

Linear Ordinary Differential Equations**EEMB247/BMSE247*****Constant-Coefficient Homogeneous Linear Differential Equations*****First Order Constant Coefficient differential equations:**

$$\frac{dN}{dt} = rN \quad \text{have solutions of the form: } N(t) = N_0 e^{rt}$$

Second order constant coefficient differential equations:

$$a \frac{d^2 x}{dt^2} + b \frac{dx}{dt} + cx = 0$$

One way to solve such a differential equation is to guess that its solution will also be of the form:

$$x(t) = e^{\lambda t}$$

where λ is a constant. If we assume this, then

$$x'(t) = \lambda e^{\lambda t}$$

and

$$x''(t) = \lambda^2 e^{\lambda t}$$

substituting these in the equation gives:

$$a \lambda^2 e^{\lambda t} + b \lambda e^{\lambda t} + c e^{\lambda t} = 0$$

divide through by the common factor:

$$a \lambda^2 + b \lambda + c = 0$$

This characteristic equation has two roots:

$$\lambda_{1,2} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

so the 2 solutions to the equation are:

$$x_1(t) = e^{\lambda_1 t}, \quad x_2(t) = e^{\lambda_2 t}$$

In general, once we have two linearly independent solutions to the differential equation, then we can find all solutions. (Not scalar multiples of each other)

If x_1 and x_2 are two solutions, then the general solution is:

$$\boxed{x(t) = c_1 e^{\lambda_1 t} + c_2 e^{\lambda_2 t}}$$

where c_1 and c_2 are arbitrary constants, determined from other information, such as the initial conditions.

case 1: roots real and unequal, $a^2 - 4b > 0$

example:

$$y'' + 3y' - 10y = 0$$

The characteristic equation is:

$$\lambda^2 + 3\lambda - 10 = 0$$

The roots are: $\lambda_1 = 2, \lambda_2 = -5$

The general solution is:

$$y(t) = c_1 e^{2t} + c_2 e^{-5t}$$

If we specify initial conditions $y(0) = 1$ and $y'(0) = 3$, then we can determine the constants c_1 and c_2 .

$$y(0) = 1 = c_1 e^{2 \cdot 0} + c_2 e^{-5 \cdot 0} \quad \Rightarrow \quad c_1 + c_2 = 1$$

differentiating:

$$y'(0) = 3 = 2c_1 e^{2 \cdot 0} - 5c_2 e^{-5 \cdot 0} \quad \Rightarrow \quad 2c_1 - 5c_2 = 3$$

$$c_1 = 8/7 \text{ and } c_2 = -1/7$$

The unique solution to the initial value problem is:

$$y(t) = 1/7 * (8 e^{2t} - 1 e^{-5t})$$

As t gets large, this will be dominated by the term with the larger eigenvalue, so the solution will grow exponentially.

case 2: roots real and equal, $b^2 - 4ac = 0$

In this case, the equation has a double root, $\lambda_1 = \lambda_2 = -b/(2a)$.

$x_1(t) = e^{-bt/(2a)}$ is a solution to the equation. If it is possible to find one solution, there are methods for finding a second, linearly independent solution, that I won't go into.

It turns out that the second solution is always of the form:

$$x_2(t) = t e^{-bt/(2a)}$$

So the general solution is: $x(t) = c_1 e^{-bt/(2a)} + c_2 t e^{-bt/(2a)}$

example:

$$y'' - 6y' + 9y = 0$$

The characteristic equation is:

$$\lambda^2 - 6\lambda + 9 = (\lambda - 3)^2 = 0, \text{ yielding the double root, } \lambda = -b/2a = 3.$$

The general solution is:

$$x(t) = c_1 e^{3t} + c_2 t e^{3t}$$

If λ is less than 0, then both $e^{\lambda t}$ and $t e^{\lambda t}$ will approach 0 as t gets large, and the population will decay to zero.

If λ is greater than 0, then both $e^{\lambda t}$ and $t e^{\lambda t}$ will get large as t gets large, and the population will explode.

