Math Intro's / Refreshers

Stochastic processes
Dynamical Systems

Introduction to Stochastic Processes

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Goal: This tutorial will cover basic probability theory, to give you a set of tools to model variability in biological data. You will also be able to understand and interpret common comparisons made between biological data and the behavior of standard stochastic processes, such as a Poisson process. We will derive equations for the mean and variance of a Poisson process, to build your intuition for these results instead of simply presenting these equations as facts to memorize. We will explore the limiting case where a Poisson distribution approaches a Gaussian distribution, another useful result of probability theory often used in biology.

1   Randomness in biology

This tutorial highlights an important and pervasive aspect of biological systems: stochasticity. (NB: 'stochasticity', 'variability', 'uncertainty', 'noise', and 'fluctuations' will all be used interchangeably here, though most of these terms have more technical and specific uses in other contexts.) Many of the variables that we observe in biological recordings fluctuate, sometimes because we cannot control all the states of the external and internal world of the organism, other times because thermal noise and other microscopic factors make the state of the biological system we interrogate inherently noisy. It is useful to model not only a median value for a fluctuating variable, but the full shape of its distribution of values.

For example, if we observe the firing of neurons in the brain to repeats of the same external stimulus, the precise times of spikes will vary between repeats. By fitting the statistics of this noise to models, we deepen our understanding of the neural response.

To build your intuition about quantifying uncertainty, let's start with a toy problem I first encountered in David MacKay's lectures on information theory and inference.

2   Testing your intuition: the bent coin lottery

A biased coin is used to generate sequences of digits, 1 for heads, 0 for tails, in a lottery. The coin is tossed 25 times to determine the winning sequence. The probability of heads is 0.1. Tickets for the lottery cost \$1 and the prize is \$$10,000,000$.

Exercise 2.1

1. You are only allowed to purchase one ticket. Which ticket would you buy?

Solution. The most likely ticket is the all-zeros ticket

$$00000\ 00000\ 00000\ 00000\ 00000,$$

with a probability of $P(000\ldots0) = (0.9)^{25} = 0.7178$.

To compute the probability of any given sequence, you multiply together the probability of every coin flip, so

$$P(000\ldots0) = P(0)P(0)P(0)\ldots P(0).$$

How do we know this ticket has the highest probability? For any 0 that we replace by a 1, the probability correspondingly changes one of the 25 $P(0)$'s to $P(1)$, since $P(1)$ is 0.1 (which is less than $P(0) = 0.9$), then the resulting product must be less than the probability of all-zeros.

2. How many tickets to would you have to buy to cover every possible outcome?

Solution. The total number of tickets is $2^{25} = 33,554,432$.

3. Is this lottery worth playing?

Solution. At first glance, the prize money ($10,000,000) is less than the cost of buying all the tickets ($33,554,432), so we might think the lottery is not worth playing. However, not all tickets are equally likely, so we don't want to buy all the tickets. We only want to buy the most likely tickets. This doesn't guarantee that there are enough likely tickets to make lottery worthwhile, but we will show later that there are.

3   Binomial distribution

Each flip of a coin like this with probability, p, of heads is an example of a Bernoulli trial, the general term for an experiment with only two output states, success or failure. The number of heads in the sequence of independent coin flips generated by our lottery will follow a binomial distribution.

Exercise 3.1

1. Write down the probability of observing k heads in n coin flips, if the probability of heads is p.

Solution. The probability of observing k heads in n coin flips is the same as the probability of observing **any** sequence of length n with k heads. We can find this probability by adding together the probabilities of every **particular** sequence of length n with k heads. That's a lot of terms to sum up. Luckily, the probability of a sequence of length n with k heads is $p^k(1-p)^{n-k}$, regardless of how the heads and tails are ordered. Why? As in Exercise 1.1, we find the probability of a sequence by multiplying the probabilities of each coin flip. Since the order of multiplication doesn't matter, the product is always $p^k(1-p)^{n-k}$.

Now we just need to count how many sequences there are of length n with k heads, since the sum of their probabilities will equal the product of their count with $p^k(1-p)^{n-k}$. It turns out that counting sequences like this comes up a lot, so there is a notation for their count, $\binom{n}{k}$, pronounced "n choose k," and known as a binomial coefficient. This binomial coefficient counts the number of ways you

can choose k out of n objects. (Why is that equivalent to the number of sequences of length n with k heads?) It is defined as

$$\binom{n}{k} = \frac{n!}{k!(n-k)!}.$$

Then we have the probability of k heads in a sequence of n coin flips is

$$\binom{n}{k} p^k (1-p)^{n-k}$$

This is the binomial distribution. Rather than memorize this particular form, remember how to write it down as the product of intuitive terms. If we consider the limit of a very small p, we can relate the binomial distribution to the Poisson distribution.

4 Poisson distribution

The Poisson distribution describes the probability of finding k events in a fixed interval if we know the rate of occurrence of these events, λ, in that interval. In terms of the variables we have been working with for the bent coin lottery,

$$\lambda = p * n. \tag{4.1}$$

We are going to take the limit where p is very small and n is very large, but their product remains fixed.

