

Figure 1.16: A capacitor  $C$  and resistor  $R$  connected in parallel. The voltage drop  $V$  is the same across the two elements of the circuit, while the currents flowing through the two circuit element must add to zero, as expressed in Eq (1.165).

## 1.5 Simple circuits and population dynamics

Most of you remember a little bit about electrical circuits from your high school physics classes. In Fig 1.16 we show a capacitor  $C$  and a resistor  $R$  connected in parallel. Here “parallel” means that the voltage difference  $V$  between the two plates of the capacitor is the same as the voltage difference across the resistor. In this simple case the circuit is closed and there is no path for current to flow out, so the current that flows through the capacitor and resistor must add up to zero. This condition of zero current (an application of Kirchoff’s laws, if that jogs your memory) allows us to write down the equation for the dynamics of the voltage  $V$  in this circuit.

Recall that the current which flows through the resistor is just  $I_1 = V/R$ . We usually think of the capacitor as being described by  $Q = CV$ , where  $Q$  is the charge on the capacitor plates, but of course if the charge changes with time there is a current flow (by definition), so that the current which

flows through the capacitor is  $I_2 = d(CV)/dt = C(dV/dt)$ . Adding these currents must give zero, and this must be true at every moment of time  $t$ :

$$I_1 + I_2 = \frac{V(t)}{R} + C \frac{dV(t)}{dt} = 0. \quad (1.165)$$

It is slightly more convenient to write this as

$$RC \frac{dV(t)}{dt} + V(t) = 0. \quad (1.166)$$

We recognize Eq (1.166) as the same equation we have seen before, both in the mechanics of motion with drag and in first order chemical kinetics. By now we know that the solution is an exponential decay,

$$V(t) = V(0)e^{-t/\tau}, \quad (1.167)$$

where the time constant  $\tau = RC$ . As you might guess by looking at the circuit—there is no battery and no current source—any initial voltage  $V(0)$  decays to zero, and this decay happens on a time scale  $\tau = RC$ . This is important because most circuits that we build, including the circuits on the chips in your computer, have some combination of resistance and capacitance, and so we know that there is a time scale over which these circuits will lose their memory. In memory chips we want this to be a very long time, so (roughly speaking) one tries to design the circuit so that  $R$  is very large. Conversely, on the processor chips things should happen fast, so  $RC$  should be small. You may recall that the capacitance  $C$  is determined largely by geometry—how big are the plates and how far apart are they?—so if we want to squeeze a certain number of circuit elements into a given area of the chip the capacitances are more or less fixed, and the challenge is to reduce  $R$ .

Almost the same equations arise in a very different context, namely population growth. Imagine that we put a small number of bacteria into a large container, with plenty of food; you will soon do more or less this experiment in the lab part of the course. Let's call  $n(t)$  the number of bacteria present at time  $t$ . Because the bacteria divide,  $n(t)$  increases. As a first approximation, it's plausible that the rate at which new bacteria appear is proportional to the number of bacteria already there, so we can write

$$\frac{dn(t)}{dt} = rn(t), \quad (1.168)$$

where  $r$  is the “growth rate.” This is just like the equations we have seen so far, but the sign is different.

When we had an equation of the form

$$\frac{dx}{dt} = -kx, \quad (1.169)$$

we found that the solution is of the form  $x(t) = A \exp(-kt)$ , where the constant  $A = x(t = 0)$ . More generally we can say that this solution is of the form  $x(t) = A \exp(\lambda t)$ , and it turns out the  $\lambda = -k$ . As will become clearer in the next few lectures, this exponential form is very general, and helps us solve a large class of problems. So, let's try it here.

