5. Applications

The Exponential Equation is a Standard Model Describing the Growth of a Single Population

The easiest way to capture the idea of a growing population is with a single celled organism, such as a bacterium or a cilliate. In Figure 1, a population of *Paramecium* in a small laboratory depression slide is pictured. In this population the individuals divide once per day. So, starting with a single individual at day 0, we expect, in successive days, 2, 4, 8, 16, 32, and 64 individuals in the population. We can see here that, on any particular day, the number of individuals in the population is simply twice what the number was the day before, so the number today, call it N(today), is equal to twice the number yesterday, call it N(yesterday), which we can write more compactly as $N(\text{today}) = 2N(\text{yesterday})$.
Since the basic rule of cell division applies not only to today and yesterday, but to any day at all, we would have $N(6) = 2N(5)$, or $N(4) = 2N(3)$, etc.

So it makes sense to write this as, $N(t) = 2N(t - 1)$ where t could take on any value at all.
Now we can generalize this idea a bit if we note that at day six the number is equal to twice the number at day five, or $N(6) = 2N(5)$ and at day five the number is equal to twice the number at day four, or $N(5) = 2N(4)$, etc.
So in the equation for day 6 we can substitute for the value of $N(5)$ — which we know to be $2N(4)$ — getting $N(6) = 2[2N(4)]$, which is the same as $N(6) = 22N(4)$.

But $N(4) = 2N(3)$, so we can substitute for $N(4)$ getting $N(6) = 22N(4) = 22[2N(3)] = 23N(3)$. And if we follow the same pattern we see that $N(3) = 23N(0)$, which we can substitute for $N(3)$ to get $N(6) = 26N(0)$. Thus we can see a relatively simple generalization, namely

$$\text{Equation 1:} \quad N(t) = 2^{t}N(0)$$

where t stands for any time at all (e.g., if $t = 6$, $N(6) = 26[N(0)]$).
Finally we note that this equation was derived from the specific situation shown in Figure 1, where one division per day was the hard and fast rule. That is where the 2 comes from in Equation 1 — from each individual *Paramecium* we obtain two individuals the next day. Of course the division rate could be anything. If there were two divisions per day but one cell always died, we would expect three individuals from each single individual and Equation 1 would be $N(t) = 3tN(0)$. So the division rate could be any number at all and the general equation becomes,

$$\text{Equation 2:} \quad N(t) = R^{t}N(0)$$

where R is usually called the finite rate of population increase (in the actual case of dividing *Paramecium* the finite rate of population increase is equal to the division rate). In Figure 2 we illustrate this equation for various values of R. It is normally referred to as the exponential equation, and the form of the data in Figure 2 is the general form called exponential.

