

# Modeling the Growth of Biological Populations<sup>1</sup>

## Population Ecology

The central questions of population ecology relate to the **factors that influence the distribution and abundance of animals and plants**. An important step towards answering these questions has been to develop mathematical models that attempt to predict the growth patterns of populations in different environments. Population ecology modelers construct their models by identifying all relevant variables (often called parameters) needed to predict changes in population size and then by attempting to determine the exact manner in which they interact to explain population growth. The models are then tested in the usual manner -- by seeing if the predictions match the actual behavior of populations. To the extent there is a match, a population ecologist becomes more certain that she understands the factors that actually determine the population's growth.

As an introduction to the field, we will review **two general models of population growth**:

- One for a situation where **resources are essentially unlimited** and therefore **individuals do not compete**
- The other for situations where there are **limited resources** and therefore **members of the population must compete** for these resources.

It shouldn't surprise you to know that population ecology is mathematical in nature. After, models are usually mathematical abstractions of nature! Let's look over some of the main ideas as painlessly as possible and then apply them to populations where resources are or are not limiting. Here are some of the main parameters:

**$N$**  -- the population size (not necessarily the most important parameter, believe it or not). Usually we specify population size in terms of time starting at some arbitrary point. Thus:

**$N_0$**  -- the population size at some arbitrary starting time (time zero)

**$N_t$**  -- the population size at some future time  **$t$**  where  **$t$**  can have any positive value -- for example,  **$N_2$  would** be the population size two time units (whatever they are -- seconds, years, generations, breeding seasons) in the future.

If we take the ratio of the population size in two adjacent time periods (for instance  $t = 0$  and  $t = 1$ ), we obtain the factor by which the population increases during one unit of time. We call this factor lambda,  **$\lambda$** . Thus:

eq. 1. 
$$\lambda = \frac{N_1}{N_0} \text{ or restated in an equally useful way: } N_1 = \lambda N_0$$

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Thus, if a population goes from 100 to 200 in time = 1 unit, then  $\lambda$  is 2; if 100 to 300 then  $\lambda$  is 3, etc.

If  $\lambda = 4$  (a very high number) and the original population is 100, what is it after time 1? After two time units?

Ans: 400, 1600 -- in the second case, the population went from 100 to 400 in time one and then increased by a factor of four again to 1600.

If we are interested in the **average rate of change of a population's size**,  $\frac{\Delta N}{\Delta t}$ , then we can state that:

$$\text{eq. 2.} \quad \frac{\Delta N}{\Delta t} = B + I - D - E$$

where:

**B** is the birth rate (usually the number of individuals or females born per unit time)

**D** is the death rate (number of individuals or females dying per unit time)

**I** is the immigration rate (individuals or females migrating into the population per time) and

**E** is the emigration rate (individuals or females migrating out of the population per time)

there are additional parameters that can be used to calculate B and D (factors such as age-specific mortality rates and age-specific birth rates).

To keep things simple, let's assume that:

$$\text{eq. 3.} \quad I = E$$

and therefore:

$$\text{eq. 4.} \quad \frac{\Delta N}{\Delta t} = B - D$$

Average rates are fine but they have limitations. One is that they implicitly refer to a particular time interval, for example a year. This is fine if the individuals in a population all reproduce at essentially one time during the year. and if deaths occur in a predictable manner. This is in fact the pattern in many species, especially if only adults are counted. But what if reproduction is going on continuously. Is there a way that we can predict the rate of growth at any moment in time (and therefore, we will see, predict the population size at any instant)?

Without getting into how they are estimated, let's define a new series of variables that will be useful in predicting the rate that a population changes in number.

- The instantaneous birth rate **b** is the number of individuals born (usually female offspring per adult (usually female) per instant in time.

- The instantaneous death rate ***d*** is likewise the number of individuals (usually females) that die per instant in time per number of individuals in the population (again, usually per female).

If we wish, we can also define terms ***e*** and ***i*** for instantaneous emigration and immigration rates.

Note that all of these measures (***b***, ***d***, ***i***, and ***e***) all have units of Number/(Number per time) – in other words, **inverse time ( $t^{-1}$  or  $1/t$ )**.

