

## Student Background Readings for Bug Dynamics: The Logistic Map

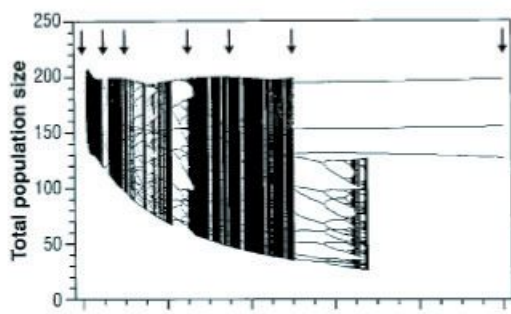
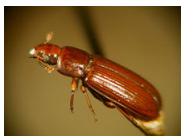


Figure 1 The population as a function of a growth rate parameter observed in the experiment of [Bugs]. Graphs such as this are called bifurcation diagrams in reference to the splitting (pitchforks) of a population into two.

### 1. Observations

We previously explored population growth and decay without limits. These are simple mathematically, but lack some of the limits that the real world often places on systems. For example, many animal species appear to have populations that remain essentially constant from year to year. For instance, the number of frogs in a pond might be 30 one year and 32 another, which is essentially constant. Clearly, a constant population number means that the number of births in a year (the birth rate) equals the number of deaths in a year (death rate). While births obviously arise from mating, deaths may arise from various causes such as aging, disease, predation, environmental stress and starvation. If there were no deaths, and if the number of births in a year were *proportional* to the number of animals present, then the population would increase exponentially with no limit (we describe exponential behavior in another module). This actually happened, to the eventual detriment to the Australian continent, when a marine toad was introduced into Australia to eat beetle grubs.



Usually, the increase in deaths as a population gets larger limits the growth of a population, and often a maximum level is reached that proves to be rather stable. How can we represent the growth or change in the population in order to predict its change in the future?

### 2. Problem

The flour beetle *Tribolium* pictured here has been studied in a laboratory in which the biologists experimentally adjusted the adult mortality rate (number dying per unit time). For some values of the mortality rate, an equilibrium population resulted. In other words, the total number of beetles did not change even though beetles were continually being born and dying. Yet, when the mortality rate was increased beyond some value, the population was found to undergo periodic oscillations in time. Under some conditions, the variation in population level became *chaotic*, that is, with no discernible regularity or repeating pattern. **Why do we get such different-looking patterns of population dynamics? What general mathematical model could produce both sets of patterns?**

In the words of the scientists themselves:

“The mathematical theory of nonlinear dynamics has led population biology into a new phase of experimental and theoretical research. Explanations of observed fluctuations of population numbers now include dynamical regimes with a variety of asymptotic behaviors: stable equilibria, in which population numbers remain constant; periodic cycles, in which population numbers oscillate among a finite number of values; quasiperiodic cycles, which are characterized by aperiodic fluctuations that are constrained to a stable attractor called an invariant loop; and chaos, where population numbers change erratically and the pattern of variation is sensitive to small differences in initial conditions.”

A population pattern that change radically in time due to small shifts in environmental conditions is considered chaotic. Explaining such behavior is an example of a problem that the traditional algebraic and analytic math taught in high school cannot model, yet for which computers are well suited.

**Your problem** is to develop and test the simplest mathematical model you can think of for a population that contains growth, yet also contains a mechanism to limit growth so that it remains below a maximum value. Once you have this model, you should then explore whether it can produce the types of behaviors described in the paragraph above.

### 3. From Biology to Math

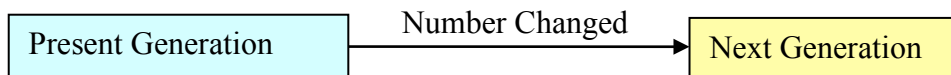
#### 3.1 System Statements, Key Components and Their Relationships

System statements are brief sentences that describe a phenomenon. They define how components of the system relate to each other. We start by determining the **components**. **For the bugs example, the components of the system are bugs and their interactions.** Next we link the components by hypothesizing what might be the relationships (processes) among the components that make them change. This is the process of writing **system statements**. Each person can have slightly different system statements as they *verbally* describe a phenomenon. The main purpose of the system statements is to bring us closer to the mathematical description of a phenomenon. The simpler the system statements are, the easier it will be to convert them into mathematics. An example of system statements for the phenomenon for the bugs system would be:

1. We start with a certain number of bugs that are currently alive, the present generation.
2. In the next generation, the change in the number of bugs due to births and deaths depends on the number of bugs in the previous generation.
3. Births clearly arise from breeding. Deaths arise from factors such as aging, disease and predation. Death rates tend to increase as populations grow, particularly due to increased competition for food and increased rates for disease. Because the change in population arises from both births and deaths, the change will be positive when births outnumber deaths, and negative when deaths outnumber births.
4. We lump births and deaths together into the simple statement that “the population tends not to grow beyond some maximum value”, without any further explanation.
5. We calculate the change in population, add it to the present population, and thus obtain the population for the next generation.