Exercise 4.1

1. Derive an expression for the probability of observing k heads in n tosses in the limit of small p and large n.

   Solution. We just showed that the binomial distribution is given by

   $$P(k) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}.$$

   Equation 4.1 tells us $p = \lambda/n$, so

   $$P(k) = \frac{n!}{k!(n-k)!} \left(\frac{\lambda}{n}\right)^k \left(1 - \frac{\lambda}{n}\right)^{n-k}.$$

   To make things easier, let's split that expression up and look at what happens to each part when we make n large. First, we'll take the first two terms:

   $$\frac{n!}{k!(n-k)!} \left(\frac{\lambda}{n}\right)^k = \frac{n \cdot (n-1) \cdot (n-2) \ldots (n-k+1) \cdot (n-k) \cdot (n-k-1) \ldots 1}{k! \cdot (n-k) \cdot (n-k-1) \ldots 1} \left(\frac{\lambda}{n}\right)^k$$

This expansion makes it more apparent that the last $n - k$ terms of $n!$ are the same as $(n - k)!$, so we can simplify the above equation to

$$\frac{n!}{k!(n-k)!}\left(\frac{\lambda}{n}\right)^k = \frac{n\cdot(n-1)\cdot(n-2)\ldots(n-k+1)}{k!}\left(\frac{\lambda}{n}\right)^k$$

$$= \frac{n\cdot(n-1)\cdot(n-2)\ldots(n-k+1)}{k!\cdot\underbrace{n\cdot n\ldots n}_{k\text{ times}}}\lambda^k$$

$$= \frac{n}{n}\cdot\frac{n-1}{n}\ldots\frac{n-k+1}{n}\cdot\frac{\lambda^k}{k!}.$$

As $n \to \infty$, all but the last fraction goes to one, so that the product is

$$\frac{n!}{k!(n-k)!}\left(\frac{\lambda}{n}\right)^k \xrightarrow[n\to\infty]{} \frac{\lambda^k}{k!}$$

Now let's look at the other half of the original equation,

$$\left(1-\frac{\lambda}{n}\right)^{n-k} = \left(1-\frac{\lambda}{n}\right)^{n}\left(1-\frac{\lambda}{n}\right)^{-k}.$$

The part with $-k$ in the exponent goes to one as n gets large. For the other part, we need to remember from calculus that $e^x = \lim_{n\to\infty}(1+\frac{x}{n})^n$, so

$$\left(1-\frac{\lambda}{n}\right)^{n-k} \xrightarrow[n\to\infty]{} e^{-\lambda}.$$

Combining both parts, we have

$$P(k) \xrightarrow[n\to\infty]{} \frac{\lambda^k}{k!}e^{-\lambda}$$

We have just written down the Poisson distribution. You will see this used as a model for biological variability again and again, either explicitly or implicitly. It is important to think about whether or not it is a good model for the system under study each time you come across it or are deciding to use it for your own research.

4.1   Intervals between events

We can also write down the distribution of intervals between events in a Poisson process. This distribution has an exponential form.

Exercise 4.2

1. Derive an expression for the distribution of an interval, τ, between two events in a Poisson process with rate, λ, in this interval.

   Solution. Let's start by translating this problem back to the language of binomial distributions of sequences. Imagine we divide time into small, discrete bins of length Δt, such that the time interval of length τ is divided into n bins. We'll say the bins are so small that we can ignore the possibility of more than one event occurring in a single bin, so that the bins are essentially Bernoulli random variables. In this scheme, the probability that we observe an interval τ between two events is the same as the probability that we observe n bins with no event followed by a bin with an event.

   Let r denote the rate per unit time of this process, so that $\lambda = r\tau$, and the probability for the Bernoulli random variable describing each bin is $r\Delta t$.

   In this case $n \to \infty$ provides the best approximation (since we don't really want to discretize time), so the probability that we observe n bins with no event is given by Poisson $P(0) = e^{-\lambda}$. The probability of one event in the last time bin is simply a Bernoulli random variable with probability $r\Delta t$. Therefore we can write the density function of the interval, τ, as

   $$\frac{P(\tau)}{\Delta t} = re^{-r\tau}.$$

5   Gaussian distribution

A Gaussian or 'normal' distribution (also called a bell-curve) of a variable x with mean μ and variance σ takes the form

$$p(x) = \frac{1}{\sigma\sqrt{2\pi}}e^{-\frac{(x-\mu)^2}{2\sigma^2}} \tag{5.1}$$

Exercise 5.1

As λ gets very large, show that the Poisson distribution approaches a Gaussian distribution with mean λ and variance λ.

