

BioModule: LOGISTIC GROWTH

The overall goal of this BioModule is to reinforce the mathematics you are learning in MATH 155 and show how they directly relate to biological material that you learn as part of the curriculum for Biology and related majors here at Colorado State University.

MATHEMATICAL OBJECTIVES (Covers material from sections 2.6, 2.7, 2.9, 3.2, 4.1, 4.5):

1. Review exponential and logarithmic functions through their use in logistic growth
2. Work with biological applications of differentiation
3. Understand the practical use of rescaling for interpretation of mathematical results
4. Initial, conceptual introduction to the Fundamental Theorem of Calculus

BIOLOGICAL OBJECTIVES (Covers material from BZ 220 Introduction to Evolution and LIFE 320 Ecology):

1. Understand the concept of logistic growth in ecology and evolution
2. Develop the biological interpretation of logistic growth models

I. BACKGROUND: WHAT IS LOGISTIC GROWTH?

What is logistic growth? Logistic growth is the growth of some quantity (there are several possibilities) with respect to an independent variable (like time) that can be described by a logistic function or curve. The logistic function describes a sigmoidal or “s-shaped” curve as seen in Figure 1. The main features of the curve are:

- 1) Early on, the rate of change is positive/increasing and approximately exponential
- 2) The rate of change in the quantity next becomes negative/slowing
- 3) Saturation eventually occurs and the quantity stops changing

So, what is this “quantity” that we are talking about?

Logistic growth occurs in a variety of settings. The logistic function and its application to describing growth were first investigated by Pierre Francois Verhulst in 1838. Verhulst used logistic growth in an ecological context to describe the growth of a population experiencing intraspecific competition. In this BioModule, we will focus on logistic growth in ecology and in evolution where it is used to

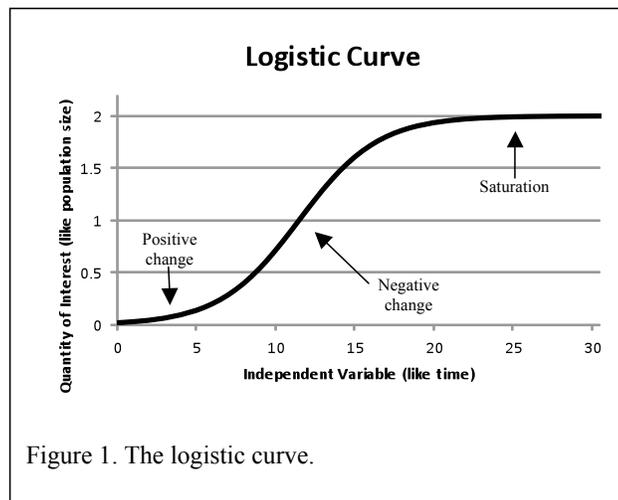


Figure 1. The logistic curve.

describe changes in allele frequencies under natural selection. Other applications occur in neural networks, statistics, tumor growth, autocatalytical reactions and several other fields. While logistic growth ends up being a relatively simple model mathematically and biologically, we will see that it does explain some actual biological observations. Furthermore, simple models like these can and often are expanded into more complicated models that are used to explain more complicated biological systems in real research.

II. THE MODEL: HOW DO WE WRITE IT MATHEMATICALLY AND INTERPRET IT BIOLOGICALLY?

Mathematically: In class, you have mostly worked with discrete time models, difference equations and maps, including the logistic map. In this BioModule, we will discuss a continuous time logistic model. The continuous time model looks like:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K} \right) \quad (1)$$

The left hand side of the equation tells us that we are now working with a differential equation (that's the type of equation we use for a continuous time model). The left hand side describes the rate of change in our quantity, x , per unit of time, t . " dx " and " dt " are often interpreted as being infinitesimally small changes in x and t , hence dx/dt gives us the instantaneous or continuous time change in x . Continuous time models can roughly be related to discrete time models by thinking about the unit of time in the discrete model as being very, very small (i.e., infinitesimally small).

The right hand side of the equation describes exactly what the rate of change in x looks like. It is controlled by two parameters. r is roughly a parameter that controls the rate of growth and K is a parameter that controls the value of the quantity of interest where saturation occurs.

Biologically: In order to understand any results of our analysis of this equation in a biological context, we need to know how to interpret biologically. This same equation can be interpreted in several different ways depending on if we are talking about ecology, evolutionary biology, neural networks or tumor growth. In this BioModule, we will focus on the ecological and evolutionary interpretations of the model.

