

# MATHEMATICA TUTORIAL for the Second Course. Part III: Predator-Prey Equations

Email: Prof. Vladimir Dobrushkin (mailto:Vladimir\_Dobrushkin@brown.edu?Subject=Mathematica)  
(Tuesday, November 8, 2022 9:06:02 AM)

## Preface

This section studies some first order nonlinear ordinary differential equations describing the time evolution (or “motion”) of those hamiltonian systems provided with a first integral linking implicitly both variables to a motion constant. An application has been performed on the Lotka--Volterra predator-prey system, turning to a strongly nonlinear differential equation in the phase variables.

### Contents [hide]

#### Preface

(<http://www.cfm.brown.edu/people/dobrush/am34/Mathematica/index.html>)

#### 0. Introduction

1. Part I: ([../ch1/part1.html](#)) Matrix Algebra
2. Part II: ([../ch2/part2.html](#)) Linear Systems of Ordinary Differential Equations
3. Part III: ([../ch3/part3.html](#)) Non-linear Systems of Ordinary Differential Equations

#### **Part III C:** ([../ch3/chaos.html](#)) Chaos

4. Part IV: ([../ch4/part4.html](#)) Numerical Methods
5. Part V: ([../ch5/part5.html](#)) Fourier Series
6. Part VI: ([../ch6/part6.html](#)) Partial Differential Equations
  - Part VI P:** ([../ch6/parabolic.html](#)) Parabolic Equations
  - Part VI H:** ([../ch6/hyperbolic.html](#)) Hyperbolic equations
  - Part VI E:** ([../ch6/elliptic.html](#)) Elliptic equations
7. Part VII: ([../ch7/part7.html](#)) Special Functions

Return to computing ([../am33/computing33.html](#)) page for the first course APMA0330

Return to computing ([../computing.html](#)) page for the second course APMA0340

Return to Mathematica ([../am33/Mathematica/index.html](#)) tutorial for the first course APMA0330

Return to Mathematica ([../index.html](#)) tutorial for the second course APMA0340

Return to the main page ([../am33/index.html](#)) for the first course APMA0330

Return to the main page ([../index.html](#)) for the second course APMA0340

Return to Part III (part3.html) of the course APMA0340  
Introduction to Linear Algebra

(<http://www.cfm.brown.edu/people/dobrush/cs52/index.html>) with *Mathematica*

## Glossary ([../glossary/](#))

## Predator-Prey Equations

Some situations require more than one differential equation to model a particular situation. We might use a system of differential equations to model two interacting species, say where one species preys on the other. For example, we can model how the population of Canadian lynx (*lynx canadensis*) interacts with a the population of snowshoe hare (*lepus americanis*) (see <https://www.youtube.com/watch?v=ZWucOrSOdCs>).

A good historical data are known for the populations of the lynx (<https://en.wikipedia.org/wiki/Lynx>) and snowshoe hare ([https://en.wikipedia.org/wiki/Snowshoe\\_hare](https://en.wikipedia.org/wiki/Snowshoe_hare)) from the Hudson Bay Company ([https://en.wikipedia.org/wiki/Hudson%27s\\_Bay\\_Company](https://en.wikipedia.org/wiki/Hudson%27s_Bay_Company)). This large Canadian retail company, which owns and operates a large number of retail stores in North America and Europe, including Galeria Kaufhof, Hudson's Bay, Home Outfitters, Lord & Taylor, and Saks Fifth Avenue, was originally founded in 1670 as a fur trading company. The Hudson Bay Company kept accurate records on the number of lynx pelts that were bought from trappers from 1821 to 1940. The company noticed that the number of pelts varied from year to year and that the number of lynx pelts reached a peak about every ten years. The ten year cycle for lynx can be best understood using a system of differential equations.

The primary prey for the Canadian lynx is the snowshoe hare. We will denote the population of hares by  $H(t)$  and the population of lynx by  $L(t)$ , where  $t$  is the time measured in years. We will make the following assumptions for our predator-prey model.

- If no lynx are present, we will assume that the hares reproduce at a rate proportional to their population and are not affected by overcrowding. That is, the hare population will grow exponentially,

$$\frac{dH}{dt} = a H \quad (\text{where } a \text{ is a constant}).$$

- Since the lynx prey on the hares, we can argue that the rate at which the hares are consumed by the lynx is proportional to the rate at which the hares and lynx interact. Thus, the equation that predicts the rate of change of the hare population becomes

$$\frac{dH}{dt} = a H - b H L, \quad (\text{where } a, b \text{ are constants}).$$

We are thinking of  $H L$  as the number of possible interactions between the lynx and the hare populations.