Solution. To do this, we need to use moment generating functions (MGFs), which are an alternative (often more useful) way of describing a probability distribution. An MGF is the expectation of e^{tX}, where X is the random variable. We will show that the standardized Poisson variable approaches the standardized Gaussian variable as $\lambda \to \infty$. So, letting X be our Poisson random variable with mean and variance λ,

$$E\left[e^{t\frac{X-\lambda}{\sqrt{\lambda}}}\right] = \exp\left(-t\sqrt{\lambda}\right) E\left[\exp\left(\frac{tX}{\sqrt{\lambda}}\right)\right]$$

$$= \exp\left(-t\sqrt{\lambda}\right) \sum_{k=0}^{\infty} P(k) \exp\left(\frac{tk}{\sqrt{\lambda}}\right)$$

$$= \exp\left(-t\sqrt{\lambda}\right) \sum_{k=0}^{\infty} e^{-\lambda}\frac{\lambda^k}{k!} \exp\left(\frac{tk}{\sqrt{\lambda}}\right)$$

$$= \exp\left(-t\sqrt{\lambda}-\lambda\right) \sum_{k=0}^{\infty} \frac{\left(\lambda\exp\left(\frac{t}{\sqrt{\lambda}}\right)\right)^k}{k!}$$

$$= \exp\left(-t\sqrt{\lambda}-\lambda\right) \exp\left(\lambda\exp\left(\frac{t}{\sqrt{\lambda}}\right)\right)$$

$$= \exp\left(\lambda\exp\left(\frac{t}{\sqrt{\lambda}}\right) - t\sqrt{\lambda}-\lambda\right)$$

$$= \exp\left(-t\sqrt{\lambda}-\lambda+\lambda\left(1+t\lambda^{-1/2}+\frac{t^2\lambda^{-1}}{2!}+\dots\right)\right)$$

$$= \exp\left(-t\sqrt{\lambda}-\lambda+\lambda+t\lambda^{1/2}+\frac{t^2}{2!}+\frac{t^3\lambda^{-1/2}}{3!}\dots\right)$$

$$= \exp\left(\frac{t^2}{2!}+\frac{t^3\lambda^{-1/2}}{3!}\dots\right)$$

$$\xrightarrow[\lambda\to\infty]{} \exp\left(\frac{t^2}{2!}\right).$$

This limit is the MGF of a standard Gaussian distribution! Therefore the Poisson distribution approaches the Gaussian distribution with the same mean and variance λ, for large λ.

Exercise 5.2

1. Derive the mean of a Poisson distribution with rate λ:

   Solution. If K is our random variable with a Poisson distribution,

$$E[K] = \sum_{k=0}^{\infty} kP(k)$$

$$= \sum_{k=0}^{\infty} k\frac{\lambda^k}{k!}e^{-\lambda}$$

$$= 0 + e^{-\lambda}\sum_{k=1}^{\infty} \frac{\lambda^k}{(k-1)!}$$

$$= 0 + \lambda e^{-\lambda}\sum_{k=1}^{\infty} \frac{\lambda^{k-1}}{(k-1)!}$$

We now substitute $j = k - 1$ to shift the sum,

$$= \lambda e^{-\lambda} \sum_{j=0}^{\infty} \frac{\lambda^j}{j!}$$
$$= \lambda e^{-\lambda} e^{\lambda}$$
$$= \lambda$$

just as we wanted.

2. Derive the variance of a Poisson distribution with rate λ:

Solution.

$$\sigma^2 = E\left[K^2\right] - E\left[K\right]^2$$
$$= \sum_{k=0}^{\infty} k^2 P(k) - \lambda^2$$
$$= \sum_{k=0}^{\infty} k^2 \frac{\lambda^k}{k!} e^{-\lambda} - \lambda^2$$
$$= 0 + \lambda e^{-\lambda} \sum_{k=1}^{\infty} k \frac{\lambda^{k-1}}{(k-1)!} - \lambda^2$$
$$= \lambda e^{-\lambda} \sum_{k=1}^{\infty} \left((k-1)\frac{\lambda^{k-1}}{(k-1)!} + \frac{\lambda^{k-1}}{(k-1)!}\right) - \lambda^2$$
$$= \lambda e^{-\lambda} \left(\sum_{k=1}^{\infty} (k-1)\frac{\lambda^{k-1}}{(k-1)!} + \sum_{k=1}^{\infty} \frac{\lambda^{k-1}}{(k-1)!}\right) - \lambda^2$$
$$= \lambda e^{-\lambda} \left(0 + \sum_{k=2}^{\infty} (k-1)\frac{\lambda^{k-1}}{(k-1)!} + \sum_{k=1}^{\infty} \frac{\lambda^{k-1}}{(k-1)!}\right) - \lambda^2$$
$$= \lambda e^{-\lambda} \left(\lambda \sum_{k=2}^{\infty} \frac{\lambda^{k-2}}{(k-2)!} + \sum_{k=1}^{\infty} \frac{\lambda^{k-1}}{(k-1)!}\right) - \lambda^2$$

and we again substitute $j = k - 1$ and $l = k - 2$ to shift the sums,

$$= \lambda e^{-\lambda} \left(\lambda \sum_{l=0}^{\infty} \frac{\lambda^l}{l!} + \sum_{j=0}^{\infty} \frac{\lambda^j}{j!}\right) - \lambda^2$$
$$= \lambda e^{-\lambda} \left(\lambda e^{\lambda} + e^{\lambda}\right) - \lambda^2$$
$$= \lambda^2 + \lambda - \lambda^2$$
$$= \lambda$$

just as we wanted.

