

Models of growth and decay

Some of the most well-known applications of quantitative analysis in the life sciences relate to describing changes in processes or ecosystem properties with time. Among the most important examples is population change, where the number of individuals N in a population is expressed as a function of the independent variable t : $N = f(t)$. In this chapter we will explore two types of exponential functions and a polynomial function that form the basis for describing and predicting population change and a lot more.

13.1 Exponential functions & population models

An exponential function is one in which the independent variable appears in the exponent, or power, of some other quantity. The equation $y = a^x$ is an example of a simple exponential function if x is the independent variable and y is the dependent variable. In this case, the constant a can be called the *base*, since it is the quantity that is raised to a power. From our high school math classes, we learned about exponential and logarithmic (the inverse of exponential) functions mostly with bases of 10 and e , where e is Euler's number (~ 2.718) and is sometimes written $\exp(\text{something})$. But we can have an exponential function with any arbitrary base.

Exponential functions arise frequently in economics, physics, and in some contexts in ecology. Imagine, for example, a population of marbled murrelets in a coastal bay in the Pacific Northwest¹. At some time, suppose their population was 100 individuals. With time, this can change as individuals die or reproduce. If we assume no murrelets emigrate or immigrate (are added to or subtracted from the population), changes in population with time are controlled only by birth and death rates, and we can say the population N after one year is:

$$N_1 = N_0 + B - D \quad (13.1)$$

In this equation, we take N_0 to be a constant, initial population. The

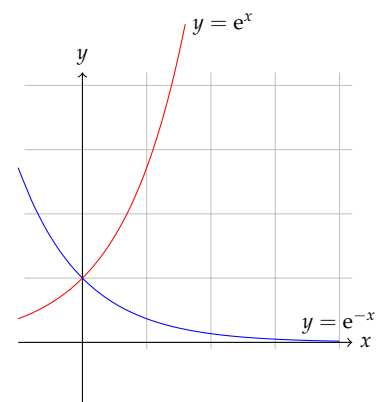


Figure 13.1: The typical ever-changing growth and decay of the exponential function.

¹ Why murrelets you might ask? As you'll see shortly, it is convenient to begin with "simple" populations, where the causes of population changes estimated from visual surveys are limited.

birth and death rates may scale with the population, such that they can be represented like this:

$$B = b \times N, \quad D = d \times N \quad (13.2)$$

where b and d are birth and death rates per individual. So, for example, if the birth rate is approximately 0.15 individuals per murrelet per year², and death rate is 0.05 individuals per murrelet per year, we can write our equation for population as:

$$N = N_0 + 0.15N_0 - 0.05N_0 \quad (13.3)$$

If we simplify the right-hand side of this, we have N after one year as a simple function of N_0 :

$$N = (1 + 0.15 - 0.05)N_0 \quad (13.4)$$

$$N = 1.1N_0 \quad (13.5)$$

If you plug in 100 for N_0 , this gives us an unsurprising result that population is 110 murrelets. This makes sense, since we get $0.15 \times 100 = 15$ births and $0.05 \times 100 = 5$ deaths during that year.

Now if we project into future years (where t is the number of years after our initial measurement of population N_0) with the same relationship, we'll see that after another year of births and deaths, we'll get:

$$N_{t=2} = 1.1(1.1N_0) \quad (13.6)$$

where the quantity in parentheses is the population after one year, now incremented by another series of births and deaths. We can rearrange that equation slightly to yield:

$$N_{t=2} = N_0 \times 1.1^2 \quad (13.7)$$

After another year, we'll get:

$$N_{t=3} = N_0 \times 1.1^3 \quad (13.8)$$

And by now you probably see the pattern. If t is the number of years after an initial population census N_0 , our projection of population is:

$$N_t = N_0 \times 1.1^t \quad (13.9)$$

Interpreted as N as a function of t , this is an exponential function with a base of 1.1 and a constant N_0 . Note that a very similar function could describe compounding interest on a loan, savings account or credit card balance, if the principal (the amount saved or borrowed) remains unchanged over time.

² Note that this birth rate is given per individual. Obviously males cannot give birth to offspring, so a better way to express fertility or fecundity is in terms of birth rates per female; however the per individual or *per capita* birth rate is easier to work with.

WE COULD HAVE WRITTEN our equation above a bit differently. Instead of keeping a constant reference to N_0 , we could have said that population next year depends only on the population this year and the birth and death rates this year. This alteration would give us:

$$N_{t+1} = N_t + B - D = N_t + N_t(b - d) = N_t(1 + r) \quad (13.10)$$

where $r = b - d$ can be defined as the population's **intrinsic growth rate**. There is no difference in the result of this equation if we apply the same assumptions and constraints as we did in the first version, but this form of the equation is a bit more versatile. It will also become useful to us in a few days. We can call it a *discrete difference* equation.