6. We call the *next* generation's population the *present* generation's population, and start the process over again.
7. Once we have a mathematical expression that relates the next generations' population to the present population, we use the computer to predict the population for all latter times.

We can express these statements graphically via the concept map below. What is not visible in the map is how we represent time. We substitute the term "generation" for "population" to include reference to the passing of a time period in which the population changes.



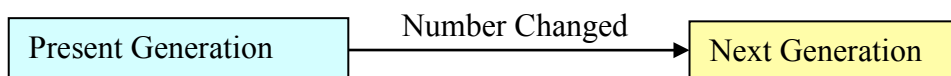
### 3.2 Underlying Theory

We postulate or theorize 1) that a balance between the rates of bug breeding and dying leads to a stable population, and that 2) there is a maximum population number for each set of rates. Specifically, we postulate that the overall rate of change in population decreases as the maximum population is reached.

Note: To keep our model simple, we will not concern ourselves with the actual causes and dynamics of dying, but rather just impose the environmental constraint that there is a maximum number of bugs possible. The effects observed in this simple model should also be present in more complete models.

### 3.3 Building a Concept Map of Model as Prelude to Equations

Concept maps graphically describe the system statements. We are going to break down the process of creating a model, writing mathematical equations, into two steps. First, let us consider the statement "The population changes from one generation to the next".

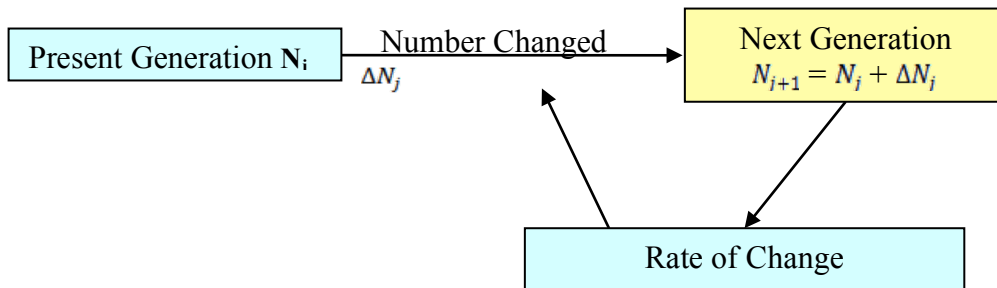


On the left we have a box that represents the number of bugs living now, during the present generation. The generation time differs for different species, with a year being typical for bugs. (For humans it might be 20 years, with the "population" of that generation being the average over the entire generation time). The average number of bugs in the next generation is obtained by adding in the total change, which includes both births and deaths. And since some generations may have more deaths than births, the change can be a negative number.

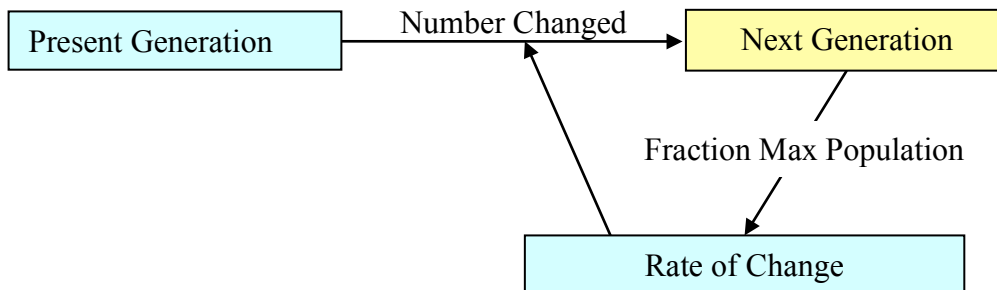
In terms of an equation, let us say the number of bugs we start with is  $N_0$ , that in the next generation it is  $N_1$ , that in the second generation it is  $N_2$ , and so forth. The diagram above states that *present + change = next*. If stated in reverse order, the concept map is *next = present + change*. In terms of symbols, we express the diagram above as the equation

$$(1) \quad N_{j+1} = N_j + \Delta N_j$$

Here  $N_j$  is the number in the present generation ( $j$ -th),  $N_{j+1}$  is the number in the next generation ( $j+1$ ), and  $\Delta N_j$  is the total change that takes generation  $j$  to generation  $j+1$ .