These quantities are often summarized as the ratio of the variance and the mean, or Fano Factor (FF). The FF for a Poisson process is clearly equal to one.

Exercise 5.3

1. Does observing an FF $= 1$ in data mean that the underlying stochastic process is a Poisson process?

   Solution. No! Suppose you have a process such that the waiting time, W, is either 2 or 0 with equal probability. The average waiting time is $E\left[W\right] = \frac{1}{2} \cdot 0 + \frac{1}{2} \cdot 2 = 1$. The variance of the waiting time is also 1 because

   $$\begin{aligned}
   \sigma^2 &= E\left[(W - E\left[W\right])^2\right] \\
   &= \sum_{w=0,2} p(w)(w-1)^2 \\
   &= \frac{1}{2}(0-1)^2 + \frac{1}{2}(2-1)^2 \\
   &= 1
   \end{aligned}$$

   Since the mean and variance are both 1, then the Fano factor is also 1. However, the process is certainly not Poisson. Therefore we have constructed a counterexample that shows that a Fano factor of 1 does not imply that the underlying process is Poisson.

6 Winning the bent coin lottery

Now that we have all of these distributions at our fingertips, let's return to the bent coin lottery.

Exercise 6.1

1. Derive how many tickets you need to buy to guarantee yourself a 99% chance of winning.

   Solution. Let's use the Gaussian approximation for the probability of getting k heads out of n coin flips. Recall that the probability of one head is $p = 0.1$ and the number of coin flips is $n = 25$. Then we can calculate the mean number of heads is $np = 2.5$, and the variance is $np(1-p) = 2.25$, which gives a standard deviation of $\sigma = \sqrt{2.25} = 1.5$.

   The nature of a Gaussian distribution is that 95% of the distribution is within two standard deviations of the mean. That means that if we get all the lottery tickets less than two standard deviations above the mean, we will have at least a 95% chance of winning. In fact, we will have a higher chance of winning because the left tail of the distribution is heavier than a Gaussian, since the probability of $k = 0$ is so high. That means we want to buy up to 5.5, which doesn't really make sense since you can't have half a head. Instead, rounding up we guess that if you buy all tickets with 6 or fewer heads, we will have $\sim 99\%$ chance of winning.

   Now we can count how many tickets we need to buy according to our approximation:

   $$\binom{25}{0} + \binom{25}{1} + \binom{25}{2} + \ldots + \binom{25}{6} = 1 + 25 + 300 + \ldots 177,100$$

   That's way less than $10,000,000$, so at a dollar per ticket the lottery is definitely worth playing!

6.1 Generating samples of a stochastic process

When modeling biological systems, it is often necessary to generate sequences from a Poisson or other stochastic process. We did this to generate our draws from the bent coin lottery.

6.2 Markov processes

One feature of the stochastic processes we have been considering today is that they are independent. A flip of the coin doesn't depend on the flip before, or any of the other previous flips. In biological systems, what came before often influences a fluctuating quantity. For example, having spiked, a neuron is unable to spike for a millisecond or two. Modeling this type of variability falls requires using stochastic processes that have an explicit history dependence. Markov processes depend only on the previous time step, in generating the current state.

A Brief Introduction to Dynamical Systems

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Dynamical Systems

Goal: This tutorial will serve as an introduction to nonlinear dynamics. We will cover some basic notation for describing time-varying quantities, like many we encounter in biology. We will introduce tools for graphical analysis of equations that are analytically intractable. This approach has the advantage of giving us an intuitive picture of the dynamics of complex systems before we even try to numerically simulate them.

1 What is a dynamical system?

A dynamical system is anything that changes in time. In biology, dynamics are important from the molecular to the ecological scale, and at every level in between. Often, the time evolution of a biological system is complex. This tutorial will introduce you to some basic and powerful tools for analyzing dynamics in nonlinear systems.

2 Basic notation

We begin by defining a general dynamical system with a set of n variables, x_i. The dynamics of this collection of variables is generally written as

$$\dot{\vec{x}} = \vec{f}(\vec{x}),\tag{2.1}$$

where $\dot{x} = \frac{dx}{dt}$, and $\vec{x} = (x_1, x_2, \ldots, x_n) \in \mathrm{R}^n$ is called the 'phase space' or 'state space' of the dynamical system. This equation can be broken out, component-wise, so that we have an equation for each variable

$$\dot{x}_1 = f_1(x_1, x_2, \ldots, x_n)$$
$$\dot{x}_2 = f_2(x_1, x_2, \ldots, x_n)$$
$$\vdots$$
$$\dot{x}_n = f_n(x_1, x_2, \ldots, x_n).\tag{2.2}$$

The system is linear if all of the x_i's on the right hand side appear to first power only. Some examples of nonlinear terms are: x_1^2, $\sin x_1$, and $x_1 x_3$. Note that we can transform non-autonomous systems, those with explicit time dependence, into this form via:

$$\dot{\vec{x}} = \vec{f}(\vec{x}, t)$$
$$\dot{t} = 1\tag{2.3}$$

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3   A simple pendulum is not so simple