We guess a solution in the form  $n(t) = Ae^{\lambda t}$ , and substitute into Eq (1.168):

$$\begin{aligned} \frac{dn(t)}{dt} &= rn(t) \\ \frac{d}{dt}[Ae^{\lambda t}] &= r[Ae^{\lambda t}] \end{aligned} \quad (1.170)$$

$$A \frac{d}{dt}[e^{\lambda t}] = \quad (1.171)$$

$$A\lambda[e^{\lambda t}] = Ar[e^{\lambda t}]. \quad (1.172)$$

Now the exponential of any finite quantity can never be zero, so we can divide both sides of the equation by  $[e^{\lambda t}]$  to obtain

$$\begin{aligned} A\lambda[e^{\lambda t}] &= Ar[e^{\lambda t}] \\ A\lambda &= Ar. \end{aligned} \quad (1.173)$$

As for the constant  $A$ , if this is zero we are in trouble, since then our whole solution is zero for all time (this is sometimes called the “trivial” solution; we'll try to avoid using that word in this course). So we can divide through by  $A$  as well, and we find that  $\lambda = r$ . The important point is that by choosing an exponential form for our solution we turned the differential equation into an algebraic equation, and in this case even the algebra is easy. So we have shown that the population behaves as  $n(t) = Ae^{\lambda t}$ , where  $\lambda = r$  and you should be able to show that  $A$  is the population at  $t = 0$ , so that

$$n(t) = n(0)e^{rt}. \quad (1.174)$$

Thus, rather than decaying exponentially, the population of bacteria grows exponentially with time. Instead of a half-life we now have a doubling time  $\tau_{\text{double}} = \ln 2/r$ , which is the time required for the population to become twice as large.

We have (perhaps optimistically) ignored death. But death only happens to bacteria that are alive (!), so again its plausible that the rate at which

the population *decreases* by death is proportional to the number of bacteria,  $-dn(t)$ , where  $d$  is the death rate. Then

$$\frac{dn(t)}{dt} = rn(t) - dn(t) = (r - d)n(t), \quad (1.175)$$

so if we define a new growth rate  $r' = r - d$  everything is as it was before. In fact, if we are just watching the total number of bacteria we can't tell the difference between a slower growth rate and a faster death rate.

These equations for the population of bacteria are approximate. Let's make a list of some of the things that we have ignored, and see if we can improve our approximation:

- We've assumed that the discreteness of bacteria isn't important—you can't have 305.7 bacteria, but we pretend that  $n(t)$  is a continuous function. Probably this isn't too bad if the population is of a reasonable size.
- We've assumed that all the bacteria are the same. It's not so hard to make sure that they are genetically identical—just start with one and don't let things run long enough to accumulate too many mutations. It takes more effort to insure that all the bacteria experience the same environment.
- We've assumed that the bacteria don't murder each other, and more gently that the consumption of food by the ever increasing number of bacteria doesn't limit the growth.
- We've assumed that the growth isn't synchronized.

These last two points deserve some discussion.

We can model the “environmental impact” of the bacteria by saying that the effective growth rate  $r'$  gets smaller as the number of bacteria gets larger. Certainly this starts out being linear, so maybe we can write  $r' = r_0[1 - an(t)]$ , so that

$$\frac{dn(t)}{dt} = r_0[1 - an(t)]n(t). \quad (1.176)$$

But then this defines a critical population size  $n_c = 1/a$  such that once  $n = n_c$  the growth will stop ( $dn/dt = 0$ )—the environment has reached its capacity for sustaining the population. It's natural to measure the population size as a fraction of this capacity, so we write  $x = n/n_c$ , so (being

careful with all the steps, since this is the kind of thing you'll need to do many times)

$$\begin{aligned}\frac{dn(t)}{dt} &= r_0[1 - an(t)]n(t) \\ \frac{d}{dt} \left( n_c \frac{n(t)}{n_c} \right) &= r_0 \left[ 1 - a \left( n_c \frac{n(t)}{n_c} \right) \right] \left( n_c \frac{n(t)}{n_c} \right)\end{aligned}\tag{1.177}$$

$$n_c \frac{dx(t)}{dt} = [1 - (an_c)x(t)]n_c x(t)\tag{1.178}$$

$$\frac{dx(t)}{dt} = r_0 x(t)[1 - x(t)],\tag{1.179}$$

where at the last step we cancel the common factor of  $n_c$  and use the fact that (by our choice of  $n_c$ )  $an_c = 1$ .