You may be familiar with the idea of instantaneous rates from differential calculus. I will not go into how such rates are calculated. Please just accept the fact that these are instantaneous rates. You will see actual examples of how such rates are calculated in calculus class.

If we once again assume that emigration and immigration rates are equal (eq. 3) then we can define the instantaneous rate of population increase, ***r*** as:

eq. 5             $r = b - d$

and we can write an equation that describes the instantaneous rate of change in population number (usually females),  $\frac{dN}{dt}$ , as:

eq. 6             $\frac{dN}{dt} = rN$

Notice that the units of ***r*** and ***N*** give instantaneous rate of population increase as number per instant in time.

If equation 6 gives the change in a population size over a very short period of time, then if we want to know the size of the population at some point in time  $t$  ( $N_t$ ) we would sum all of the changes in population size over all of the time instants between a starting time ( $t = 0$ ) and finishing time ( $t = t$ ). This is done using the calculus techniques called referred to as integration. If one solves eq. 6 by integration we find that:

eq. 7             $N_t = N_0 e^{rt}$

where ***e*** is the base of natural logarithms (about 2.718) and ***t*** is any time period. Thus, the equation will tell us the population size at time  $t$  starting from its size at some starting time ( $N_0$ ) Although it may seem a bit more formidable than eq. #1, it is actually easier to use and has a number of mathematical advantages. Notice, incidentally, that equation #8 has the same general form as equation #1 ( $N_1 = \lambda N_0$ ) where  $e^r$  is the

factor by which the size of a population changes per individual for any time interval  $t$  akin to  $\lambda$  as the factor by which the population changes per individual for a certain discrete time interval.

Below are the actual steps in the integration – please, **you do not need to know this for this course**. The mechanics of this solution are for your math courses. It is provided only to give you a taste, if you haven't already had one, of the use of calculus in biology.

$$\frac{dN}{dt} = rN$$

collect population and time terms

$$\frac{dN}{N} = rdt$$

integrate the previous equation

$$\ln N_t - \ln N_0 = rt + 0$$

$$\ln \frac{N_t}{N_0} = rt$$

$$\frac{N_t}{N_0} = e^{rt}$$

$$N_t = N_0 e^{rt}$$

Now, let's see how equation 7 looks when we graph it and also consider how it applies to some biological populations.

**Growth in an Unlimited Environment:** Suppose that organisms find themselves in an ideal physical environment where they are not limited by food, space, access to mates, or any other thing that might impede their growth. Examples are species that are recent invaders of new habitats to which they are well-adapted -- for instance, microbes in a nutrient broth, aphids on an undefended plant, seeds in a freshly tilled, fertilized and watered plot.

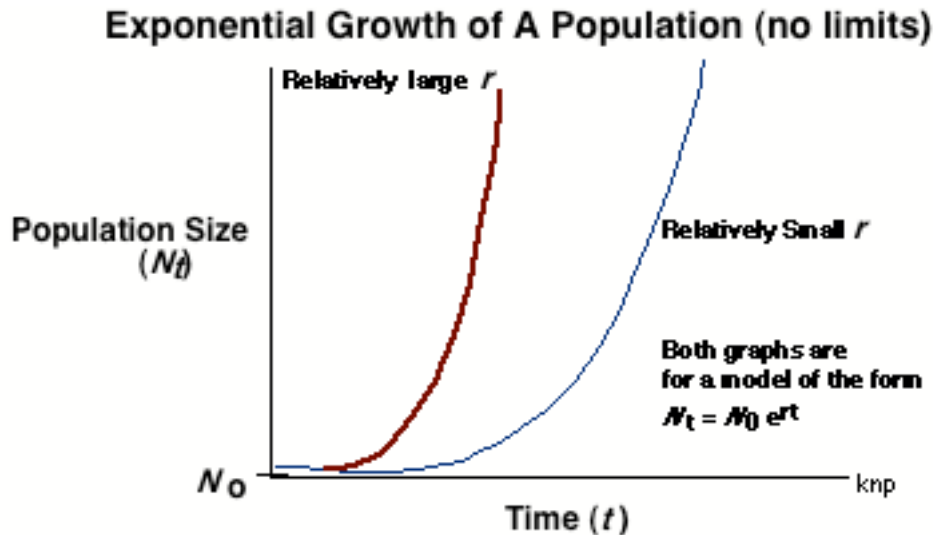
For as long as there is no competition for these resources (in ecology we say that **none of the resources are limiting**) the population's growth will be entirely determined by its intrinsic rate of increase,  $r_0$ .