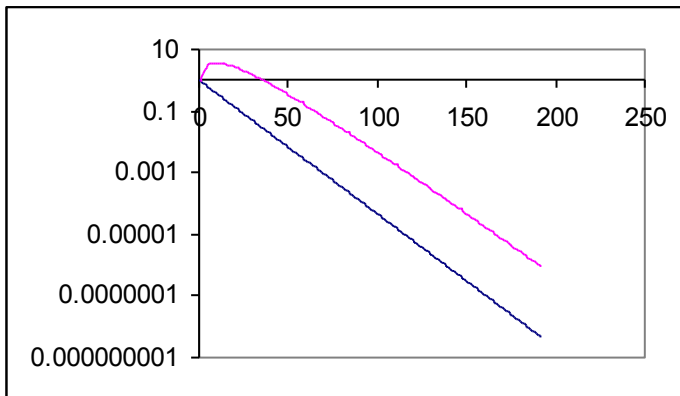


Figure shows the case if λ is negative.

case 3: Complex Conjugate Roots, $b^2 - 4ac < 0$

The roots of the characteristic equation is the complex conjugates:

$$\lambda_1 = \alpha + i\beta, \quad \lambda_2 = \alpha - i\beta,$$

where $\alpha = -\frac{b}{2a}$, and $\beta = \frac{\sqrt{4ac - b^2}}{2a}$, and $i = \sqrt{-1}$.

Thus, two solutions to the equation are:

$$x_1(t) = e^{\lambda_1 t}, \quad x_2(t) = e^{\lambda_2 t}$$

But in differential equations, whenever you know 2 solutions, any linear combination of solutions is also a solution, so it is useful to instead consider the solutions:

$$x_1^* = \frac{e^{\lambda_1 t} + e^{\lambda_2 t}}{2} \text{ and } x_2^* = \frac{e^{\lambda_1 t} - e^{\lambda_2 t}}{2i}$$

and remember from trigonometric identities:

$$e^{i\theta} = \cos \theta + i \sin \theta$$

$$e^{-i\theta} = \cos \theta - i \sin \theta$$

This means that:

$$e_1^t = e^{\alpha t + i\beta t} = e^{\alpha t} e^{i\beta t} = e^{\alpha t} (\cos \beta t + i \sin \beta t)$$

and

$$e_2^t = e^{\alpha t - i\beta t} = e^{\alpha t} e^{-i\beta t} = e^{\alpha t} (\cos \beta t - i \sin \beta t)$$

$$x_1^* = \frac{e^{\lambda_1 t} + e^{\lambda_2 t}}{2} = e^{\alpha t} \cos \beta t, \quad \text{and } x_2^* = \frac{e^{\lambda_1 t} - e^{\lambda_2 t}}{2i} = e^{\alpha t} \sin \beta t$$

This allows us to get rid of the imaginary terms, and express things just in terms of sines and cosines.

Therefore the general solution is:

$$\boxed{x(t) = e^{\alpha t} (c_1 \cos \beta t + c_2 \sin \beta t)}$$

where c_1 and c_2 are arbitrary constants.

Example: Simple Harmonic Motion

$$\frac{d^2 y}{dt^2} + Ky = 0$$

This has the characteristic equation:

$$\lambda^2 + K = 0,$$

with roots $\lambda = \pm i\sqrt{K}$

In this case, $\alpha = 0$, and $\beta = \sqrt{K}$

The general solution is

$$y(t) = c_1 \cos \beta t + c_2 \sin \beta t$$

If we know the initial conditions, that $y(0) = y_0$ and $y'(0) = v_0$

then $y_0 = c_1 \cos 0 + c_2 \sin 0 \Rightarrow c_1 = y_0$

$$v_0 = dy/dt = -\beta c_1 \sin \beta t + \beta c_2 \cos \beta t$$

$$v_0 = c_2 \beta \Rightarrow c_2 = v_0 / \beta$$

This equation is something that cycles with a radian frequency of β , or a period of $2\pi/\beta$, but it would be more convenient to have this in the form of:

$$y(t) = A \sin(\beta t + \phi)$$

Where A is the amplitude, and β is the radian frequency, and ϕ is the phase shift.

