the exponential growth with harvesting model,

$$P_{\text{next year}} = 1.5P_{\text{this year}} - 0.2,$$

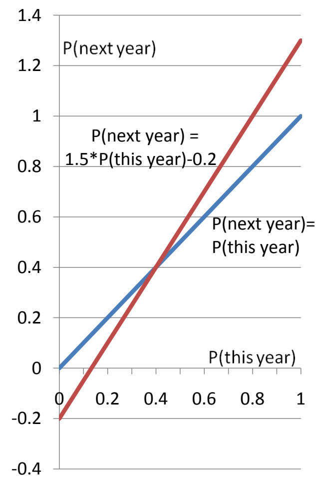

Figure 8: Graph of the exponential model with harvesting with $k = 1.5$ and $H = 0.2$, along with the diagonal.

using the same initial populations. If we start with $P(0) = 0.3$, then for the exponential growth model, we have already seen that

$$P(N) = 1.5^N 0.3.$$

The oredictions of the model with harvesting is more difficult to compute. Let $P_H(t)$ be the population at time t for the harvesting model. Then we are given that $P_H(0) = 0.3$. To compute $P_H(1)$, we compute

$$P_H(1) = 1.5 \cdot P_H(0) - H = 1.5 \cdot 0.3 - 0.2 = 0.25,$$

$$P_H(2) = 1.5 \cdot P_H(1) - H = 1.5 \cdot 0.25 - 0.2 = 0.175,$$

and

$$P_H(3) = 1.5 \cdot P_H(2) - H = 1.5 \cdot 0.175 - 0.2 = 0.0625.$$

Finally,

$$P_H(4) = 1.5 \cdot P_H(3) - H = 1.5 \cdot 0.0625 - 0.2 = -0.10625.$$

What does this mean? The population decreases from years zero to one, one to two and two to three. In year four the population has gone negative. This isn't “physically realizable”, but in order to become negative, $P_H(t)$ must have gone through a population of zero at some

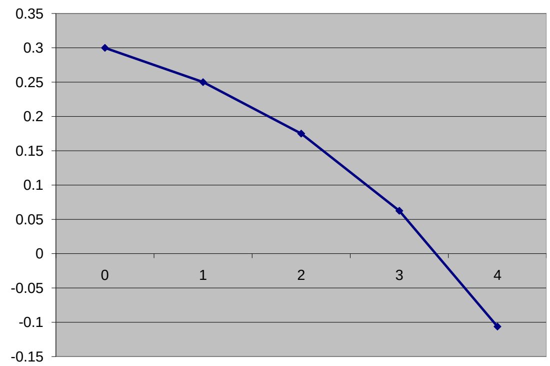

Figure 9: Population as a function of time for the exponential model with harvesting for $P(0) = 0.3$ with $k = 1.5$, $H = 0.2$.

time between $t = 3$ and $t = 4$. So a negative population is interpreted as extinction (see Fig. 9).

If this were an invasive species, this would be good news. For $P_H(0) = 0.3$, harvesting at a rate of 0.2 per year is enough to drive this species extinct in four years.

While there is not anything difficult involved in computing $P_H(N)$, it is tedious. We were lucky that the population went extinct fairly quickly. If we take $P_H(0) = 2.0$, and repeat the process above to compute the predicted populations

$$P_H(1) = 1.5 * P_H(0) - 0.2 = 1.5 * 2.0 - 0.2 = 2.8,$$

that is, the population has grown. Future populations continue to grow and we must do a lot of arithmetic to compute the precise prediction. Comparing the population predictions with and without harvesting, we see very similar exponential growth in both cases (see Fig. 10).

For the exponential growth model, there is a formula for $P(N) = k^N P(0)$. We can compute the population in year N directly from $P(0)$. For the exponential growth model with harvesting, to compute $P_H(N)$, we need to compute all the years from $t = 0$ to $t = N-1$ before we can compute $P_H(N)$.

2.4 Avoiding the arithmetic

We would like to be able to predict the long-term behavior of the population for the harvesting model for any initial population without having to do an exorbitant amount of arithmetic.