This equation predicts that if we start with a very small ( $x \ll 1$ ) population, the growth will be exponential with a rate  $r_0$ , but as  $x$  gets close to 1 this has to stop, and the population will reach a steady, saturated state. These dynamics will be important in your experiments, so let's actually solve this equation.

**Problem 20:** In the previous paragraph we made some claims about the behavior of  $x(t)$ , based on Eq (1.179), but without actually solving the equation (yet). Can you explain why these claims are true, also without constructing a full solution? To get started, can you make a simpler, approximate equation that should describe the dynamics accurately when  $x \ll 1$ ?

We use the same idea as before, "moving" the  $x$ 's to one side of the equation and the  $dt$  to the other:

$$\frac{dx}{dt} = r_0 x[1 - x]\tag{1.180}$$

$$\frac{dx}{x(1 - x)} = r_0 dt.\tag{1.181}$$

If you remember how to do the integral

$$\int \frac{dx}{x(1 - x)},$$

you can proceed directly from here. If, like me, you remember that

$$\int \frac{dx}{x} = \ln x,$$

but aren't sure what to do about the more complicated case, then you need to turn the problem you have into the one you remember how to solve.

**Problem 21:** Starting with

$$\int \frac{dx}{x} = \ln x, \tag{1.182}$$

remind yourself of why

$$\int \frac{dx}{1-x} = -\ln(1-x). \tag{1.183}$$

The trick we need here is that fractions which have products in the denominator can be expanded so that they just have single terms in the denominator. What this means is that we want to try writing

$$\frac{1}{x(1-x)} = \frac{A}{x} + \frac{B}{1-x}, \tag{1.184}$$

but we have to choose  $A$  and  $B$  correctly. The way to do this is to work backwards:

$$\frac{A}{x} + \frac{B}{1-x} = \frac{A(1-x)}{x(1-x)} + \frac{Bx}{x(1-x)} \tag{1.185}$$

$$= \frac{A(1-x) + Bx}{x(1-x)} \tag{1.186}$$

$$= \frac{A + (B-A)x}{x(1-x)}. \tag{1.187}$$

Now it is clear that if we want this to equal

$$\frac{1}{x(1-x)},$$

then we have to choose  $A = 1$  and  $B = A = 1$ . So we have

$$\frac{1}{x(1-x)} = \frac{1}{x} + \frac{1}{1-x}, \quad (1.188)$$

and now we can go back to solving our original problem:

$$\begin{aligned} \frac{dx}{x(1-x)} &= r_0 dt \\ \frac{dx}{x} + \frac{dx}{1-x} &= r_0 dt \end{aligned} \quad (1.189)$$

$$\int_{x(0)}^{x(t)} \frac{dx}{x} + \int_{x(0)}^{x(t)} \frac{dx}{1-x} = \int_0^t r_0 dt \quad (1.190)$$

$$\ln(x) \Big|_{x(0)}^{x(t)} - \ln(1-x) \Big|_{x(0)}^{x(t)} = r_0 t \quad (1.191)$$

$$\ln[x(t)] - \ln[x(0)] - \ln[1-x(t)] + \ln[1-x(0)] = r_0 t \quad (1.192)$$

$$\ln \left[ \frac{x(t)}{x(0)} \cdot \frac{1-x(0)}{1-x(t)} \right] = r_0 t \quad (1.193)$$

$$\frac{x(t)}{x(0)} \cdot \frac{1-x(0)}{1-x(t)} = \exp(r_0 t) \quad (1.194)$$

$$\frac{x(t)}{1-x(t)} = \frac{x(0)}{1-x(0)} \exp(r_0 t). \quad (1.195)$$

Note that in the last steps we use the fact that sums (differences) of logs are the logs or products (ratios), and then we get rid of the logs by exponentiating both sides of the equation. The very last step puts the time dependent  $x(t)$  on left side and the initial condition on the right.

