

1. Introduction – comparison of difference and differential equations.

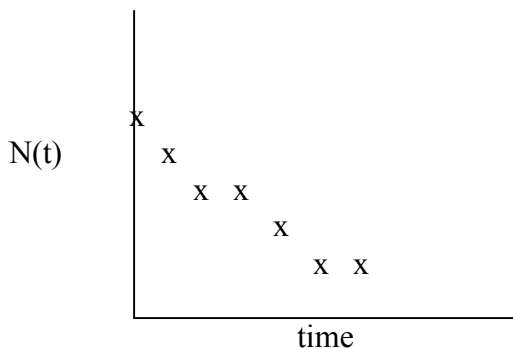
$$N_{t+\Delta t} = F(N_t)$$

In difference equations we use an **updating function**.

Given the state of a system (such as a population size) at one point in time, the updating function gives the state of the system at a later time.

These are called **difference equations** because they specify the relationship between a system state at 2 different times.

When we are dealing with difference equations, we only know the state of the systems at discrete points in time. This is a **discrete-time dynamical system**.



The state of the system at the next point in time depends only on the state at the previous point in time (and possibly also discrete points before that).

- Difference equations are a useful modeling tool only if we can write down an explicit formula relating the values of the state variables at successive times.

When the time interval Δt is large, a valid update rule has to describe the outcome of a complex set of interrelated biological processes, and it may be very difficult to come up with an appropriate formula.

An alternative approach is to use **differential equations** and to model in **continuous time**.

In many cases in biology, we are interested in the future state of the system, but all we know is the current state of the system, and the rates of processes (such as births and deaths) that can change the state of the system.

Continuous-time models describe the state of the system at all points in time, rather than just at discrete points.

We use differential equations to go from:

the rate of change of a variable \rightarrow new value of a variable

speed \rightarrow position

growth rate \rightarrow biomass

birth and death rates \rightarrow population size

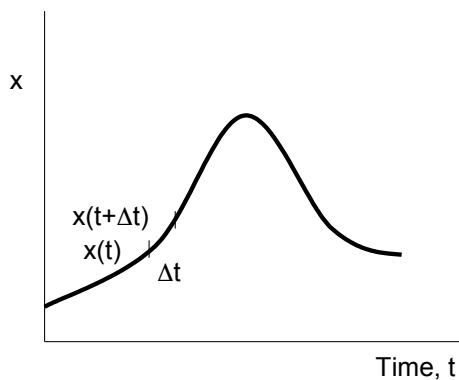
rate of production \rightarrow amount of a chemical

rate of inputs and outputs from lake \rightarrow concentration in the lake

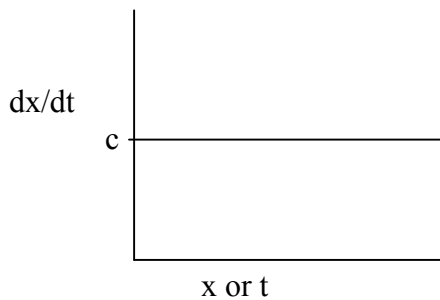
Remember what we mean by the derivative:

$$\frac{dX}{dt} = \lim_{\Delta t \rightarrow 0} \frac{X(t + \Delta t) - X(t)}{\Delta t}$$

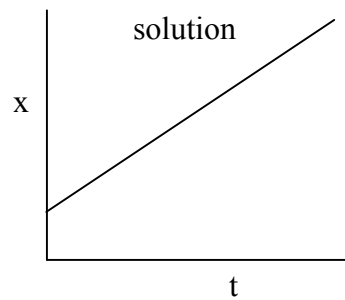
If we plot $X(t)$ versus time, dX/dt is the slope of the tangent to the curve.