One version of  $r$ , called  $r_0$  is called the **intrinsic rate of increase** and is a measure of the **biotic potential of population**, i. e. , its ability to increase under ideal conditions).

Since  $r_0$  is largely a measure of how rapidly organisms of a certain type can turn resources into reproduction, the higher the  $r_0$  value, the faster the population grows.

From your math classes you should recognize eq. 8 as an **equation for**

**exponential growth.** When solved and plotted, it produces what is often called a **J-shaped or exponential curve**:



However, no population can increase exponentially forever. Sooner or later it will encounter some form of environmental resistance, e.g., individuals will either run out of resources, or encounter a catastrophic change in the environment which causes the population to crash. This latter event is the more usual for a number of species, especially insects and algae. These organisms exhibit exponential growth when conditions are favorable, but when the environment changes, the population crashes to very low density only to rise again when conditions improve. A good example of this type of population growth is seen every spring with algal blooms due to the mixing of water in a pond or lake. After the ice melts, the water has a fairly uniform temperature and this allows nutrients in the sediment at the bottom to mix in the water at all levels. Algae near the surface use sunlight and these nutrients to reproduce exponentially and soon the pond's surface has a greenish color. As summer approaches and the sun warms the surface water, a strong temperature barrier is created which prevents the nutrients from reaching the surface. Consequently, the population of algae crashes until the next spring. Populations of species which follow a series of J-shaped curves as their growth pattern, as with this example, are usually controlled by **physical aspects of the environment**, e. g. , **weather**, which change abruptly. Since the effect of these abiotic factors is independent of the density of the population, this pattern is called **density-independent growth**. Density-independent growth patterns controlled by abiotic factors such as weather characterize species variously referred to as **opportunistic species** (because they take advantage of favorable conditions to realize their biotic potential), **colonizing species** (because they often disperse to new areas when their density is high), or **fugitive species** (because they cannot persist for long periods in any one area due to competition with more stable or equilibrium species). We will see them discussed below under evolutionary ecology as "**r-selected species**". Notice that individuals in these "r-selected" species compete with each other by being

able to disperse better and/or to produce more offspring in a shorter period of time. Note the obvious relation of the second to the term "r-selected".

**Growth in a Limited Environment:** More often than not, there is some degree of competition for resources. In fact, in many species and for much of the time, individuals compete intensely for resources. How can we model the growth of such populations?

Population ecologists introduce the term **carrying capacity (K)** which is defined as the maximum number of individuals of a certain population that can survive in a given habitat. It is assumed that any number of individuals beyond **K** simply cannot survive -- either they die or they are driven off or they emigrate to find a better place to live. Obviously, if the actual population, **N**, is very close to **K**, then the population should not be able to grow. On the other hand, if the population is a long way away from **K**, (*i.e.*, very few individuals compared to the available resources - available open slots for members of this species) then population growth should be very rapid and in fact should approach exponential growth. Here is one way to treat this mathematically:

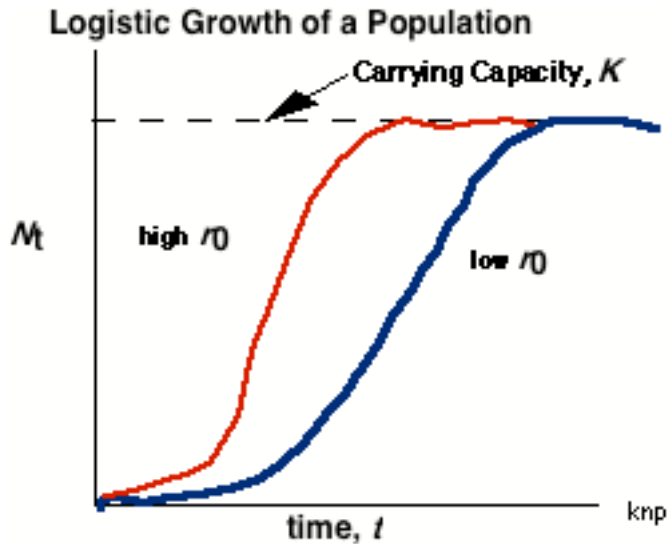
$$\text{eq. 8} \quad \frac{dN}{dt} = rN \frac{(K - N)}{K} = rN \left(1 - \frac{N}{K}\right)$$