We can do this if we know a little trigonometry:

If $y(t) = A \sin(\beta t + \phi)$, from the formula for $\sin(x+y)$ we know:

$$y(t) = A \sin(\beta t + \phi) = A \sin(\beta t) \cos \phi + A \cos(\beta t) \sin \phi = c_1 \cos \beta t + c_2 \sin \beta t$$

By equating the coefficients of the $\sin \beta t$ and $\cos \beta t$ terms this means that:

$$A \sin(\beta t) = c_1 \text{ and}$$

$$A \cos(\beta t) = c_2$$

$$\text{and } c_1^2 + c_2^2 = A^2 \sin^2 \phi + A^2 \cos^2 \phi = A^2 (\sin^2 \phi + \cos^2 \phi) = A^2$$

$$A = \sqrt{c_1^2 + c_2^2}$$

$$\cos \phi = \frac{c_2}{\sqrt{c_1^2 + c_2^2}}$$

$$\sin \phi = \frac{c_1}{\sqrt{c_1^2 + c_2^2}}$$

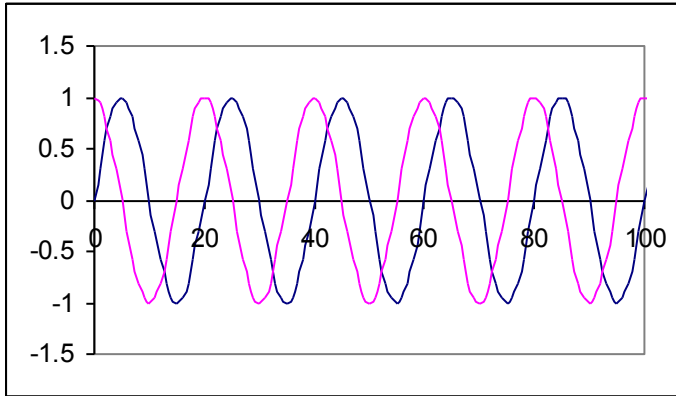
$$\tan \phi = \frac{\sin \phi}{\cos \phi} = \frac{c_1}{c_2}$$

$$\phi = \tan^{-1} \left(\frac{c_1}{c_2} \right)$$

Thus the solution to the equation for simple harmonic motion is:

$y(t) = A \sin(\beta t + \phi)$, where the radian frequency is \sqrt{K} . The amplitude and phase depend on the initial conditions in these ways.

In this case, the damping term is equal to zero, so the cycles will continue indefinitely. If α was less than zero, then cycles would decay with time, if α was greater than zero, then the cycles would diverge with time.



Higher-Order Linear Constant Coefficient Differential Equations:

The results of the 2nd order system extend directly into higher order systems.

The general nth order homogeneous linear constant coefficient differential equation is:

$$\frac{d^n y}{dt^n} + a_{n-1} \frac{d^{n-1} y}{dt^{n-1}} + \dots + a_2 \frac{d^2 y}{dt^2} + a_1 \frac{dy}{dt} + a_0(t)y = 0$$

Extending what we did with second order systems, we can go directly from this to the **characteristic equation**:

$$\lambda^n + a_{n-1}\lambda^{n-1} + \dots + a_2\lambda^2 + a_1\lambda + a_0 = 0$$

From this we can find the roots, $\lambda_1, \lambda_2, \dots, \lambda_n$. This is usually the most difficult step.

There are a number of ways that you can find the root to the characteristic equation. In

the second order system, we used the old quadratic equation: $\lambda_{1,2} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$.

There are equivalents to this for third and 4th, maybe even 5th order systems, but they get quite messy. Other ways are to factor the equation, if possible, or to use a computer program to find the roots. Mathematica, MatLab, or R can do this for you.

❖ For each unique (simple) real root (i.e. there is a single copy) λ_k , there is a solution $y_k = e^{\lambda_k t}$.

❖ For each root, λ_k , of which there are m copies, there are m solutions:

$$y_1 = e^{\lambda_k t}, y_2 = t e^{\lambda_k t}, \dots, y_m = t^{m-1} e^{\lambda_k t}$$

❖ If $\alpha + i\beta$ and $\alpha - i\beta$ are simple roots (1 copy each), then two solutions are:

$$y_1 = e^{\alpha t} \cos \beta t \text{ and } y_2 = e^{\alpha t} \sin \beta t$$

❖ If there are m copies each of roots $\alpha + i\beta$ and $\alpha - i\beta$ then $2m$ solutions are:

$$y_1 = e^{\alpha t} \cos \beta t, y_2 = t e^{\alpha t} \cos \beta t, \dots, y_m = t^{m-1} e^{\alpha t} \cos \beta t$$

$$y_{m+1} = e^{\alpha t} \sin \beta t, y_{m+2} = t e^{\alpha t} \sin \beta t, \dots, y_{2m} = t^{m-1} e^{\alpha t} \sin \beta t$$