From our first course in general physics, we learn to solve for the equation of motion of a simple harmonic oscillator, $m\ddot{x} + kx = 0$, arriving at the familiar equation, $x(t) = A\cos(\sqrt{\frac{k}{m}}t + \phi)$. We can convert this nonlinear-looking second-order equation into the above form by making the substitution $x_1 = x$ and $x_2 = \dot{x}$ to arrive at a coupled system of linear equations

$$\dot{x}_1 = x_2$$
$$\dot{x}_2 = -\frac{k}{m}x_1. \tag{3.1}$$

Here we see the power of writing out the equations component-wise. In this formulation the two variables now correspond to the position and velocity of the oscillator. These equations only describe the motion of a real pendulum for small perturbations around 0. The implicit approximation made here is that $\sin x \approx x$ for small x. The true equation for a pendulum is $\ddot{\theta} + \frac{g}{l}\sin(\theta) = 0$, where g is the acceleration due to gravity and l is the length of the pendulum. We can also write this out component-wise, defining a change of variable names, $x_1 = \theta, x_2 = \dot{\theta}$,

$$\dot{x}_1 = x_2$$
$$\dot{x}_2 = -\sin x \tag{3.2}$$

and we see that this is a nonlinear dynamical system that looks quite difficult to solve. Oftentimes in biological systems, your equations will look like this and seem quite intractable. What can we do when faced with a problem like this?

4   Phase portraits and stability analysis

The big idea here is to run our construction in reverse. Instead of solving for the equations that govern the motion of our variables, we instead try to figure out what trajectories look like in phase space and thereby gain knowledge about those solutions. We will do that all without solving the equations! Instead, we will construct a 'phase portrait' of all of the qualitatively different trajectories in the phase space.

As an example, consider a one-dimensional version of the pendulum equation we just encountered, $\dot{x} = -\sin x$, and let's try to solve for $x(t)$ in the usual way and then try to analyze the system graphically. This equation is non-linear, but it is also separable

$$-\int \frac{dx}{\sin x} = \int dt = t + C. \tag{4.1}$$

We can now work with just the left-hand side of this equation to obtain

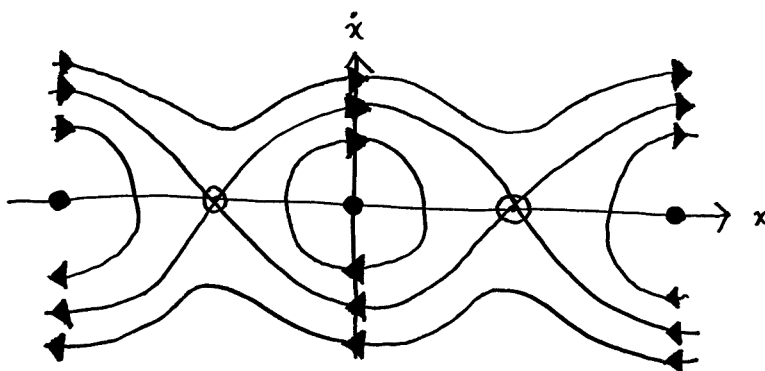$$\int \csc x \, dx = \ln|\csc x + \cot x|. \tag{4.2}$$

With initial condition, $x(0) = x_0$, we can write down an equation for t in terms of x

$$t = \ln\left|\frac{\csc x + \cot x}{\csc x_0 + \cot x_0}\right|, \tag{4.3}$$
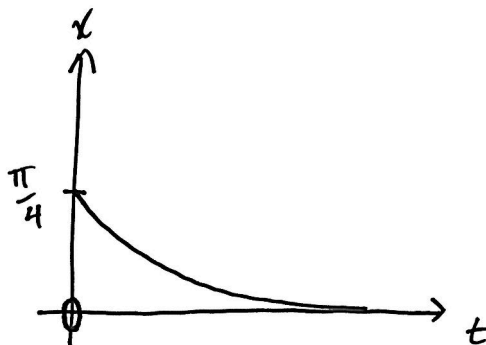
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but we want x in terms of t. This equation is hard to invert and is not particularly illuminating. We can make progress, however, by instead plotting $\dot{x}$ versus x and analyzing some basic features of this phase portrait of the system.

Exercise 4.1

1. Sketch the phase portrait of this system, labeling stable and unstable fixed points.

2. Sketch $x(t)$ when $x_0 = \frac{\pi}{4}$.

5   Exponential Growth

We now consider some basic continuous growth models in population biology. Continuous growth models are especially suited for populations where reproduction can happen at any point in time.

For a discrete time model, we have:

$$r = \frac{N(t + \Delta t) - N(t)}{N(t)} \tag{5.1}$$

meaning that the rate of increase is equal to the increase in the number of individuals $N(t + \Delta t) - N(t)$ divided by the initial number of individuals. What happens if we make the interval Δt shorter and shorter? For Δt going to zero, we obtain:

$$r = \frac{1}{N(t)} \frac{dN(t)}{dt} \tag{5.2}$$

rearranging:

$$\frac{dN(t)}{dt} = rN(t) \tag{5.3}$$

which is the differential equation for the exponential (Malthusian) growth you should be familiar with.