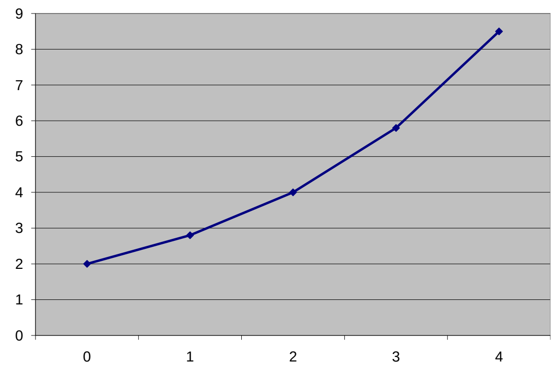

Figure 10: Population as a function of time for the exponential model with harvesting for $P(0) = 2$ with $k = 1.5$, $H = 0.2$.

The key to doing this is to look carefully at the graph of the population this year vs. the population next year.

Given the population this year, $P_H(0)$, we can obtain the population next year $P_H(1)$, by starting on the horizontal axis at $P_H(1)$, going vertically to the graph, then going horizontally to the vertical axis. The point on the vertical axis is $P_H(1)$.

We have been putting the diagonal $P_{\text{next year}} = P_{\text{this year}}$ on our graphs for reference, now we can use the diagonal to help describe the behavior of the model. Note that the graph for the model crosses this diagonal in exactly one point. If the population this year is small enough, then the graph for the model is below the diagonal. This means that the population next year is smaller than the population this year (the graph of the model is below the diagonal for $P_{\text{this year}}$ small). If the population this year is sufficiently large, the graph for the model is above the diagonal, so the population next year is larger than the population this year.

The dividing point between these two behaviors is the point where the graph of the model crosses the diagonal. This is the point where the model predicts that the population next year equals the population this year. Such a point is called a “fixed point”, since the population stays fixed from year to year. We can compute the exact location of this point by noting that this point satisfies both equations

$$P_{\text{next year}} = 1.5P_{\text{this year}} - 0.2$$

and

$$P_{\text{next year}} = P_{\text{this year}},$$

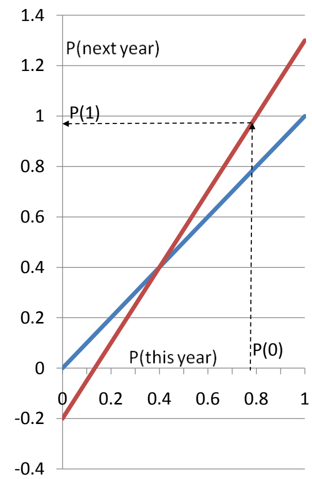

Figure 11: Graph of the exponential growth model with harvesting for $k = 1.5$, $H = 0.2$.

so we solve

$$P_{\text{this year}} = 1.5P_{\text{this year}} - 0.2$$

for $P_{\text{this year}}$. This occurs at $P = 0.4$. So if $P_H(0) < 0.4$ then the population dies out, but if $P_H(0) > 0.4$ then the population grows. Eventually, it grows like the exponential growth model

2.5 Types of functions

The exponential growth model with harvesting gives us a new view of what kinds of functions can occur by using models and gives us two different ways to look at the same model. For $H = 0$, that is, just the exponential growth model, every non-zero initial condition leads to a rapidly growing population.

For $H > 0$, and $P_H(0)$ sufficiently large, the model still predicts a rapidly growing population.

However, for $H > 0$ and a small initial population ($P_H(0)$ close to zero), the model predicts the population that quickly crashes to extinction.

Finally, for each value of $H > 0$, the exponential growth model with harvesting predicts the existence of a fixed point–that is, the model predicts a population where harvesting and natural deaths are exactly balanced by births, so the population stays the same from year to year. In this case the graph of the population as a function of time is just a constant function.

2.6 The power of a clever idea

Again we see that the power of mathematics comes not in massively complicated equations or hugely elaborate arithmetic. The great ideas in mathematics come when somebody looks at some problem in a new way. The idea of looking at a model by graphing the population this year vs the population next year does not require hard computations, so far our graphs have been lines. However, the idea of drawing this picture and using it to say things about what the model predicts for different initial populations is very useful. We exploit this idea in the next section.

While the problems of population biology can be both very interesting and extremely important (ask anyone who has been knocked out of their boat by a large silver carp), don't forget the bigger picture. We are following the process of modelling–making a model, learning things about the model, then refining the model to do a better job reflecting the situation of the original problem.

3 Limited growth

We know that growth, particularly exponential growth, can not go on forever in a finite environment. For populations with the ability to spread widely (like people) we forget this because the earth is very big and we are relatively small. However, eventually, growth must subside–you just run out of room.