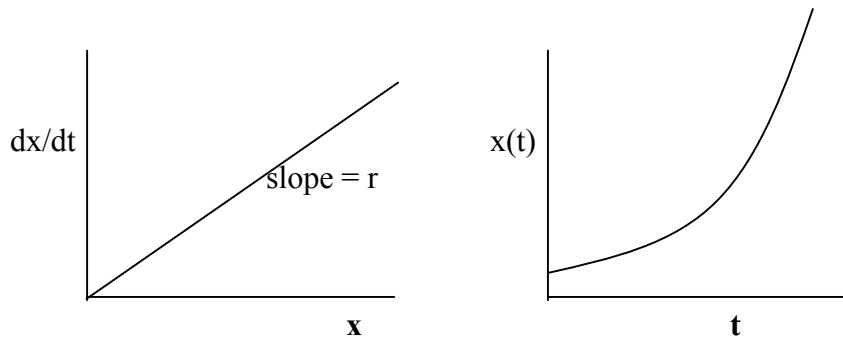
If dX/dt is constant, then X will have a constant rate of change and $X(t)$ will look like a straight line with a constant slope, increasing or decreasing depending on whether the derivative is positive or negative.



$$dx/dt = c$$



If dX/dt increases linearly with X , then the rate of change of X increases linearly as X increases, and X will grow or decline exponentially through time (depending on whether the slope of the relationship with X is positive or negative):



2. Terminology

An **ordinary differential equation** is any statement linking the values of a state variable to its derivative and to a single independent variable:

$$F\left(t, y, \frac{dy}{dt}, \frac{d^2y}{dt^2}, \dots, \frac{d^ny}{dt^n}\right) = 0$$

the single independent variable in this case is time, t .

The **order** of the differential equation is n , the degree of the highest derivative that appears in the equation.

$$\frac{dy}{dx} = 2x \quad \text{first order}$$

$$\frac{d^2y}{dt^2} + 3\frac{dy}{dt} - 2y = 0 \quad \text{second order}$$

The **solution** of an ordinary differential equation is a function, $y=f(t)$ that satisfies the equation for every value of the independent variable.

For example, if C is any real number, then the solution of

$$\frac{dy}{dt} = 2t \quad \text{is: } y = f(t) = t^2 + C$$

because substituting $f(t)$ in for y leads to $2t = 2t$.

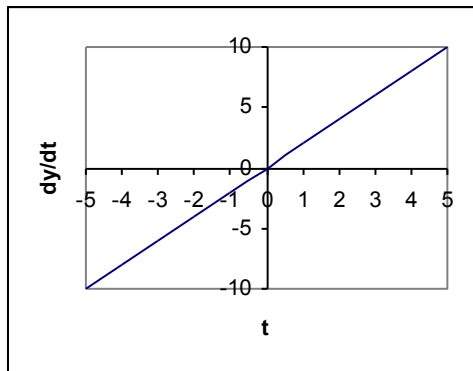
We call $t^2 + C$ a general solution of $\frac{dy}{dt} = 2t$, since every solution will have this form.

All that the differential equation is telling us is the slope of y at each value of t . Therefore it is defining a solution that is a family of curves, shifted up or down depending on the value of C .

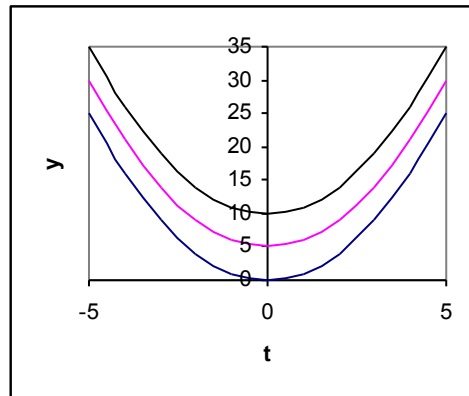
This differential equation is of **first order** and contains 1 arbitrary constant, C .

A second order differential equation will have 2 arbitrary constants.

The **general solution** of an n^{th} order differential equation will contain n independent parameters.



differential equation tells us slope



solution is a family of curve

Particular solution We can obtain a particular solution by plugging in the value of y that we know at one point in time t . For example, if we know that at $t=0$, $y = 5$, then $5 = 0^2 + C$, and C is 5.

Much of the work in differential equations involves coming up with ways to find the solutions of differential equations. We'll find out that in most cases it is not possible to come up with an exact solution of $y = f(t)$, and in these cases there are a number of tricks that people do in order to find out something about the behavior of the solution to a differential equation when you can actually solve it. We'll spend most of the next 3 weeks talking about these.