If y_1, y_2, \dots, y_n are the n linearly independent solutions obtained in this way from the characteristic equation, then the general equation is:

$$y(t) = c_1 y_1(t) + c_2 y_2(t) + \dots + c_n y_n(t)$$

Example: $\frac{d^5 y}{dt^5} - 2 \frac{d^4 y}{dt^4} + 8 \frac{d^2 y}{dt^2} - 12 \frac{dy}{dt} + 8y = 0$

Characteristic Equation: $\lambda^5 - 2\lambda^4 + 8\lambda^2 - 12\lambda + 8 = 0$

Roots: $(\lambda + 2)(\lambda^2 - 2\lambda + 2)^2 = 0$

$$\lambda_1 = -2, \lambda_{2,3} = 1 + i, \lambda_{4,5} = 1 - i$$

Five linearly independent solutions are:

$$y_1 = e^{-2t}, \quad y_2 = e^t \cos(t), \quad y_3 = e^t \sin(t), \quad y_4 = t e^t \cos(t), \quad y_5 = t e^t \sin(t)$$

The general solution is:

$$y(t) = c_1 e^{-2t} + c_2 e^t \cos(t) + c_3 e^t \sin(t) + c_4 t e^t \cos(t) + c_5 t e^t \sin(t)$$

In many ecological problems that we'll run into, instead of having a single n^{th} order differential equation, we may have a system of n first-order differential equations.

$$\begin{aligned}\frac{dx_1}{dt} &= a_{11}x_1 + a_{12}x_2 + \cdots + a_{1n}x_n \\ \frac{dx_2}{dt} &= a_{21}x_1 + a_{22}x_2 + \cdots + a_{2n}x_n \\ &\vdots \\ \frac{dx_n}{dt} &= a_{n1}x_1 + a_{n2}x_2 + \cdots + a_{nn}x_n\end{aligned}$$

This is equivalent to a single n^{th} order differential equation.

For example, if you have two first order differential equations, this can be re-written as a single second-order differential equation:

$$\frac{dx}{dt} = a_{11}x + a_{12}y \quad (1)$$

$$\frac{dy}{dt} = a_{21}x + a_{22}y \quad (2)$$

Take the second order equation and solve it for x :

$$x = \frac{1}{a_{21}} \frac{dy}{dt} - \frac{a_{22}}{a_{21}} y \quad (3)$$

differentiate both sides of (3) and equate to the right hand side of (2)

$$\frac{dx}{dt} = \frac{1}{a_{21}} \frac{d^2y}{dt^2} - \frac{a_{22}}{a_{21}} \frac{dy}{dt} = a_{11}x + a_{12}y$$

substitute in (3) for x :

$$\frac{1}{a_{21}} \frac{d^2y}{dt^2} - \frac{a_{22}}{a_{21}} \frac{dy}{dt} - \frac{a_{11}}{a_{21}} \frac{dy}{dt} + a_{11}a_{22}y - a_{12}y = 0$$

Multiply both sides by a_{21} , and we have a 2^{nd} -order differential equation in terms of y only:

$$\frac{d^2y}{dt^2} - (a_{11} + a_{22}) \frac{dy}{dt} + (a_{11}a_{22} - a_{12}a_{21})y = 0$$

From this we could use the techniques that we have already learned to deal with second order linear differential equations.

We could write the characteristic equation:

$$\lambda^2 - (a_{11} + a_{22}) \lambda + (a_{11}a_{22} - a_{12}a_{21}) = 0$$

Alternatively we could use the matrix techniques that I will describe in a minute to solve the system of differential equations directly.

We can also do the reverse, if we have a 2nd order linear differential equation, we can transform it into a system of 2 first order linear differential equations:

$$\frac{d^2 y}{dt^2} + \beta \frac{dy}{dt} + \gamma y = 0$$

we can create a new variable, x , such that:

$$x = \frac{dy}{dt}$$

$$\frac{dx}{dt} = \frac{d^2 y}{dt^2}$$

Then substituting in to the equation above:

$$\frac{dx}{dt} + \beta x + \gamma y = 0$$

$$\frac{dx}{dt} = -\beta x - \gamma y$$

$$\frac{dy}{dt} = x$$

So we have created a system of 2 first order equations.