5.1 Analysis

Given the initial condition:

$$N(0) = N_0 \geq 0 \tag{5.4}$$

we can solve the equation. The equation is separable:

$$\frac{dN(t)}{dt N(t)} = r \tag{5.5}$$

Integrating both sides:

$$\int_0^T \frac{dN(t)}{N(t)} = \int_0^T r dt \tag{5.6}$$

$$[\ln(N)]_{N(0)}^{N(T)} = [rt]_0^T \tag{5.7}$$

$$\ln(N(T)) - \ln(N(0)) = rT \tag{5.8}$$

$$\ln\left(\frac{N(T)}{N(0)}\right) = rT \tag{5.9}$$

$$\frac{N(T)}{N(0)} = e^{rT} \tag{5.10}$$

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$$N(T) = N(0)e^{rT} \tag{5.11}$$

The interpretation of the solution is the following: for $r > 0$ the population grows exponentially. For $r < 0$ the decay is exponential. For $r = 0$ the population is constant.

6 The Logistic Growth Model

6.1 Intraspecific Competition

We have considered a model in which populations grow without constraint. However, due to the finiteness of resources, an environment cannot sustain an infinite population. When resources start being scarce, a fierce competition among individuals of the same species begins. We call this effect intraspecific competition (i.e., within the same species).

To set the stage, let's examine some data from Gause (1932). To test the effects of intraspecific competition, Gause used brewer's yeast (*Saccharomyces cerevisiae*). His experiments were based on the growth of yeast in an environment with a limited nutrients. He started the population at some low level and then he measured the volume of the cells in time. The data is represented in Figure 1.
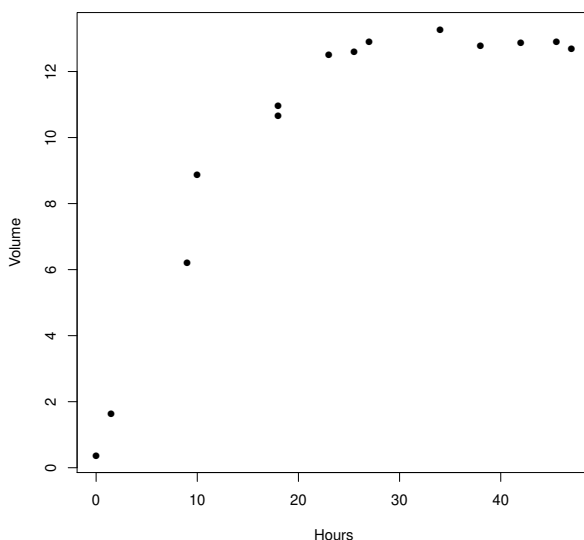

Figure 1: Data measured by Gause. Growth of brewer's yeast in an environment with limited nutrients.

Clearly, yeast does not grow to infinity. Rather, after 1 day or so the population stops growing and remains around a given volume. Suppose that a population can grow up to a certain threshold K, usually known as carrying capacity. This model can be represented by the differential equation:

$$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right) \tag{6.1}$$

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where r can be measured as the growth rate at very low density and K is the carrying capacity for the system, i.e., the density of individuals the habitat can support. (Note that $r > 0$ and $K > 0$, otherwise this equation does not make biological sense. If $r < 0$, why doesn't this make sense?)

6.2   Analysis

Plot $\frac{dN(t)}{dt}$ vs. $N(t)$ (see Figure 2). Using this graphical method we can count the number of equilibria and investigate their stability.
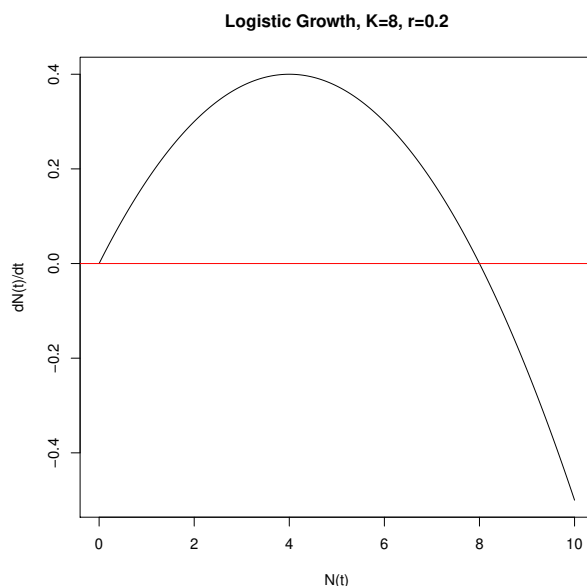

Figure 2: Graphical methods for logistic growth.

We define an equilibrium point (or steady state, or fixed point or critical point) a point in which $\frac{dN}{dt} = 0$. In this point, the growth rate is zero: left alone, the population will not grow nor decay. In the logistic growth equation we have two fixed points: $N^* = 0$, $N^* = K$. This can be seen in the graph whenever $\frac{dN}{dt}$ crosses the zero line.