Continuing with terminology:

Linear differential equations have the special form:

$$\frac{d^n y}{dt^n} + a_{n-1}(t) \frac{d^{n-1} y}{dt^{n-1}} + \cdots + a_2(t) \frac{d^2 y}{dt^2} + a_1(t) \frac{dy}{dt} + a_0(t)y = g(t)$$

where there are no non-linearities in y or its derivatives.

The coefficients a_0, a_1, \dots, a_n can be functions of the independent variable, t .

But the case of **constant coefficients** (where a_0, a_1, \dots, a_n are all constants) is of particular importance to stability analysis because it can in principle be solved completely.

The equation is **homogeneous** if $g(t) = 0$, i.e. there isn't a term that depends just on the independent variable.

Autonomous differential equations are differential equations that just involve y and the derivatives of y . They do not depend on the independent variable (time) directly.

$$F\left(y, \frac{dy}{dt}, \frac{d^2y}{dt^2}, \dots, \frac{d^ny}{dt^n}\right) = 0$$

The equation for logistic growth of a population is a first order, autonomous, non-linear differential equation.

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

Many of the basic population models that we run into are autonomous differential equations. But if the carrying capacity, K , is a function of time, rather than being a constant, then this equation would become **non-autonomous**:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K_1 + K_2 \sin(\omega t + c)}\right)$$

The rate of change of the population no longer depends only on N , but it depends on time as well.

Examples:

$$\frac{d^2x}{dt^2} + 2x\frac{dx}{dt} + x^2 = \sin t \quad \begin{array}{l} \text{second order, non-linear, non-autonomous,} \\ \text{non-homogeneous} \end{array}$$

$$\frac{d^3x}{dt^3} + 2t\frac{dx}{dt} + t^2x = 0 \quad \begin{array}{l} \text{third order, linear, non-autonomous, homogeneous} \end{array}$$

3. Differential Equations that we can solve

3.1. Pure-time Differential Equations.

In **pure-time differential equations**, the rate of change of some state variable is just some function of time.

The general form of a pure-time differential equation is:

$$\frac{dF}{dt} = f(t)$$

$F(t)$ is the unknown state variable, and $f(t)$ is its measured rate of change.

We are looking for a function $F(t)$ whose derivative is $f(t)$.

To find this, we simply take the **antiderivative of f** , which is also called the **indefinite integral** of f .

$$F(t) = \int f(t)dt$$

Every differentiable function has only one derivative, but the same function has a whole family of antiderivatives.

$$\int f(t)dt = F(t) + C \quad \text{where } C \text{ is the arbitrary constant.}$$

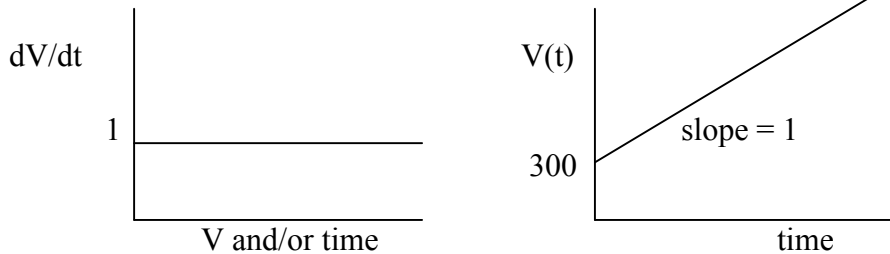
For example, if we know that water is entering a cell at a constant rate of $1.0\text{mm}^3/\text{s}$, and that the volume of the cell at $t=0$ is 300mm^3 , then we can calculate the volume of the cell at any later point in time:

$$\frac{dV}{dt} = 1$$

$$V(t) = \int 1 dt = t + C$$

$$V(0) = 0 + C = 300$$

The solution is: $V(t) = t + 300$.



I'm not going to go through all of the rules for integrals. It is pretty much an art form, and there are tables of common integrals in any calculus text book.

These days when I want to know the solution of a complex pure-time differential equation, I get the computer package, **Mathematica** to do it for me. It is a very useful package for symbolic algebra.