Equation (1.195) is almost what we want, but it would be more useful to write  $x(t)$  explicitly. Notice that what we have is of the form

$$\frac{x(t)}{1-x(t)} = F, \quad (1.196)$$

where  $F$  is some factor. You'll see things like this again, so it might be worth knowing the trick, which is to invert both sides, rearrange, and invert

again:

$$\frac{x(t)}{1-x(t)} = F$$

$$\frac{1-x(t)}{x(t)} = \frac{1}{F} \quad (1.197)$$

$$\frac{1}{x(t)} - 1 = \quad (1.198)$$

$$\frac{1}{x(t)} = 1 + \frac{1}{F} \quad (1.199)$$

$$= \frac{F+1}{F} \quad (1.200)$$

$$x(t) = \frac{F}{1+F}. \quad (1.201)$$

Armed with this little bit of algebra, we can solve for  $x(t)$  in Eq (1.195):

$$\frac{x(t)}{1-x(t)} = \frac{x(0)}{1-x(0)} \exp(r_0 t)$$

$$\Rightarrow x(t) = \frac{\frac{x(0)}{1-x(0)} \exp(r_0 t)}{1 + \frac{x(0)}{1-x(0)} \exp(r_0 t)} \quad (1.202)$$

$$= \frac{x(0) \exp(r_0 t)}{[1-x(0)] + x(0) \exp(r_0 t)}, \quad (1.203)$$

where the last step is just to make things look a little nicer.

Some graphs of Eq (1.203) are shown in Fig 1.17. You should notice that all of the curves run smoothly from  $x(0)$  up to the maximum value of  $x = 1$  at long times. Indeed, all the curves seem to look the same, just shifted along the time axis. Hopefully you'll see something like this in the lab!

**Problem 22:** It's useful to look at an expression like Eq (1.203) and "see" some of the key features that appear in the graphs, without actually making the exact plots.

(a.) Be sure that if you evaluate  $x(t)$  at  $t = 0$  you really do get  $x(0)$ , as you should if we did all the manipulations correctly.

(b.) Ask yourself what happens as  $t \rightarrow \infty$ . You should be able to see that  $x(t)$  approaches 1, no matter what the initial value  $x(0)$ , as long as it's not zero.

(c.) Show that you can rewrite Eq (1.203) as

$$x(t) = \frac{1}{1 + \exp[-r_0(t - t_0)]}, \quad (1.204)$$

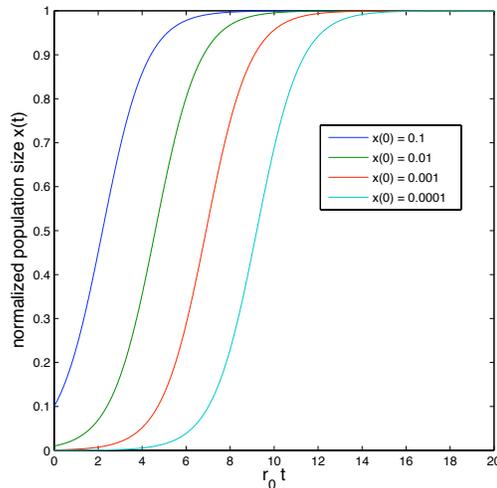


Figure 1.17: Dynamics of population growth as predicted by Eq (1.203), the solution to Eq (1.179). Time is measured in units of the growth rate  $r_0$  of small populations, and the population size is normalized the “capacity” of the environment.

where  $t_0$  depends on the initial population. What does this mean about the growth curves that start with different values of  $x(0)$ ?

**Problem 23:** As discussed in connection with the first laboratory and in Section 1.1, an object moving through a fluid at relatively high velocities experiences a drag force proportional to the square of its velocity. In the presence gravity this means that  $F = ma$  can be written as

$$m \frac{dv}{dt} = -av^2 + mg, \quad (1.205)$$

where the velocity  $v$  is positive if the object is moving downwards,  $a$  is the drag coefficient, and  $g$  as usual is the acceleration due to gravity. As noted in the lectures, a similar equations can arise in chemical kinetics.