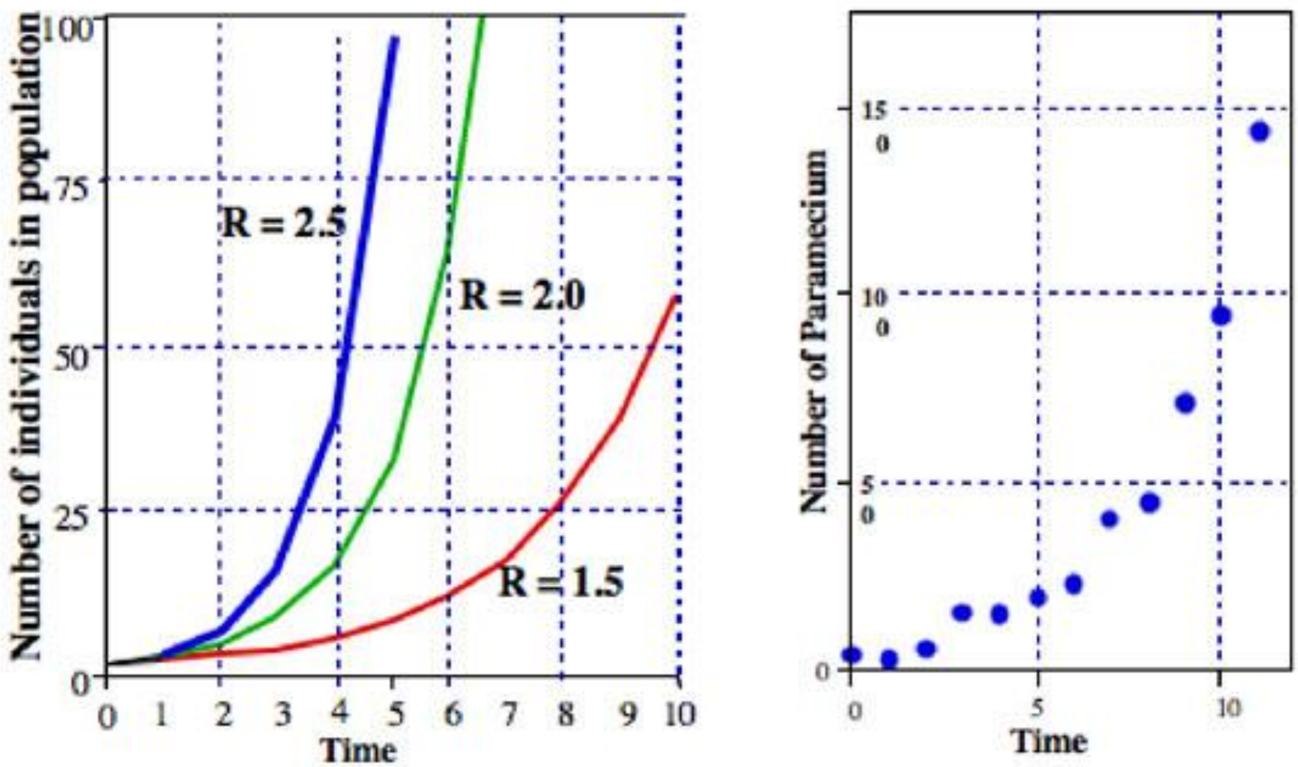

Figure 2: Left: general form of exponential growth of a population (equation 2). Right: actual numbers of Paramecium in a 1 cc sample of a laboratory culture.

Any value of R can be represented in an infinite number of ways (e.g., if *R* = 16, we could write *R* = 8 x 2, or *R* = 42, or *R* = 32/2, or *R* = 2.718282.77). That last expression (*R* = 2.718282.77) makes use of an important constant that might be recalled from elementary calculus, Euler's constant. Expressing whatever value of R as Euler's constant raised to some power is actually extremely useful — it brings the full power of calculus into the picture. If we symbolize Euler's constant as *e* we can write Equation 2 as

$$\text{Equation 3:} \quad N(t) = N(0)e^{rt}$$

Now if we take the natural log of both sides of Equation 3 — remember *ln*(*ex*) = *x* — Equation 3 becomes: *ln* [*N*(*t*)] = *ln* [*N*(0)] + *rt*
And if we began the population with a single individual (as in the example above), we have

$$\text{Equation 4:} \quad \ln(N(t)) = rt$$

from which we see that the natural log of the population, at any particular time, is some constant, times that time. The constant *r* is referred to as the intrinsic rate of natural increase (Figure 2).
All sorts of microorganisms exhibit patterns that are very close to exponential population growth. For example, in the right hand graph of Figure 2 is a population of *Paramecium* growing in a laboratory culture. The pattern of growth is very close to the pattern of the exponential equation.

Another way of writing the exponential equation is as a differential equation, that is, representing the growth of the population in its dynamic form. Rather than asking what is the size of the population at time *t*, we ask, what is the rate at which the population is growing at time *t*. The rate is symbolized as *dN*/*dt* which simply means "change in *N* relative to change in *t*," and if you recall your basic calculus, we can find the rate of growth by differentiating Equation 4, which gives us

$$\text{Equation 5:} \quad \frac{d\ln N(\mathrm{t})}{dt} = r$$

which is kind of remarkable, because it says that the rate of growth of the log of the number in the population is constant. That constant rate of growth of the log of the population is the intrinsic rate of increase.

Recall that the rate of change of the log of a number is the same as the "per capita" change in that number, which means we can write Equation 5 as

$$\frac{d\ln N}{dt} = \frac{dN}{Ndt} = r$$

where we omit the variable *t* since it is obvious where it goes, and then we rearrange a bit to come up with

$$\text{Equation 6:} \quad \frac{dN}{dt} = rN$$

where the parameter *r* is, again, the intrinsic rate of natural increase. The basic relationship between finite rate of increase and intrinsic rate is

$r = ln(R)$

where ln refers to the natural logarithm. Note that Equation 6 and Equation 3 are just different forms of the same equation (Equation 3 is the integrated form of Equation 6; Equation 6 is the differentiated form of Equation 3), and both may be referred to simply as the exponential equation.