In Mathematica I can say:

Integrate $[(t^3-1)/(t-1),t]$, meaning $\int \left(\frac{t^3-1}{t-1} \right) dt$

And it'll come back with:

$$t + \frac{t^2}{2} + \frac{t^3}{3}$$

Continuing with some types of differential equations that we can solve:

3.2. *Some Autonomous Differential Equations.*

In this class of differential equations, the rate of change depends only on the state of the system, not on external factors:

$$\frac{dN}{dt} = g(N)$$

here the stuff on the right hand side depends on N rather than on t (as in pure-time differential equations).

- In autonomous differential equations, although the rate of change does not depend explicitly on time, the solution does.

First-order autonomous differential equations: Some can be solved explicitly.

One important first order autonomous differential equation that is easy to solve is the equation for exponential growth:

$$\frac{dN}{dt} = rN$$

where the rate that the population is growing is a linear function of the current population density. $r = b - d$: the per capita birth rate – the per capita death rate. If $r > 0$ the population is increasing in size, if $r < 0$ the population is decreasing in size.

We can't directly integrate the right hand side, as we did in pure-time differential equations, because here integrating the function rN requires knowing the solution $N(t)$. But, we'd like to be able to turn this problem into an integration problem, because we know how to solve most integrals.

3.2.1 Separation of Variables

One of the most useful methods for solving first-order differential equations is separation of variables.

The trick of separation of variables, as the name implies, is to separate the two variables, so that all of the stuff that involves N is on one side of the equation, and all of the stuff that involves t is on the other side.

If we divide both sides by N we get:

$$\frac{1}{N} \frac{dN}{dt} = r$$

then if we integrate both sides with respect to t we get:

$$\int \frac{1}{N} \frac{dN}{dt} dt = \int r dt$$

and by the change of variables procedure for integrals in calculus we get:

$$\int \frac{1}{N} dN = \int r dt$$

$$\int \frac{1}{N} dN = \ln(|N|) + c_1$$

$$\int r dt = rt + c_2$$

The absolute value bars around N (required by the integral of $1/x$) are unnecessary, if N represents a population, and therefore must be positive.

$$\ln(N) + c_1 = rt + c_2$$

c_1 and c_2 are both arbitrary, so we can combine them into a single constant.

$$\ln(N) = rt + c$$

We can solve for N by exponentiating both sides:

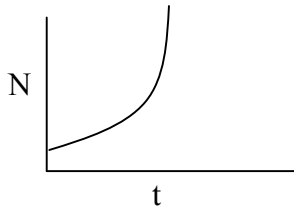
$$N(t) = e^{rt+c} = e^{rt}e^c = Ce^{rt}$$

we can find the constant by substituting in the initial condition:

If N at time 0 is N_0 ,

$$\text{then } N_0 = C e^{r \cdot 0} \Rightarrow C = N_0$$

$$N(t) = N_0 e^{rt}$$



Separation of variables works in some cases, but not all cases.

Logistic Growth:

Another familiar case where it works is in the model for logistic growth of a population:

$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$, where r is the maximum population growth rate at low densities, and K is the carrying capacity.

Separate the variables:

$$\int \frac{dN}{N\left(1 - \frac{N}{K}\right)} = \int r dt$$

If you look at a table of integrals, there is one that says:

$$\int \frac{du}{u(a + bu)} = \frac{1}{a} \ln \left| \frac{u}{a + bu} \right| + c$$

This will work for us if:

$$u = N$$

$$a = 1$$

$$b = -\frac{1}{K}$$

This gives us:

$$\ln \left(\frac{N}{1 - \frac{N}{K}} \right) + c_1 = rt + c_2$$

$$\frac{N}{1 - \frac{N}{K}} = Ce^{rt}$$

From this we can plug in N_0 for N at time 0, so that:

$$C = \frac{N_0}{1 - \frac{N_0}{K}}$$

$$N = Ce^{rt} \left(1 - \frac{N}{K} \right)$$

$$N \left(1 + \frac{Ce^{rt}}{K} \right) = Ce^{rt}$$

$$N = \frac{Ce^{rt}}{1 + \frac{Ce^{rt}}{K}}$$

Plugging in C, this can be written as:

$$N(t) = \frac{KN_0 e^{rt}}{K - N_0 + N_0 e^{rt}}$$

If you try plotting this out, it looks like the familiar curve for logistic population growth.