The heart of the model, of course, is what we use for the change  $\Delta N_j$ . We know from our module *Spontaneous and Exponential Decay*, that if the increase in population were proportional only to the number present, then we would get exponential growth or decay. We want to somehow build in the fact that the population has a maximum value. We imagine that the *Total Change* should decrease in magnitude as we get closer to reaching the maximum population number. We might show this graphically, as step two, by indicating that the *Number Changed* depend upon the rate of change (the change per generation), and that the rate changes as we get closer to the maximum population  $N_{\max}$ :



### 3.4 From a Concept Map to a Mathematical Model (With Derivation)

It is often too hard to try to guess the final form of a model all in one fell swoop. So let's start with what we already know, namely our work in the *Spontaneous and Exponential Decay* module, and try to extend it to bug populations. The extension is based on the relations in the concept map above, and essentially adds mathematical symbols to the elements in the figures.

As we did in the *Spontaneous and Exponential Decay* module, we measure time in discrete intervals of  $\Delta t$ , and label each step or generations by a discrete integer  $j = 0, 1, 2, \dots$  :

$$(2) \quad t = j \Delta t$$

Accordingly, the number of bugs present at time  $t = j \Delta t$  is called  $N_j$  :

$$(3) \quad N_j = N(t = j \Delta t)$$

Recall, if the change in the number of atoms during a time interval were a constant  $\lambda$ ,

$$(4) \quad \Delta N_j = \lambda$$

then that number would increase *linearly* with time

$$(5) \quad N(t) = \lambda t$$

Here the proportionality constant  $\lambda$  is called the *growth rate* and has the dimension of *number per unit time*, which is the same as just *per unit time*. If, instead, the change in number  $\Delta N$ , in addition to being proportional to the length of the time interval, were also proportional to the number of species present during the time interval,

$$(6) \quad \Delta N_j = \lambda N_j \Delta t,$$

then, exponential growth results,

$$(7) \quad N(t) = N(0)e^{\lambda t}$$

where  $N(0)$  is the number present at time  $t=0$ . The important point here is that exponential growth results from the change or rate being proportional to the number present.

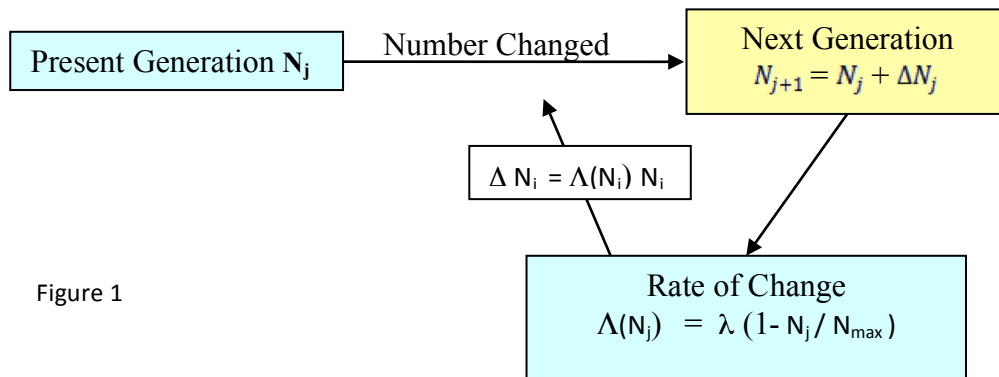


Figure 1

Equation (6) is a good starting model for our model of bug populations. With the change proportional to the number present, we would obtain exponential growth in the number of bugs with growth rate  $\lambda$ . Yet we want the model to contain a mechanism such that growth rate slows down as the number of bugs reaches its maximum  $N_{max}$ , the *carrying capacity* of the environment. And so, as shown in the concept map above, we extend the model by postulating that the growth rate parameter, which we now call  $\Lambda(N_j)$ , is no longer a constant but instead decreases as the number of bugs  $N_j$  gets close to  $N_{max}$ :

$$(8) \quad \Lambda(N_j) = \lambda (1 - N_j / N_{\max})$$

Here  $\lambda$  is still a constant, which can be thought of as a growth rate, while  $\Lambda(N_j)$  is now a function of the variable  $N_j$ , which incorporates births and a population limit. Indeed, if  $N_j$  become greater than  $N_{\max}$ , then Eq. (8) leads to a negative value for  $\Lambda(N_j)$ , which would mean a decrease in the number of bugs (death). Our expression then for the change in the number of bugs in generation  $j$  is

$$(9) \quad \Delta N_j = \Lambda(N_j) N_j \Delta t$$

$$(10) \quad = \lambda (1 - N_j / N_{\max}) N_j \Delta t.$$

The full model, which is also the algorithm we use for the calculation, is then

$$(11) \quad N_{j+1} = N_j + \lambda (1 - N_j / N_{\max}) N_j$$

where we have set  $\Delta t = 1$ , which means that we measure time in units of *generations*.