An equilibrium point N^* is stable if when we slightly perturb the system that is resting at N^*, $\lim_{t \to \infty} N(t) = N^*$. We can think about stability using the cartoon in Figure 3.

The red ball is at an unstable equilibrium point: slightly perturbing its position will set it in motion ending up at another point. The blue balls, on the other hand, will return to the same point once slightly perturbed: they are at stable equilibrium points.

For the logistic growth, we have that $N_1^* = 0$ is unstable, while $N_2^* = K$ is stable. If you start with zero bacteria, say, you will always have zero, but as soon as you have a single organism, you get exponential growth. Close to this fixed point, the system does not 'feel' the carrying-capacity. For single species dynamics, whenever growth rate is > 0 on the left of the fixed point and < 0 on the right of the fixed point we have stability. Therefore, if a species has density 0 and we slightly increase its density (decreasing it
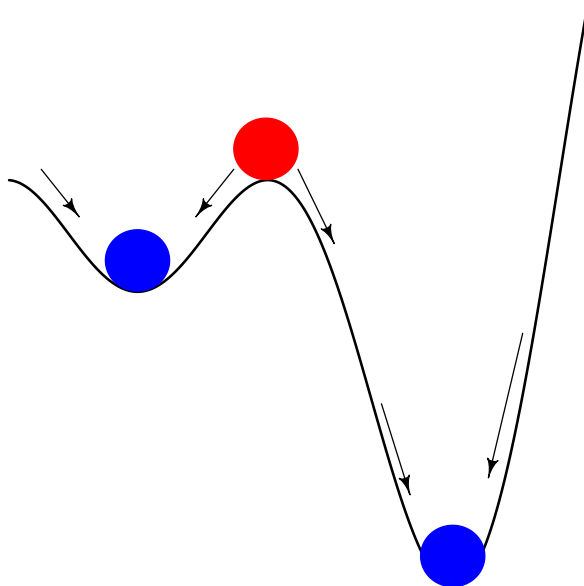
Figure 3: Stability as a metaphor.

would be a biological nonsense) it will start growing until it reaches density K, when it will stop growing. It stops growing exponentially, and with the same rate that it exploded near 0.

We will now use some mathematics to get a qualitative understanding of equilibria. First, we want to find the equilibria. By definition, we want to solve the equation:

$$rN^* \left(1 - \frac{N^*}{K}\right) = 0 \tag{6.2}$$

There is a trivial solution:

$$N^* = 0 \tag{6.3}$$

while the other solution can be found using:

$$1 - N^*/K = 0 \tag{6.4}$$

$$N^*/K = 1 \tag{6.5}$$

$$N^* = K \tag{6.6}$$

We now want to measure the growth rate in the vicinity of an equilibrium. First, let us assume that $N(0) \ll K$ (i.e., the population at time 0 is at a much lower level than the carrying capacity). Then, $(1 - N(0)/K) \approx 1$. This means that the growth rate equation is approximately:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \approx rN \tag{6.7}$$

the population, when close to 0, will grow almost exponentially. In the same way, we can evaluate what happens when $N(0) \approx K$. In this case $(1 - N(0)/K) \approx 0$ and therefore:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \approx 0 \tag{6.8}$$

the population will remain constant.

Finally, when $N(0) \gg K$ the term $(1 - N(0)/K)$ becomes negative (say the value is some unspecified $-y$). Then the approximate growth becomes:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \approx -rNy \tag{6.9}$$

the population decreases exponentially.

We want to know where the population grows at the fastest rate. To do so, we first take the derivative:

$$\frac{\partial \frac{dN}{dt}}{\partial N} = r - \frac{2rN}{K} \tag{6.10}$$

and equate it to zero:

$$r - \frac{2rN}{K} = 0 \tag{6.11}$$

$$N = \frac{K}{2} \tag{6.12}$$

we find that when the population is half-saturated, it grows at the fastest rate. Piecing these facts together, we can draw a qualitative solution for the differential equation (Figure 4).

This qualitative drawing captures the essential features of the solution:

$$N(t) = \frac{K}{1 + (K/N_0 - 1)e^{-rt}} \tag{6.13}$$

The solution can be obtained using partial fractions, and is reported below.
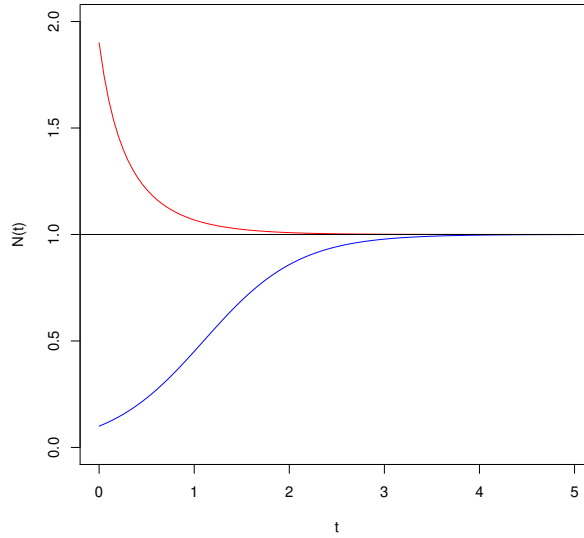
Figure 4: Logistic Growth: $K = 1, r = 2$. Blue: $N(0) = 0.1$, Red: $N(0) = 1.9$