Situations where the limits to growth effect the sizes of populations are not hard to find. Populations restricted to small islands, species whose biology restrict them to the high altitudes of mountain peaks and plants and animals in isolated ponds face these limits relatively quickly. For example, on Lovells and Gallops islands in Boston Harbor, it is hard to walk down a path without encountering a large fluffy rabbit. (By the way, this is a lovely day trip when it is nice out.) These populations are large for the size of the islands and the dynamics of the population is very interesting.

3.1 A model incorporating a limit to growth

To modify the exponential model so that growth does not continue forever, we make the following assumptions

1. The exponential growth model works well for small populations.

2. There is some population size, call it C, such that if the population ever gets to C or above then all the resources are consumed and the next time period the population is zero.

The new parameter C is the absolute upper bound to growth. We will call C the "crash population". If the population reaches C (or above), then the population immediately goes extinct. Presumedly, a population near C would consume almost all the resources, so there would be many more deaths than births and the population would crash to close to zero.

There are many ways to build a model that satisfies these assumptions, but we remember Occum's Razor and try to find a simple model. There are two ways to proceed. First we could try algebra. Since the assumption says that exponential growth is a good model for small populations, our model should look like

$$P_{\text{next year}} = kP_{\text{this year}}$$

when $P_{\text{this year}}$ is small. However, when $P_{\text{this year}}$ is C then $P_{\text{next year}}$ is zero. We can include this in the exponential model by multiplying on the right hand side by a term which is zero when $P_{\text{this year}} = C$, for example,

$$P_{\text{next year}} = kP_{\text{this year}}\left(1 - \frac{P_{\text{this year}}}{C}\right).$$

Note if $P_{\text{this year}}$ is near zero, then $(1 - P_{\text{this year}}/C)$ is near one so the model is near the exponential model, as we require.

We can also construct our new model graphically. Assumption 1 above says that the exponential model does a good job when the population is near zero, so the graph of $P_{\text{this year}}$ vs. $P_{\text{next year}}$ should look like the exponential model near $P_{\text{this year}} = 0$. That is, like a straight line going through the origin with a slope bigger than one (see Fig. 12).

Assumption 2 says that for $P_{\text{this year}}$ near the value of the crash population, C, the value of $P_{\text{next year}}$ must be near zero. When $P_{\text{this year}} = C$ then $P_{\text{next year}} = 0$. Putting these two requirements on the graph, we get the picture in Fig. 12.

What happens when $P_{\text{this year}}$ is between zero and C? We fill in the graph in a simple way with a smooth curve, say a nice parabola. This is exactly the kind of graph we get when we plot the function

$$P_{\text{next year}} = kP_{\text{this year}}\left(1 - \frac{P_{\text{this year}}}{C}\right).$$

This model is called the "Discrete Logistic model" of population growth in a limited environment. Since negative populations don't make any sense, we usually add the requirement that for $P_{\text{this year}}$ larger than C, the population next year is zero (i.e., extinct).

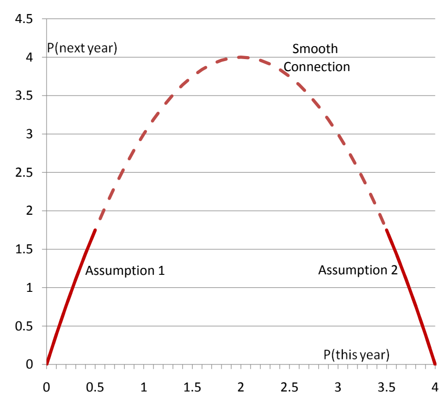

Figure 12: Building the limited growth model from the two assumptions.

3.2 What does this model predict?

To see what kinds of population dynamics this model predicts, we look at some specific examples. Suppose we are counting the population of thousands of rabbits on a small island. So we will count rabbits in units of 1000, i.e., $P = 1$ means a population of 1000 rabbits, etc.

Suppose for this island, the crash population (the population at which the rabbits eat everything an immediately go extinct) is 4000, or $C = 4$. If $P_{\text{this year}}$ is 4 or larger, then next year the population will be extinct ($P_{\text{next year}} = 0$).

We try a number of different values of the growth rate constant k.

3.2.1 Small k

We start with a relatively small value of k, say $k = 1.5$. Since $k > 1$ the population grows quickly when it is small

We look first at the graph of $P_{\text{this year}}$ vs. $P_{\text{next year}}$ (see Fig. 13). This graph shows that there are fixed populations at $P = 0$ (extinct is forever) and for P near 1.33. For populations below 1.33 the population next year will be larger. For populations just above 1.33, the population next year will be slightly smaller.