(a.) For any given system, the usual units of time, speed, etc. might not be very natural. Perhaps there is some natural time scale  $t_0$  and a natural velocity scale  $v_0$  such that if we measure things in these units our equation will look simpler. Specifically, consider variables  $u \equiv v/v_0$  and  $\tau \equiv t/t_0$ . Show that by proper choice of  $t_0$  and  $v_0$  one can make all the parameters ( $m, g, a$ ) disappear from the differential equation for  $u(\tau)$ .

(b.) Solve the differential equation for  $u(\tau)$ . Does this function have a universal shape? Since we have gotten rid of all the parameters, is there anything left on which the shape could depend? If you need help doing an integral it’s OK to use a table (or perhaps an electronic equivalent), but you need to give references. Translate your results into predictions about  $v(t)$ .

(c.) Suppose that the initial velocity  $v(t = 0)$  is very close to the terminal velocity  $v_\infty = \sqrt{mg/a}$ . Show that your exact solution for  $v(t)$  is approximately an exponential

decay back to the terminal velocity. Then go back to Eq (1.205) and write  $v(t) = v_\infty + \delta v(t)$ , and make the approximation that  $\delta v$  is small, and hence  $\delta v^2$  is even smaller and can be neglected. Can you now show that this approximate equation leads to an exponential decay of  $\delta v(t)$ , in agreement with your exact solution?

(d.) Explain the similarities between this problem and the population growth problem that starts with Eq (1.179) and leads to the results in Fig 1.17. Can you make an exact mapping from one problem to the other?

What about synchronization? Cell growth and division is a cycle, and if this cycle runs like a clock then we can imagine getting all the clocks aligned so that the population of bacteria holds fixed for some length of time, then doubles as all the cells proceed complete their cycle, then holds fixed, doubles again, and so on. In fact, real single celled organisms lose their synchronization if they don't communicate. On the other hand, many organisms (including big complicated ones not so different from us) get synchronized by the seasons—we are all familiar with the nearly simultaneous appearance of all the baby birds at the same time of year. This suggests that rather than writing down a differential equation, we should use one year as the natural unit of time and ask how the number of organisms in one year  $n(t)$  depends on the number that were there last year  $n(t-1)$ . Again if we just think about growth we would argue that the number of new organisms is proportional to the number that we started with, hence

$$n(t) = Gn(t-1), \quad (1.206)$$

where  $G > 1$  means that we are describing growth from season to season while  $G < 1$  means that the population is dying out. It's interesting that in this case the seasonal synchronization doesn't make any difference, because the solution still is exponential:  $n(t) = n(0)e^{t/\tau}$ , where  $\tau = 1/(\ln G)$ .

**Problem 24:** Verify that Eq (1.206) is solved by  $n(t) = n(0)e^{t/\tau}$ , with  $\tau = 1/(\ln G)$ . As a prelude to things which will be important in the next major section of the course, consider a population in which some fraction of the organisms wait for two seasons to reproduce, so that

$$n(t) = G_1 n(t-1) + G_2 n(t-2). \quad (1.207)$$

Can you still find a solution of the form  $n(t) \propto e^{t/\tau}$ ? If so, what is the equation that determines the value of the time constant  $\tau$ ?