Notice that the expression  $\left(\frac{K - N}{K}\right)$  describes a "braking factor" on the population's growth. The closer **N** comes to **K** the smaller that fraction (the more  $\frac{(K - N)}{K}$  approaches zero) and the more slowly the population grows. When **N** = **K** there is no growth, if **N** > **K** then the population's growth rate (dN/dt) is negative.

If we integrate equation 9 we can find an expression for the population size at any time **t**:

$$\text{eq. 9} \quad N_t = \frac{K}{1 + \left(\frac{(K - N_0)}{N_0 e^{rt}}\right)}$$

Here is a plot of eq. 9 for different values of **r**<sub>0</sub>:



This model, which incorporates the effect of carrying capacity, is called the **logistic model**. Very few species follow the logistic model exactly; *Paramecium* is an example of one that does – at least in some environments. Multicellular organisms depart from the model by showing oscillations around the value of  $K$  rather than a smooth, flat line. The reason for this difference is the unrealistic assumptions built into the model.

(Unrealistic) Assumptions of the Logistic Model:

- **All individuals are identical** and so are represented by  $N$ . In fact individuals differ in their probability of reproducing and dying and these differences are age-specific. Such age differences are minimal for paramecia that simply divide when they reach a certain size. However, this assumption tends to approximate reality for entire populations where individual differences are averaged out.
- **There are no time lags in the system.** The model assumes that any change in density immediately depresses further growth reducing reproduction and increasing mortality. Biological systems in general do not respond instantaneously to environmental perturbations, as anyone who has been injured knows. Any effect of density on growth rate takes time, especially as regards changes in reproductive output due to the lower food level resulting from the density increase.
- **$K$  is fixed** and cannot be surpassed. Since  $K$  is determined by resources which are often alive themselves, e. g., food, it seems very unlikely that such resources will not themselves fluctuate over time. Such fluctuations will then result in  $K$  being a variable rather than a fixed parameter.

Despite the fact that the logistic model does not fit empirical data exactly, the model is useful in illustrating the principle of **density-dependent growth** mediated by **intraspecific competition**. Deviations from the model occur at the upper limit when density is high due to time lags in the adjustment of individual physiology to the increase in density. Time lags can be added as constants to the logistic equation based on the physiological responses of an **individual species** to provide a better fit to empirical data, but the model loses generality when its realism is increased.

If there are  $r$ -selected species, then there must also be " **$K$ -selected species**". These are generally characterized as being very specialized from intra-specific competition. They often have low intrinsic rates of growth and they are often characterized by relatively heavy investment in a few offspring. They often are not specialized for dispersal. We will consider more about  $K$ -selected species when we look at competitive interactions.

### General Comments About Models

Models attempt to capture **three features** in explaining a phenomenon: generality, precision and realism. **Generality** means that the model has wide application and so applies to many different species. **Precision** refers to the extent to which the model is stated in quantitative terms that can correspond to empirical data. **Realism** means how close to model conforms to nature and does not depend upon oversimplified assumptions. Models generally can maximize two of these three attributes at a cost in the third. The logistic model maximizes generality and precision but suffers in realism due to its unrealistic assumptions. It expresses the idea density-dependent growth characteristic of all equilibrium species (generality) and can accommodate real data (precision).

### Questions:

1. Be able to explain the different characteristics of  $r$  and  $K$  selected species.
2. Why do you think that there are "over" and "under" shoots of population size ( $N$ ) when near  $K$ ? Think about human populations (we definitely show the characteristics of  $K$  selected species).
3. Can you tell if a species is  $r$  or  $K$  selected simply by looking at its population growth shortly after it invades a new habitat? Explain.