

Population Ecology The Growth of Biological Populations¹

Conservation Biology
Spring 2009

"BEFORE YOUR START" NOTE: Do not be intimidated by all of the math here. If you are not comfortable with math, please look at it as a chance to learn a bit about reading equations and translating them into graphs (and reading graphs). You will not need to be able to solve any of these equations (except #1) but you will need to understand what they mean. There are actually some uses for understanding these sorts of equations that go beyond the course. For instance, the exponential growth equations are also the basis for understanding important topics like compounded interest – something that is important to everyone. These are examples of what are called deterministic models of population growth. **AS ALWAYS, IF YOU DON'T UNDERSTAND SOMETHING IN HERE, PLEASE COME AND VISIT ME DURING MY OFFICE HOURS ASAP – I AM ALWAYS HAPPY TO SEE YOU.**

INTRODUCTION: 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.

THE BASICS. EXPONENTIAL GROWTH: 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)

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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, λ . Thus:

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

Thus, if a population goes from 100 to 200 in time = 1 unit, then λ is 2; if 100 to 300 then λ 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 rate of change of a population's size, $\frac{\Delta N}{\Delta t}$, then we can state that:

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

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, lets assume that:

eq. 3.
$$I = E$$

and therefore:

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

We can define two other parameters:

b the birth rate for some particular time interval normalized to the population size (usually number of breeding females) and

d , the death rate for some particular time interval normalized to the population size (again, usually number of breeding females).:

eq. 5 $b = \frac{B}{N}$ (but where B is offspring produced per very short instant of time)

eq. 6 $d = \frac{D}{N}$ (but where D is offspring produced per very short instant of time)

Thus b and d are the rate of change of the population due to birth or death per individual per very short moment of time.

Note again -- we express b and d as **instantaneous rates** -- birth and deaths per mother over an infinitesimally small change in time (dt). By contrast, B , D and λ are typically expressed over much longer time intervals -- for instance, per breeding cycle, year, or generation. If you have had calculus you will be familiar with this idea. However, calculus is not required for this course and there is no need for me to show you how such a rate is calculated. And, in any case, you can brag to your friends that you are taking a science course where you use some calculus (an almost infinitesimally small amount, but they don't need to know that unless asked)! The usefulness of using instantaneous rates comes when we work with populations where generations overlap (like humans) -- where there is more or less continuous reproduction. Many species fall into this category. On the other hand, many others are seasonal -- breeding occurs once a year in a very defined season and not outside of it. For such populations, of which there are perhaps even more examples, the "Delta" form of the equation is perfectly useful.

We can now re-write equation #4 :

eq. 7 $\frac{dN}{dt} = B - D = bN - dN = (b - d) * N$

where dN/dt is the instantaneous rate of change in population size.
Now, if we define **the rate of increase (r)**:

eq. 8 $r = b - d$

and we substitute r for $(b-d)$ we get:

eq. 9 $\frac{dN}{dt} = r * N$

Eq. 9 gives the "instantaneous rate" of population change -- the change in the number of individuals over a very short period of time. If we want to predict the actual number of individuals, N , after some time period, we must use a different equation. This one is the result of using a calculus technique called integration -- essentially summing the changes in population given by eq. 9 for a very short time interval over many intervals to give the population after a longer period of time. The result of this integration is:

eq. 10
$$N_t = N_0 e^{rt}$$

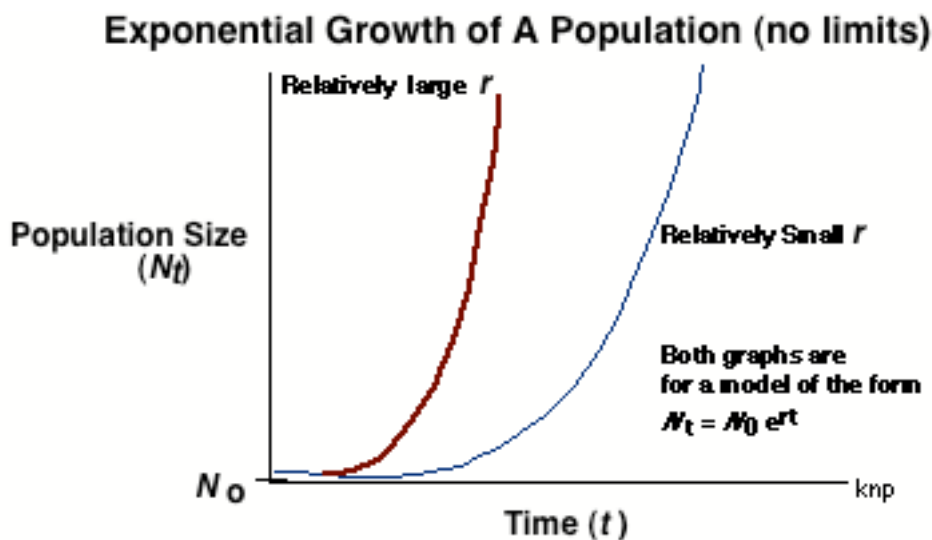
where **e** is the base of natural logarithms (about 2.718) and **t** is any time period. Although it may seem a bit more formidable than eq. #1, it is actually easier to use and has a number of mathematical advantages – but if it helps you to understand, just remember that this equation has the same general uses as equation #1.

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). More about this below.

Now we can finally use some of the math and apply them to model populations of organisms

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 (see above). 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. 10 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. More about this in the next set of notes.

LOGISTIC GROWTH: Populations 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)**. It 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:

eq. 11
$$\frac{dN}{dt} = rN \frac{(K - N)}{K} = rN \left(1 - \frac{N}{K}\right)$$

where *r* is growth rate (the maximum rate possible for this species when nothing is limiting).

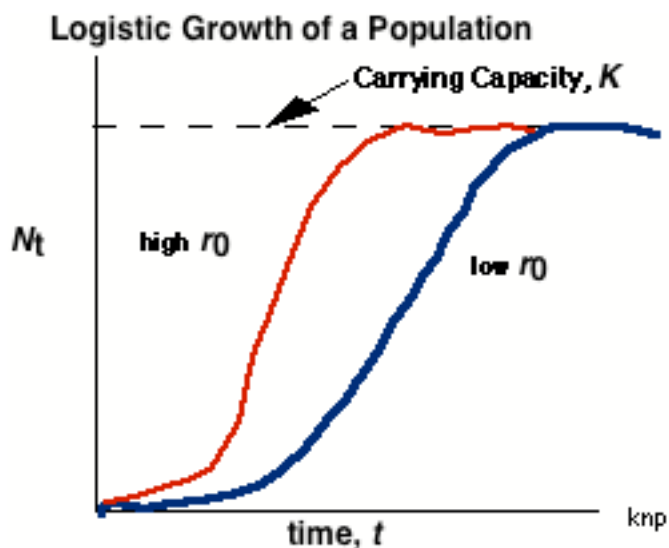
Notice that the expression $\left(\frac{K - N}{K}\right)$ describes a "braking factor" on the population's growth. The closer N comes to K the smaller that fraction (the more $\frac{K - N}{K}$ approaches zero) and the more slowly the population grows. When $N = K$ there is no growth, if $N > K$ then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

If we integrate equation 11 we can find an expression for the population size at any time t :

eq. 12
$$N_t = \frac{K}{1 + \left(\frac{K - N_0}{N_0} e^{-rt}\right)}$$

Please don't freak out here if you don't know calculus - you are not expected to .. I am only putting this in for those who have the training to understand this integration.

Here is a plot of eq. 12 for different values of r and the same carrying capacity:



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.

General Comments About Models (Important)

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. Know the difference between **exponential growth** and **logistic growth**.

Know what graphs of each look like.

Know the relationships between b , d and growth rate.

Know what r and r_0 are and what happens to the shape of exponential and logistic graphs if r increases and in the case of logistic graphs, if K changes.

Know what dN/dt means – what will a graph of dN/dt vs. time look like where dN/dt is positive, negative, and equal to zero?

Know the difference between a graph of dN/dt vs. time and N vs. time.

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. Know what "density-dependence" and "density-independence" mean (also covered in class). Know some good examples that show both effects.

4. **Understand what a model is** from these examples and be able to explain how the different parts of the logistic equation (#11) are used to model unlimited growth and density dependent effects.