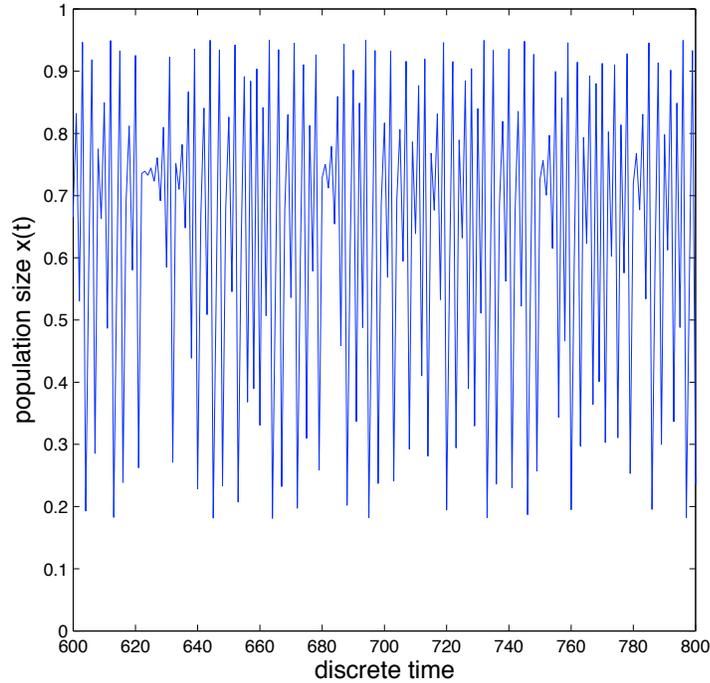


Figure 1.18: Simulation of Eq (1.208) with  $G_0 = 3.8$  starting from an initial condition  $x(1) = 0.1$ . This is in the chaotic regime. We see a general alternation from odd to even times, but no true periodicity.

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Really interesting things happen when we combine the discreteness of seasons with the impact of other organisms on the growth rate. As before, we can try a linear approximation, so that  $G = G_0[1 - n(t)/n_c]$ , and we can rewrite everything in terms of the fractional population  $x$ :

$$x(t) = G_0 x(t-1)[1 - x(t-1)]. \quad (1.208)$$

If  $G_0 < 1$ , no matter where we start, eventually the population dies out and we approach  $x = 0$  at long times. If  $G_0$  is somewhat bigger than 1, then a small initial population grows and eventually saturates. But if  $G_0$  gets even bigger, some interesting things happen. For example, when  $G_0 = 3$ , the population oscillates from season to season, being alternately large and small, and this oscillation continues forever—there is no decay or growth

to a steady state. When  $G_0 = 3.5$ , there is an oscillation with alternating seasons of large and small population, but it takes a total of four seasons before the population repeats exactly. We say that at  $G_0 = 3$  we observe a “period 2” oscillation, and at  $G_0 = 3.5$  we observe a “period 4” oscillation. If we keep increasing  $G_0$  we can observe period 8, period 16, ... all the powers of 2 (!). The transitions to longer and longer periods come more quickly as  $G_0$  increases, until we exceed a critical value of  $G_0$  and the trajectories  $x(t)$  start to look completely random, even though they are generated by the simple Eq (1.208); see Fig 1.18.

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**Problem 25:** Write a program to generate the trajectories  $x(t)$  that are predicted by Eq (1.208). Run this program, exploring different values of  $G_0$ , and verify the statements made in the previous paragraph. In particular, try starting with different initial conditions  $x(0)$ , and see whether the solutions are “attracted” to some simple form at long times, or whether trajectories that start with slightly different values of  $x(0)$  end up looking very different from each other. Does this dependence on initial conditions vary with the value of  $G_0$ ? Can you see what this might have to do with the problem of predicting the weather?

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The random looking trajectories of Fig 1.18 are called *chaotic*, and the discovery that such simple deterministic equations can generate chaos changed completely how we look at the dynamics of the world around us. What is remarkable is that the surprising properties of this simple equation (which you can rediscover for yourself even with a pocket calculator) are provably the properties of a broad class of equations, and one can observe the sequence of period doublings and the resulting chaos in real physical systems, matching quantitatively the predictions of the simple model to key features of the data.

This has been a scant introduction to a rich and beautiful subject. Please ask for more references if you are intrigued.

## 1.6 The complexity of DNA sequences

This section remains to be written. Current students should see the less formal notes posted to blackboard.

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**Problem 26:** The total genomic DNA of a newly-discovered species of newt contains 1200 copies of a 2 kb repeated sequence, 300 copies of a 6 kb repeated sequence as well as 3000 kb of single-copy DNA.

(a.) What will the “Cot curve” (i.e. plot of the fraction of DNA remaining single-stranded vs.  $C_0t$ ) look like? Be sure to label the axes, and indicate the fractional contribution of the different kinds of DNA.

(b.) Devise a procedure to prepare reasonably pure samples of the three kinds of DNA. Explain how you would calculate the times of annealing required for each step.

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