If we start with an initial population, of $P(0) = 0.2$ then tedious computation (or Excel) shows us that in subsequent years the population increases, but levels off at the fixed point $P \approx 1.33$. If the initial population is large, say $P(0) = 3.95$ (very near the crash population of 4), then initially the population drops to close to zero. Then it grows slowly toward the fixed point of $P = 1.33$

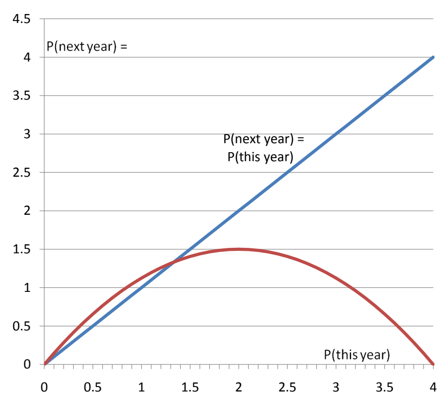

Figure 13: Graph of the Discrete Logistic model for $k = 1.5$.

In fact, no matter where you set the initial population $P(0)$, in subsequent years the population tends to the fixed population $P \approx 1.33$.

This is a new type of behavior for functions and it agrees with our guess about what might happen in a limited environment. At first a small population grows, but eventually the limits to growth "kick in" and the population settles to a stable fixed value.

3.2.2 Large k

Suppose our population of rabbits is extremely prolific if the population is small–assume $k = 4$. Small populations will almost quadruple in size after a single year, so we expect that a small population will grow very quickly. The graph of $P_{\text{this year}}$ vs. $P_{\text{next year}}$ still has the same shape as before, but the slope is much greater near $P = 0$. There is still a fixed point just but now it is much larger, near $P = 3$, and it occurs where the graph is decreasing (see Fig. 15).

If we look at the prediction of this model for, say, $P(0) = 0.2$, we see an entirely new, and surprising, type of function. The population rises and falls without any particular pattern. The only things we can say for sure is that if the population is very small, then it will increase quickly and if the population is near $P = 4$, then it will crash to near zero (see Fig. 16)

3.3 A Bigger Surprise

There is something even more shocking about this model. Suppose we change the initial population just a tiny amount from $P(0) = 0.2$ to $P(0) = 0.201$ (or one more rabbit). The predictions of the model look very similar when graphed (see Fig. 17). However, if we

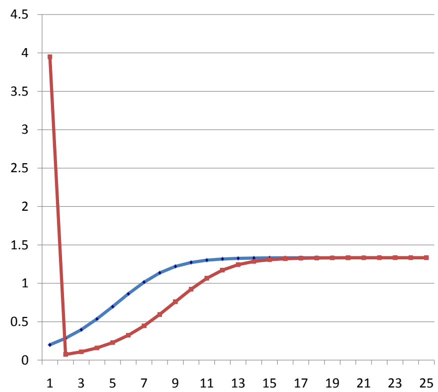

Figure 14: Population predictions for $P(0) = 0.2$ and $P(0) = 3.95$ for the Discrete Logistic model with $k = 1.5$.

graph the predictions for $P(0) = 0.2$ and $P(0) = 0.201$ on the same graph we see something shocking. The two populations evolve almost the same way for a few years, but by year 8 we can see a significant difference in the populations. By year 12, the predictions are completely different (see Fig. 17).

This is called "sensitive dependence on initial conditions" and is a hallmark of what has come to be called "chaotic dynamics" in a model.

Chaos is really shocking. Our model is simple and completely deterministic, but a tiny change in initial conditions radically changes the predictions of the model after only a few years! If one extra rabbit is born or dies, or if our initial count is off by only one, our predictions will be completely different in only a few years.

But wait–you should have that mysterious feelng of deja vu–that mysterious feeling of deja vu. The exponential model also had the property that a small change in initial conditions lead to a a large discrepancy in prediction. However, this large discrepancy wasn't so noticable because the population was so large.

In fact, the same phenomenon as in the exponential growth model is happening here. The exponential growth of small populations quickly makes any small error grow. Populations under this model don't just grow forever, but rise and crash, this error can alter the timing of the crashes. Two nearby initial populations can lead to predictions for a particular time in the future where one population is large (near 4) and the other is small (near 0).