Ecology: In ecology, the quantity of interest, x , is the population size, e.g., the number of elephants there are in a particular population. So, dx/dt represents the total rate of change in the elephant population's size. We can rewrite Eq. 1 by expanding it, which gives a more intuitive interpretation of the logistic growth equation.

$$\frac{dx}{dt} = rx - \frac{rx^2}{K} \quad (2)$$

When population size, x , is small relative to the parameter, K , then the right hand side of the equation is dominated by the rx term. Like in the discrete time models you've previously seen,

$\frac{dx}{dt} = rx$ describes exponential growth. This helps us with our interpretation of the model. When population size is low, r is the per capita growth rate. In other words, r describes the growth rate per individual when the population size is low, so rx describes the growth of the total population when population size is low. If we look at Fig. 1, we see that the first part of the logistic curve looks like exponential growth because it is when Eq. 1 is dominated by the rx term.

What happens when population size is larger? Then the second term, $-\frac{rx^2}{K}$, becomes more important. First, notice that the negative sign on this term means that it will slow down the rate of growth. We also see a slowing of the rate of growth in Fig. 1 as the population size increases and this term becomes more important. How do we interpret this term ecologically? Well, terms that include x^2 are often interpreted as the rate at which two individuals (e.g., whatever number is in the exponent) encounter one another. Because of the negative effect on growth from this term, we think of it as describing pairwise competition (where two individuals meet and negatively affect one another because of competition for resources, space, etc.). These models are also often described as models of density-dependence (because the growth slows as population density, and hence competition, increases) or intraspecific competition. The ratio r/K describes how intense the intraspecific competition is when individuals meet, and K is usually described as the carrying capacity or the maximum possible size of the population (e.g., where saturation happens).

Evolution: In evolutionary biology, the quantity of interest, x , for this model is the allele frequency in a population. An allele is the particular sequence of DNA at a locus (i.e., gene). A single locus may have multiple possible DNA sequences and each of these is an allele. Under natural selection, we expect that alleles that are more beneficial to the fitness (e.g., reproduction) of an organism will increase in frequency in the population. Alleles that are deleterious or detrimental to fitness should decrease in the population.

A logistic model is used to describe the changes in allele frequency over time for a single locus with two alleles, A and a , for a haploid organism. Remember that a haploid organism has only one complement of chromosomes, as opposed to diploids like humans who have two complements or copies of their chromosomes. The model is:

$$\frac{dx}{dt} = sx(1-x) \quad (3)$$

Where s is a measure of how strong selection is. More specifically, we set the fitness of the most fit allele, say A , at 1, and the fitness of the less fit allele, say a , at $1-s$.

III. SOLUTIONS TO THE MODEL: HOW DO WE FIND THEM MATHEMATICALLY AND WHAT DO THEY TELL US ABOUT BIOLOGY?

When we write $\frac{dx}{dt}$, we're implicitly assuming that x changes with time. In other words, x must be a function of t , $x(t)$, in order to take its derivative with respect to t , which is what $\frac{dx}{dt}$ is saying to do. We often want to know $x(t)$, because this would allow us to predict the quantity of interest (e.g., population size, allele frequency) at any time. $x(t)$ is the solution to equations of the form 1-3. We find the solution using The Fundamental Theorem of Calculus, which relates differentiation and integration, or in this case, the equation describing the rate of change to its solution. This is just a foreshadowing about The Fundamental Theorem of Calculus. You'll learn the details in a later section (4.5).

The solution of Eq. 1 (or Eq. 2 since they are the same) is:

$$x(t) = \frac{x_0 e^{r(t-t_0)}}{1 + \frac{x_0}{K} (e^{r(t-t_0)} - 1)} \quad (4)$$

In order to find the value of x at any point in time, t , we substitute in the value of the parameters, r and K , and the time point of interest, t . t_0 and x_0 are also substituted into the equation and refer to the initial conditions (the value of x at the first point in time you are considering).

IV. FITTING DATA TO THE MODEL: IS IT JUST MATH OR DOES IT MATTER FOR THE REAL WORLD?

Models are used in biology (and most applications) in two main ways. First, models can be used in a purely theoretical sense to help us develop hypotheses for how systems should behave based on first principles. For example, in the application of logistic growth in ecology, we can see that the addition of intraspecific competition changes our prediction (or hypothesis) for how population dynamics should behave. Specifically, we would predict that population size should saturate at some value, K , instead of continuing to grow exponentially (which is the prediction without intraspecific competition).

Second, models can be used to test hypotheses or explain patterns observed in specific systems. For example, if we see a population that seems to have grown to a particular level and then saturated, we might want to test whether there is density-dependent regulation in that population. To do so, we might fit the logistic growth model solution to the observed data, estimate parameters, and see how good the model fits or does at explaining the observed data. If it is pretty good, then density-dependent regulation may be a good explanation for the processes regulating the population.

Logistic growth models are quite simplistic (as we said before), but they do in fact provide good explanations of observations of some real systems. We will see more about this as we do Activities and Problems.