For every n^{th} order differential equation, there is an equivalent set of n first order differential equations, and vice versa.

Next we will consider a more efficient way of solving systems of linear constant coefficient differential equations.

Let's start with this system of 2 linear first order differential equations:

$$\frac{dx}{dt} = a_{11}x + a_{12}y \quad (1)$$

$$\frac{dy}{dt} = a_{21}x + a_{22}y \quad (2)$$

Before when we solved second order linear constant coefficient equations, we started by guessing that the solution would be of the form: $y(t) = e^{\lambda t}$.

Similar to this, here we start by guessing that the solution of these equations might be of the form: $x = Ae^{\lambda t}$, $y = Be^{\lambda t}$, where A, B, and λ are constants to be determined.

Then $dx/dt = A\lambda e^{\lambda t}$, and $dy/dt = B\lambda e^{\lambda t}$.

Substituting into equations (1) and (2) we get:

$$x' = A\lambda e^{\lambda t} = a_{11} A e^{\lambda t} + a_{12} B e^{\lambda t}$$

$$y' = B\lambda e^{\lambda t} = a_{21} A e^{\lambda t} + a_{22} B e^{\lambda t}$$

If we divide by $e^{\lambda t}$ we get the linear system:

$$(a_{11} - \lambda) A + a_{12} B = 0$$

$$a_{21} A + (a_{22} - \lambda) B = 0$$

We'd like to find values for λ such that the equations have a solution (A,B) where A and B are both non-zero. We learned earlier when we were talking about eigenvalues and eigenvectors, that this occurs whenever the determinant of the system:

$$D = \begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix} = (a_{11} - \lambda)(a_{22} - \lambda) - a_{21}a_{12} = 0$$

equals 0.

This gives us the characteristic equation:

$$\lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}) = 0$$

From there we can find the roots of the characteristic equation, and see if they are real or not, and see if the solution grows or declines exponentially, or shows oscillations.

In this case, λ once again turns out to be the eigenvalue, and $\begin{pmatrix} A \\ B \end{pmatrix}$ is the right eigenvector.

The Matrix Method for Solving Systems of Linear 1st Order Differential Equations:

$$\begin{aligned}\frac{dx_1}{dt} &= a_{11}x_1 + a_{12}x_2 + \cdots + a_{1n}x_n \\ \frac{dx_2}{dt} &= a_{21}x_1 + a_{22}x_2 + \cdots + a_{2n}x_n \\ &\vdots \\ \frac{dx_n}{dt} &= a_{n1}x_1 + a_{n2}x_2 + \cdots + a_{nn}x_n\end{aligned}$$

We can write this in matrix notation where:

$$\mathbf{x}(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix} \quad \mathbf{x}'(t) = \begin{pmatrix} x'_1(t) \\ x'_2(t) \\ \vdots \\ x'_n(t) \end{pmatrix}$$

We can define an nxn matrix \mathbf{A} :

$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix}$$

This system can then be written as:

$$\mathbf{x}'(t) = \mathbf{A}\mathbf{x}(t)$$

If λ is an eigenvalue of \mathbf{A} , with corresponding eigenvector \mathbf{v} , then $\mathbf{x}(t) = e^{\lambda t}\mathbf{v}$ is a solution to the system.

There is a theorem that states that a system like this has n linearly independent solutions. If \mathbf{A} has n linearly independent eigenvectors $\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_n$, corresponding to eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_n$, then the **general solution** is:

$$\mathbf{x}(t) = c_1 e^{\lambda_1 t} \mathbf{v}_1 + c_2 e^{\lambda_2 t} \mathbf{v}_2 + \dots + c_n e^{\lambda_n t} \mathbf{v}_n$$

Suppose we have a rather strange competitive situation:

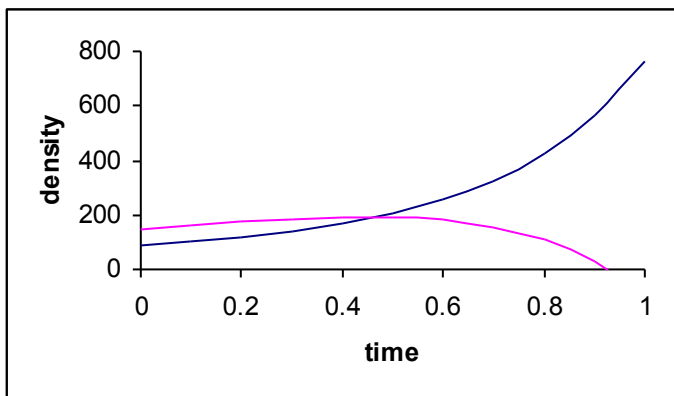
$$x_1'(t) = 3x_1(t) - x_2(t)$$

$$x_2'(t) = -2x_1(t) + 2x_2(t)$$

An increase in the population of one species causes a decline in the growth rate of another.

Suppose the initial populations are $x_1(0) = 90$ and $x_2(0) = 150$.

The competition model predicts something like this, where species 2 is excluded from the system, and species 1 grows exponentially.



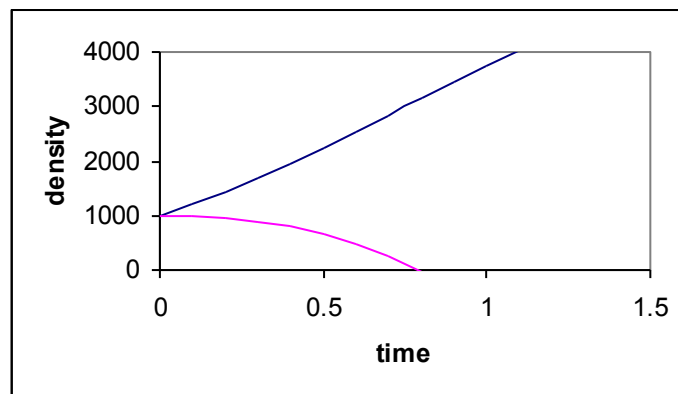
Suppose we have a similar, rather strange predator-prey situation:

predator: $x_1'(t) = x_1(t) + x_2(t)$

prey: $x_2'(t) = x_1(t) + x_2(t)$

Suppose the initial populations are $x_1(0) = x_2(0) = 1000$.

Here's what happens to the predator-prey system. The prey is driven extinct at the point when $\cos(t)$ is equal to $\sin(t)$, which happens at $t = \pi/4$.



That ends the section on differential equations that we can **solve**.

What do we do with the vast majority of differential equations in biological systems that we can't solve?

We have a number of options:

1. Simulate
2. Graphical Methods
3. Stability Analysis

Simulation

In general, even if we can't get an analytical expression for $x(t) = \dots$, we can numerically figure out what $x(t)$ will be for all values of t , for particular values of the parameters in the model.

Using R, Matlab, or other programs for numerically solving differential equations.

There are a number of numerical algorithms that allow you to determine the future state of the system based on the current state and the derivative. For all of these algorithms, you have to provide specific values to the parameters in the model, and a specific starting condition. This means that you have to do a very large set of runs to understand the behavior of the model from simulation alone.

The simplest method is the Euler method.

Say we have a differential equation:

$$\frac{dx}{dt} = f(x, t)$$

The Euler Method simply uses the definition of the derivative:

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

It says that if Δt is small, then

$$\frac{dx}{dt} = f(x, t) \approx \frac{x(t + \Delta t) - x(t)}{\Delta t}$$

This means that:

$$x(t + \Delta t) \approx x(t) + f(x, t) \Delta t$$

How good this approximation is depends on how small Δt is. The smaller Δt , the better the approximation.

There are a number of errors in any numerical approximation technique.

The Euler Method is not the best method available. It does a pretty good job if the time step is very small. A number of other modifications have been made.

One of the other options is the **Improved Euler Method**, which averages the slopes at the left and right endpoints of each step and uses the average slope to compute the next value of the state variable.

One commonly used method is the **Runge-Kutta method**, which effectively divides the time between t and $t+\Delta t$ and computes the slope at a number of points in that interval and gives a weighted average of the slopes. This is a very accurate and widely used method.

It can be very tedious work to try to figure out the behavior of a model from simulation alone. For this reason, simulation is usually combined with one or both of the other methods of graphical techniques and stability analysis, to get some idea of how the model might behave in different regions of the parameter space.