6.3   Optional - Solving the Logistic Equation

Numerical solutions for a model depend on the actual values of all the parameters and initial conditions. However, the possible behavior of the model is controlled by the relation among the parameters (e.g., if you express the mass in grams or kg, the numbers will change, but the stability of equilibria will not). A useful technique to investigate which combination of parameters is critical for the dynamics of the system is the rescaling of models so that they become dimensionless. Dimensionless models typically contain less parameters than their counterpart.

For example, take the logistic growth model above and set $x = N/K$. Because both N and K are of the same unit (e.g., biomass, or density), then x has no dimension.

$$\frac{dx}{dt} = \frac{1}{K} \tag{6.14}$$

$$\frac{dN}{dt} = \frac{1}{K} rN \left(1 - \frac{N}{K}\right) = rx(1 - x) \tag{6.15}$$

now let's set $rt = \tau$. Note that r is in units of $1/time$, so that τ is dimensionless. This makes the system dimensionless (use chain rule with $dt = d\tau/r$):

$$\frac{dx}{d\tau} = \frac{dx}{dt}\frac{dt}{d\tau} = \frac{1}{r}\frac{dx}{dt} = \frac{1}{r}rx(1 - x) = x(1 - x) \tag{6.16}$$

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6.3.1 Solving the logistic dimensionless model

This is a separable differential equation:

$$\int \frac{1}{x(1-x)} dx = \int d\tau \tag{6.17}$$

For the left part we use partial fractions:

$$\frac{1}{x(1-x)} = \frac{A}{x} + \frac{B}{x-1} \tag{6.18}$$

Multiply both sides by $x(x-1)$:

$$-1 = A(x-1) + Bx \tag{6.19}$$

When $x = 0$ we find that $A = 1$; when $x = 1$ we have $B = -1$. Therefore:

$$\int \frac{1}{x(1-x)} dx = \int \left(\frac{1}{x} - \frac{1}{x-1} \right) dx \tag{6.20}$$

Integrate by making the change of variables $u = x - 1$:

$$\int \left(\frac{1}{x} - \frac{1}{x-1} \right) dx = \int \frac{1}{x} dx - \int \frac{1}{x-1} dx = \int \frac{1}{x} dx - \int \frac{1}{u} du \tag{6.21}$$

The integrals are now very simple to solve:

$$log(x)|_{x(0)}^{x(\tau)} - log(x-1)|_{x(0)}^{x(\tau)} = \tau \tag{6.22}$$

From this, setting $x(0) = x_0$ we can write:

$$log(x(\tau)) - log(x_0) - log(x(\tau) - 1) + log(x_0 - 1) = \tau \tag{6.23}$$

$$log \frac{x(\tau)(x_0 - 1)}{(x(\tau) - 1)x_0} = \tau \tag{6.24}$$

$$\frac{x(\tau)(x_0 - 1)}{(x(\tau) - 1)x_0} = e^\tau \tag{6.25}$$

$$x(\tau)(x_0 - 1) = e^\tau ((x(\tau) - 1)x_0) \tag{6.26}$$

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$$x(\tau)(x_0 - 1 - x_0 e^\tau) = -x_0 e^\tau \tag{6.27}$$

$$x(\tau) = \frac{x_0 e^\tau}{(1 + x_0 e^\tau - x_0)} = \frac{x_0 e^\tau}{(1 + x_0(e^\tau - 1))} \tag{6.28}$$

Now we can substitute back $\tau = rt$ and $x(t) = N(t)/K$ to recover the solution of the logistic growth:

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)} \tag{6.29}$$

7 Euler method for numerical integration

The Euler method is a very basic way to perform numerical integration on an ordinary differential equation. Suppose you wish to approximate a function, $\dot{x}(t) = f(x)$. You start at some initial condition, x_0, and want to play the dynamics forward in time. The Euler method has a simple update rule, based on the definition of the derivative from your intro calculus course. For a small step in time, Δt, update x by

$$x_{n+1} = x_n + \Delta t f(x), \tag{7.1}$$

where x_n is an approximation to $x(t_n)$.

This method is very simple to code but suffers from the fact that you need to take step sizes, Δt, much smaller than any intrinsic time scale in your system to achieve good performance. Other numerical integration methods, such as Runge-Kutta, are included in most programming packages. You should simulate a system in which you know the solution to familiarize yourself with these numerical integration schemes.

8 Further reading

Would you like to know more about nonlinear dynamics and chaos? If so, a particularly accessible set of online lectures by Steve Strogatz is available on YouTube, and a link can be found at:
`https://www.youtube.com/playlist?list=PLbN57C5Zdl6j_qJA-pARJnKsmROzPnO9V`