Before we move on, notice a few things about our population model. First, population is unrestrained. The only factors influencing the growth rate are birth and death rate, and these are considered constants. In reality, these might not be constant as individuals compete for limited resources. Alterations to this model to account for this fact will be introduced next time. Also, notice that the intrinsic growth rate r is positive because we have said that the birth rate is higher than the death rate. It is, of course, possible for the reverse to be true: death rate could be larger than the birth rate, and the resulting r would be negative. As you can see from the above equations, a negative r would result in an exponential decrease in population with time.

When $r = 0$, we may say that the growth rate is zero and births balance deaths. The birth rate that balances death rate is sometimes called "replacement", since it replaces each death with a birth.

13.1.1 More exponentials

One place where exponential functions appear in the natural sciences is in animal physiology, particularly where processes are regulated by temperature. The "surface area" theory for metabolic scaling discussed above suggests that basal metabolic rate scales **allometrically** with the mass of the animal. As we hinted at above, this hypothesis stems from the postulate that metabolic rate scales with the surface area (through which heat can be lost), which is in turn a function of $[L^2]$, where $[L]$ is a characteristic length of the animal. Mass, however, scales with the volume of the animal, which is a function of $[L^3]$. If we combine the two relationships to express metabolic rate as a function of mass, we get the allometric relationship:

$$B \propto M^b \quad (13.11)$$

where B is metabolic rate, M is body mass, and b is the scaling exponent, which is equal to $2/3$ according to the surface area theory. We

briefly acknowledged that several studies in the 20th century suggest that the 2/3-power scaling is not correct, and that a 3/4-power scaling might be more appropriate. Nevertheless, the general form of the relationship is reasonable. To transform this proportionality into an equation, we could introduce a constant B_0 , so that we have

$$B = B_0 M^b \quad (13.12)$$

If we interpret B as the dependent variable and M as the independent variable, this is clearly a *power function* because M is the base. Contrast this type of equation with the population equation above, where the independent variable t was the exponent.

The simple power-law equation for metabolic rate has some simple applications for which it is useful, but it fails to describe many important phenomena that are seen by animal physiologists. One is the fact that metabolic rate is also very sensitive to temperature. A modification to the simple power law was proposed not too long ago in [this Science paper](#). The modification supposes that metabolic rate depends on the kinetics of biochemical reactions on a cellular scale, which are in turn temperature dependent. In chemistry, the temperature dependence of reactions is often expressed as an exponential function of temperature through the Arrhenius relationship:

$$R \propto e^{-\frac{E}{kT}} \quad (13.13)$$

where R is a reaction rate constant and E/k is an energy-related constant for a given reaction, and T is temperature. While this looks a bit ugly, it is an incredibly important relationship for chemistry, physics, and now biology, because it does a surprisingly good job of describing how temperature affects physical and chemical processes.

Let's look for a moment at the general form of this equation by imagining a similar function

$$R = e^{-1/T} \quad (13.14)$$

where we consider temperature T to be the independent variable. As you can see, as temperature increases, the exponent becomes smaller and approaches zero. Since $x^0 = 1$ for all x , this function approaches 1 as temperature increases, but becomes very small for small T . Of course, we cannot compute $1/T$ for $T = 0$, and for that reason the Arrhenius equation is written for T in Kelvin rather than Celsius.

In any case, a much improved relationship for the basal metabolic rate of animals that includes both a dependence on body mass and temperature can be written:

$$B \approx B_0 M^b e^{-\frac{E}{kT}} \quad (13.15)$$

This is a more complex function because it contains two independent variables (mass and temperature), but can be visualized by treating one of them as a constant while the other varies. If we imagine how metabolic rate changes for a single ectothermic organism of a given mass as body temperature changes, it might have a pattern that looks similar to the plot above, but that approaches a value of B_0 with increasing temperature.³

³ If you're interested in more on this topic, revisit [this neat article](#) written for the Nature Education Project, and the references therein, or check out [this summary](#) of the paper that examined this function.

13.2 Adding complexity

Our first population growth model was a simple exponential one. We assumed unrestrained growth with a constant per-capita (per individual) rate parameter $r = b - d$, where b and d are per capita birth and death rates. Our year-to-year prediction of population N with this growth model is

$$N_1 = N_0(1 + r) \quad (13.16)$$

Given an initial population N_0 , the population after t years was

$$N = N_0(1 + r)^t \quad (13.17)$$

While we arrived at this result with just some reason and algebra, a more general solution can be found using calculus. We won't worry too much with how this solution is obtained, nor will you be expected to reproduce it, but it is always nice to see how more advanced topics can help us with the problem at hand. So here is a quick summary of how the calculus version works:

If we re-write our first incremental population change equation above

$$N_1 = N_0 + rN_0 \quad (13.18)$$

$$N_1 - N_0 = rN_0 \quad (13.19)$$

Notice that the left-hand side is now just the population *change* over one year. One of the strategies of calculus that allows elegant solution of complex problems is to imagine "smooth" changes, where the increment over which those changes are measured in vanishingly small. While this is obviously an oversimplification of population dynamics (i.e., many animals have discrete breeding seasons so that births are clustered during a relatively small period of time, and no births occur during the remainder of the year), but in many cases we don't need to worry too much about this. We express these vanishingly-small change increments with *derivatives*, where the

derivative of N with respect to t can be translated as the instantaneous rate of population change as a function of time, i.e., the population growth rate. With this strategy, the above equation is written:

$$\frac{dN}{dt} = rN \quad (13.20)$$

Applying some second semester calculus, we'd come up with the following solution, which works at all t :

$$N = N_0 e^{rt} \quad (13.21)$$

Compare this equation with the one above, $N = N_0(1+r)^t$, which we developed with discrete differences. Graph both functions and see if they match reasonably well. They should be close, but not exactly the same. The discrete model is, in fact, subtly different, and is often called the *geometric* model for population growth, while the exponential version is the classical *Malthusian* model.

Calculus aside, the above unrestrained population models are useful as a starting point, but they neglect any mechanisms of slowing population growth. In most settings, resource limitation slows or reverses growth rates as population increases. If you're not familiar with the story of [St. Matthews Island reindeer](#), it is an interesting illustration of this effect taken to an extreme.

A fairly simple way to account for resource limitation, and to thereby restrain population growth according to some carrying capacity K , is to include an "interaction" term for our growth rate. Using the same notation as above, an increment of growth in this new population model is:

$$N_1 = (1+r)N_0 - \frac{(1+r)N_0^2}{K} \quad (13.22)$$

This looks a bit clunky, but we can clean it up with a little bit of algebra and by making the same kinds of calculus-oriented modifications that we made above:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \quad (13.23)$$

As above, the derivative term on the left hand side is the rate of population change as a function of time, or the population growth rate. If we write the equation with G for growth rate on the left-hand side, it looks a bit more manageable:

$$G = rN \left(1 - \frac{N}{K}\right) \quad (13.24)$$

$$G = rN - \frac{r}{K}N^2 \quad (13.25)$$

As you can see, the growth rate is just a second-order polynomial equation. As such, it's graph might be a bit familiar to us: it is a downward-opening parabola that crosses the x -axis at $x = 0$ and $x = K$. This is the **logistic** population growth model, perhaps the simplest way of incorporating density dependence and carrying capacity into the description of population changes in a place with finite resources.

Solving this differential equation is not particularly easy, but fortunately for us, smart people have found useful solutions. The most straight-forward solution for N as a function of t is:

$$N = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}} \quad (13.26)$$

Here is an example of a case where we can defer to the experts who came before us and simply borrow their result for our own use. The fact is, even with the above solution, there is plenty of complexity in the logistic population model since we must define, for any particular scenario, several of the parameters before we can use it to any avail: K , N_0 , and r .

13.2.1 Example: minimizing suppression and loss costs (Problem 3.5)

The hypothetical functions we have proposed for the suppression cost C and net value change V_{nc} were simple idealizations and would need to be modified according to better understandings of cost-effort relationships. Nevertheless, our cost-plus-net-value-change function can still allow an instructive optimization. Our function reads:

$$C + V_{nc} = wE + V_0 e^{-kE}, \quad (13.27)$$

where the first term on the right-hand side is the cost of suppression activities, while the second term is the net value change in case of fire. The lowest-cost state is clearly the bottom of the dip in Figure 3.2, but can we identify that point algebraically? If we use a little calculus, we can indeed.

In first-semester calculus, we learn that the maxima and minima of functions can be found by setting the derivative equal to zero. In this case:

$$\frac{d}{dE}(C + V_{nc}) = w - kV_0 e^{-kE} = 0. \quad (13.28)$$

For our purposes here, I won't explain how we arrive at this, but suffice it to say that when we solve the right-hand equality for E , we retrieve the effort corresponding to the minimum total $C + V_{nc}$. We'll

follow the algebraic manipulations through here:

$$w - kV_0e^{-kE} = 0 \quad (13.29)$$

$$w = kV_0e^{-kE} \quad (13.30)$$

$$\frac{w}{kV_0} = e^{-kE} \quad (13.31)$$

$$\ln\left(\frac{w}{kV_0}\right) = -kE \quad (13.32)$$

$$E = -\frac{1}{k} \ln\left(\frac{w}{kV_0}\right) \quad (13.33)$$

This result isn't necessarily pretty, but it provides a robust analytical solution that depends only on the coefficients we assigned to the trial functions, and that can be easily modified for different coefficient values.

Exercises

1. Review Section 13.2.1. In the equation for cost plus net value change, there is a constant k . What are its units?
2. Propose some reasonable values for the constants and coefficients for the fire-suppression problem in Section 13.2.1 and determine the optimal effort and its cost.
3. Review Section 12.1.2 and ensure that you are comfortable with the analysis presented there – or that you have developed and justified your own approach to achieving an analogous solution. Propose and execute a strategy for incorporating car trips through the county road network in order to estimate the probable number of collisions in a given span of time.
4. Review Section 12.2.1. Construct and evaluate a spreadsheet model to solve the numerical approximation of the SIR system of equations.