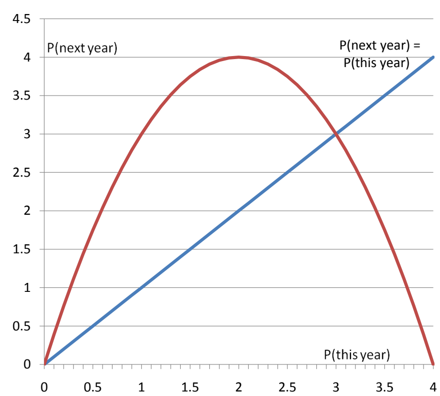

Figure 15: Graph of the Discrete Logistic model for $k = 4$.

3.4 A Glass Half Full

How you react to this observation depends on if you are a "glass half full" or "glass half empty" kind of person. On the one hand, you might say that this makes the model worthless because we can never get the initial value exactly right or guarantee that there are not any tiny external effects that are quickly magnified.

On the other hand, one of the fundamental mysteries of our world is how things got so complicated. How can we possibly "understand" such complicated behavior? Won't the explanation be at least as complicated? Remarkably, the Discrete Logistic model is really pretty simple and yet it displays very complicated (even "chaotic") behavior. If a population following the simple Discrete Logistic model can make predictions of very complicated behavior, perhaps other things in nature that look like they are extremely complicated arrise from simple rules. There is hope of understanding the rules that govern our complicated, chaotic world.

The proper response to a model exhibiting this sort of behavior, that is, sensitive dependence on initial conditions, is to be more careful which questions we ask. For example, for this Discrete Logistic model with $k = 4$, we see that while any tiny error in initial condition changes the value of future population predictions. We can confidently predict that the population will rise until it gets close to the crash population, then crash and start to rebuild. The predictions of the Discrete Logistic model for $P(0) = 0.2$ and $P(0) = 0.201$ for $P(20)$ are very different, but if we take the average population over a long period of time, we get almost the same value for both initial conditions.

One of the classic examples of a chaotic system is the weather. It isn't reasonable for us to expect an accurate weather prediction more than a few days in the future because the

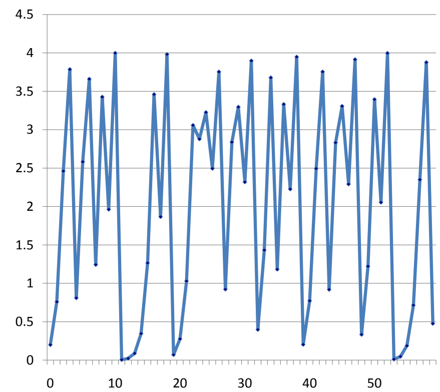

Figure 16: Population predictions for $P(0) = 0.2$ for the Discrete Logistic model with $k = 4$.

weather displays the same sort of sensitivity to initial conditions that the Discrete Logistic model does (on a larger scale). In fact, it has been said, only slightly tongue-in-cheek the the decision of a butterfly in Brazil to flap its wings an extra time can effect the weather in New York a few months later. However, this does not mean that we can't predict the future average weather. Even during a cold snap in January, we confidently predict the average temperature will be much higher in August–so predictions about climate change should be taken seriously even if a prediction of rain a week from Monday is suspect.

3.5 A final comment

All the mathematics you learned in high school was developed by mathematicians that share the following characteristics. They are male, they are dead (and have been for at least 200 years) and they are probably European. (If not European, then they have been dead for at least 500 years.)

But mathematics is still alive and growing–the material above is a great example. It is an active field of research no older than your parents. Those in the field are not entirely European– almost all other continents are all represented. Even better, you might see the person who gave the best accepted definition of a "chaotic" system, Professor Robert Devaney, walking down Commonwealth Ave. talking to Prof. Nancy Kopell, one of the great names in applying these ideas to mathematical biology.

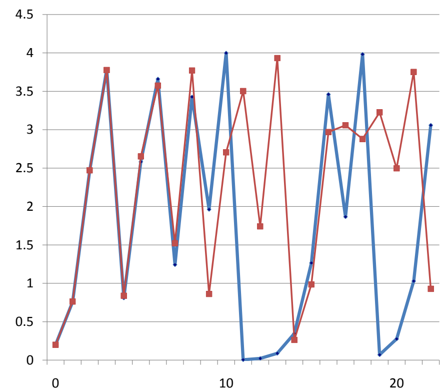

Figure 17: Population predictions for $P(0) = 0.2$ and $P(0) = 0.201$ for the Discrete Logistic model with $k = 4$.