### 3.5 From a Concept Map to a Mathematical Model (Without Derivation)

In Figure 1 we present a concept map with mathematical representations of each step included. Our goal is to turn this concept map into a mathematical model that can be simulated on a computer using a spreadsheet such as Excel, a programming language such as Python, or a specialized modeling program like Venism. In each case we need to convert the concept map into mathematical statements that we can then use as an algorithm to program a computer.

Let's try to understand every step of this process.

$N_j$ : is the "number of bugs" in our current generation.

$\Delta N_j$ : is the "change in number of bugs" as we go from the present generation into the next generation. This is just the number of bugs born minus the number of bugs who have died.

$\lambda$ : is the growth or birth rate parameter, similar to that in our exponential growth and decay model. However, as we extend our model it will no longer be the actual growth rate, but rather just a constant that tends to control the actual growth rate without being directly proportional to it.

$\Lambda(N_j) = \lambda(1 - N_j / N_{\max})$ : is our model for the effective "growth rate", a rate that decreases as the number of bugs approaches the maximum allowed by external factors such as food supply, disease or predation. (You can think of  $\lambda$  as the growth or birth rate in the absence of population pressure from other bugs.) We write this rate as  $\Lambda(N_j)$ , which is a mathematical way of saying  $\Lambda$  is affected by the number of bugs, i.e., " $\Lambda$  is a function of  $N_j$ ". It combines both growth and all the various environmental constraints on growth into a single function. This is a

good approach to modeling; start with something that works (exponential growth) and then modify it incrementally, while still incorporating the working model.

$N_{j+1} = N_j + \Delta N_j$  : This is a mathematical way to say, “The new number of bugs equals the old number of bugs plus the change in number of bugs”.

$N_j/N_{\max}$ : is what fraction a population has reached of the maximum carrying capacity allowed by the external environment. We use this fraction to change the overall growth rate of the population. In the real world, as well as in our model, it is possible for a population to be greater than the maximum population (which is usually an average of many years), at least for a short period of time. This means that we can expect fluctuations in which  $N_j/N_{\max}$  is greater than 1.

By taking a close look at the concept map, we see that it can be expressed as the mathematical relation giving the change in the number of bugs in the next ( $N_{j+1}$ ) and the present generations:

$$(12) \quad N_{j+1} = N_j + \lambda (1 - N_j / N_{\max}) N_j$$

$$(13) \quad = N_j (1 + \lambda) - \lambda N_j^2 / N_{\max}$$

This is an expression that the number of bugs in a new generation is the sum of the number of bugs in the previous generation and change in bug population between the two generations.

### 3.6 Discussion of Model

Eq. (11) is fairly simple, but because there is an  $N_j^2$  term on the right-hand-side of the equation it is a *nonlinear* equation. As we shall see, that does lead to some interesting behaviors. However, because  $N_{\max}$  is expected to be a very large number, if the bug population  $N_j$  remains small, then the nonlinear term is expected to be small and we should obtain something close to exponential growth. In fact,  $\Delta = 0$  when  $N_j = N_{\max}$ , at which point the population does not change. At the other extreme, when  $N_j$  is larger than  $N_{\max}$ , then  $\Delta$  becomes negative, and we should get *decay* back towards  $N_{\max}$ . So we would expect that the bug population would settle at a stable population, at which point there would be neither growth nor decay. That population should be *stable* since a small variation from  $N_{\max}$  leads to either growth or decay back to  $N_{\max}$ .

Just by looking at Eq. (11) there is no way to know how good a model it is. Being as simple as it is, the model is not expected to be a complete description of the population dynamics of bugs. However, if it exhibits some features similar to those found in nature, then it may well form the foundation for a more complete description. Specifically, the model has no details about the biology of bugs or of the environment, other than the carrying capacity and the birth rate. Nevertheless, now that we have a simple model in hand as Eq. (11), as scientists, we will go ahead and explore its solutions and then compare them to nature.

Equation (11) is a form of what is known as the *logistic map* or equation. It is a *map* because it “maps” the population in one year into the population of the next year. It is “logistic” in the military sense of supplying a population with its needs. It a nonlinear equation because it contains a term proportional to  $N_j^2$  and not just  $N_j$ . The logistic map Eq. (11) is also an example

of discrete mathematics. It is discrete because the time variable  $j$  assumes just integer values, and consequently the variables  $N_{j+1}$  and  $N_j$  do not change continuously into each other, as would a function  $N(t)$ . In addition to the *variables*  $N_j$  and  $j$ , Eq. (11) also contains the two *parameters*  $\lambda$ , the growth rate, and  $N_{\max}$ , the maximum population. You can think of these as "constants" whose values are determined from external sources and remain fixed as one year of bugs gets mapped into the next year. However, as part of viewing the computer as a laboratory in which to experiment, and as part of the scientific process, you should vary the parameters in order to explore how the model reacts to changes in them.

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