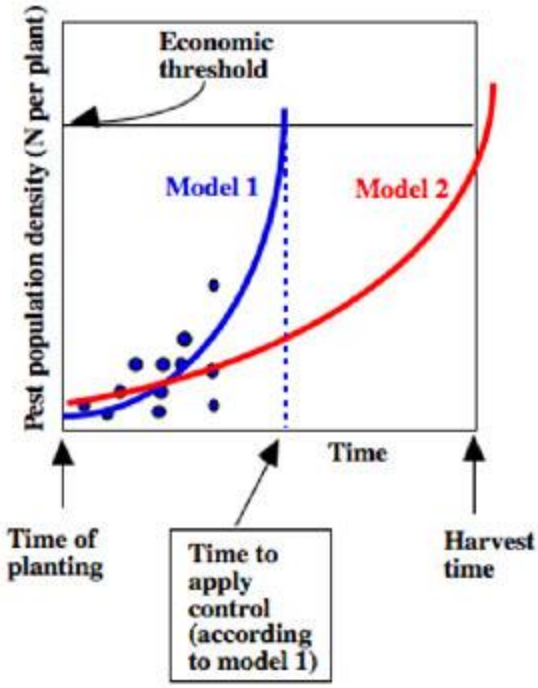

Figure 3: Hypothetical case of a pest population in an agroecosystem

According to model 1 (which has a relatively large estimate of R), the farmer needs to think about applying a control procedure about half way through the season. According to model 2 (which has a relatively small estimate of R), the farmer need not worry about controlling the pest at all, since its population exceeds the economic threshold only after the harvest. Clearly, it is important to know which model is correct. In this case, according to the available data (blue data points), either model 1 or 2 appears to provide a good fit, leaving the farmer still in limbo.

The exponential equation is a useful model of simple populations, at least for relatively short periods of time. For example, if a laboratory technician needs to know when a bacterial culture reaches a certain population density, the exponential equation can be used to provide a prediction as to exactly when that population size will be reached. Another example is in the case of agricultural pests. Herbivores are always potentially major problems for plants. When the plants subjected to such outbreaks are agricultural, which is to say crops, the loss can be very significant for both farmer and consumer. Thus, there is always pressure to prevent such outbreaks. Since WWII the major weapon in fighting such pest outbreaks has been chemical pesticides, such as DDT. However, in recent years we have come to realize that these pesticides are extremely dangerous over the long run, both for the environment and for people. Consequently there has been a movement to limit the amount of pesticides that are sprayed to combat pests. The major way this is done is to establish an economic threshold, which is the population density of the potential pest below which the damage to the crop is insignificant (i.e., it is not really necessary to spray). When the pest population increases above that threshold, the farmer needs to take action and apply some sort of pesticide, or other means of controlling the pest. Given the nature of this problem, it is sometimes of utmost importance to be able to predict when the pest will reach the economic threshold. Knowing the R for the pest species enables the farmer to predict when it will be necessary to apply some sort of control procedure (Figure 3).

The exponential equation is also a useful model for developing intuitive ideas about populations. The classic example is a pond with a population of lily pads. If each lily pad reproduces itself (two pads take the place of where one pad had been) each month, and it took, say, three years for the pond to become half filled with lily pads, how much longer will it take for the pond to be completely covered with lily pads? If you don't stop to think too clearly, it is tempting to say that it will take just as much time, three years, for the second half of the pond to become as filled as the first. The answer, of course, is one month. Another popular example is the proverbial ancient Egyptian (or sometimes Persian) mathematician who asks payment from the king in the form of grains of wheat (sometimes rice). One grain on the first square of a chess board, two grains on the second square, and so forth, until the last square. The Pharaoh cannot imagine that such a simple payment could amount to much, and so agrees. But he did not fully appreciate exponential growth. Since there are 64 squares on the chess board, we can use Equation 2 to determine how many grains of wheat will be required to pay on the last square (R raised to the 64th power, which is about 18,446,744,074,000,000,000 — a lot of wheat indeed, certainly more than in the whole kingdom).

These examples emphasize the frequently surprising way in which an exponential process can lead to very large numbers very rapidly.