Exercises:

1. Suppose a species of bacteria in a friendly environment, reproduces every twenty minutes by splitting in 2. (So if you start with 1 bacteria, after 20 minutes you hvae 2, after 40 minutes you have 4 (each of the 2 splits) and so on.)

   Let $P(N)$ be the number of bacterial at time N with time measured in hours.

   (a) How is $P(N+1)$ related to $P(N)$ (i.e., what is the model for how the population changes.)

   (b) If you start with $P(0) = 1$ bacteria, how many will you have after two hours?

   (c) If you start with $P(0) = 3$ bacteria, how many will you have after two hours?

2. Ideas and rumors sometimes spread very quickly. Suppose someone starts a rumor and it is so interesting that each person who hears the rumor starts calling friends to tell them the rumor. Suppose it takes 1 minute to tell a friend the rumor. Of course, once they hear the rumor, they start telling their friends and so on.

   (a) If one person starts the rumor, how many people will know the rumor after 1 minutes, 2 minutes, 10 minutes, 1 hour, 2 hours and 3 hours.

   (b) If $R(t)$ is the number of people who know the rumor at time t measured in minutes, what it the relationship between $R(t+1)$ and $R(t)$?

(c) While this might be a good model for the initial growth of a rumor, why is it not a good model after 3 hours? Explain how you know the model can't be accurate and what goes wrong in your assumptions made in building the model that make it not work.

3. Suppose a population of rabbits follows the exponential growth model

$$P(t+1) = kP(t)$$

where t is time in years and $P(t)$ is the population at time t. Suppose the popultion increases from 4000 to 130,000 in 6 years, (that is $P(0) = 4000$ and $P(6) = 130,000$). What is the value of k. (Hint: We know how to express $P(6)$ in terms of k and $P(0)$. You can use trial and error or, if you remember some other properties of logs, you can solve algebraically–either way is fine.)

4. Using the value of k you found in Exercise 1, what harvesting rate H in the exponential model with harvesting

$$P(t+1) = kP(t) - H$$

has $P = 4000$ as a fixed point? (Hint: Again, this is a little algebra. Remember that a fixed population P_{fixed} has the property that if $P(t) = P_{\text{fixed}}$ then $P(t+1) = P_{\text{fixed}}$ also, so

$$P_{\text{fixed}} = P(t+1) = kP(t) - H = kP_{\text{fixed}} - H,$$

and we know k from Exercise 1 and $P_{\text{fixed}} = 4000$ is given, so solve for H.)

5. Macquarie Island is a small island between Australia and Antarctica. Before 2000, it was populated with 4000 rabbits and 160 feral house cats (both introduced species), It is also used by various species of sea birds for nesting. Some of the bird species that use the island are rare so it was decided that the cats should be "removed" (i.e., killed).

   However, cats also eat rabbits. Once the cats were removed, the rabbit population exploded to 130000 by 2006. How many rabbits did each of the cats eat per month before in order to keep the population at 4000?

   (You can find more information at

   `http://www.newscientist.com/article/dn16414-rampant-rabbits-trash-world-heritag`
   `html`

   and

   `http://www.newscientist.com/article/mg20126913.200-blunder-let-bunnies-devastat`
   `html`

   and a web cam of Macquarie Island at

http://www.aad.gov.au/asset/webcams/macca/default.asp.)

Read the article in Sunday's (Jan 31) New York Times about the problems with rabbits on Robben Island (you can find it at

http://www.nytimes.com/2010/02/01/world/africa/01safrica.html?scp=1&sq=rabbit&st=cse).

There is a detail that should catch your eye that indicates that the efforts to control the rabbits are doomed. What is this detail?

(6) Use whatever technology you have available (a spread sheet program like Excel is best), to compute $P(1), \ldots, P(50)$ for the Discrete Logistic model

$$P(t+1) = kP(t)\left(1 - \frac{P(t)}{4}\right)$$

with $P(0) = 0.2$ and $k = 2.5, 2.6, 2.7, \ldots, 3.9, 4.0$. Comment on the patterns in these numbers–that is, how would you describe the behavior of the population? (For example: "For $k = 3$ the population that oscillates between ≈ 2.766 and 2.560.).