- If there is no food, the lynx population will decline at a rate proportional to itself,

$$\frac{dL}{dt} = \delta L \quad (\text{where } \delta \text{ is a constant}).$$

- The lynx receive benefit from the hare population. The rate at which lynx are born is proportional to the number of hares that are eaten, and this is proportional to the rate at which the hares and lynx interact. Consequently, the growth rate of the lynx population can be described by

$$\frac{dL}{dt} = c H L - \delta L, \quad (\text{where } c, \delta \text{ are constants}).$$

We now have a system of differential equations that describe how the two populations interact,

$$\dot{H} = a H - b H L, \quad \dot{L} = c H L - \delta L,$$

where we use the dot notation to represent the derivatives with respect to time  $t$ .



Alfred James Lotka

The system of differential equation used to model predator-prey interactions

$$\begin{aligned} \dot{x} &= x(a - \alpha y), \\ \dot{y} &= y(-\delta + bx), \end{aligned}$$

is usually referred to as Lotka--Volterra model

([https://en.wikipedia.org/wiki/Lotka%E2%80%93Volterra\\_equations](https://en.wikipedia.org/wiki/Lotka%E2%80%93Volterra_equations)).

Here  $x$  is the number of prey (for example, rabbits

(<https://en.wikipedia.org/wiki/Rabbit>));  $y$  is the number of some

predator (<https://en.wikipedia.org/wiki/Predation>) (for example, foxes

(<https://en.wikipedia.org/wiki/Fox>));  $\dot{x}$  and  $\dot{y}$  represent the

instantaneous growth rates of the two populations;  $t$  represents time;

$a$ ,  $\alpha$ ,  $\delta$ , and  $b$  are positive real parameters (<https://en.wikipedia.org/wiki/Parameter>) describing the interaction of the two species (<https://en.wikipedia.org/wiki/Species>).

The Lotka--Volterra system of equations is an example of a Kolmogorov ([https://en.wikipedia.org/wiki/Andrey\\_Kolmogorov](https://en.wikipedia.org/wiki/Andrey_Kolmogorov)) model, which is a more general framework that can model the dynamics of ecological systems with predator-prey interactions, competition, disease, and mutualism ([https://en.wikipedia.org/wiki/Mutualism\\_\(biology\)](https://en.wikipedia.org/wiki/Mutualism_(biology))). The equations which model the struggle for existence of two species (prey and predators) bear the name of two scientists: Lotka (1880--1949) and Volterra (1860--1940). They lived in different countries, had distinct professional and life trajectories, but they are linked together by their interest and results in mathematical modeling.

The predator--prey model was initially proposed by Alfred J. Lotka ([https://en.wikipedia.org/wiki/Alfred\\_J.\\_Lotka](https://en.wikipedia.org/wiki/Alfred_J._Lotka)) in the theory of autocatalytic chemical reactions in 1910. Lotka was born in Lemberg, Austria-Hungary, but his parents immigrated to the US. In 1925, he utilized the equations to analyze predator-prey interactions. Lotka published almost a hundred articles on various themes in chemistry, physics, epidemiology or biology, about half of them being devoted to population issues. He also wrote six books.



Vito Volterra

The same set of equations was published in 1926 by Vito Volterra ([https://en.wikipedia.org/wiki/Vito\\_Volterra](https://en.wikipedia.org/wiki/Vito_Volterra)), a mathematician and physicist, who had become interested in mathematical biology because of the impact by the marine biologist Umberto D'Ancona ([https://en.wikipedia.org/wiki/Umberto\\_D%27Ancona](https://en.wikipedia.org/wiki/Umberto_D%27Ancona)) (1896--1964). Vito Volterra was born in Ancona, then part of the Papal States, into a very poor Jewish family. He attended the University of Pisa, where he became professor of rational mechanics in 1883. His most famous work was done on integral equations. In 1892, he became professor of mechanics at the University of Turin and then, in 1900, professor of mathematical physics at the University of Rome La Sapienza. His daughter Luisa married Umberto D'Ancona.

The predator-prey system of equations was later extended by many researchers, including C. S. Holling ([https://en.wikipedia.org/wiki/C.\\_S.\\_Holling](https://en.wikipedia.org/wiki/C._S._Holling)), Arditi--Ginzburg model ([https://en.wikipedia.org/wiki/Arditi%E2%80%93Ginzburg\\_equations](https://en.wikipedia.org/wiki/Arditi%E2%80%93Ginzburg_equations)), Rosenzweig-McArthur model ([http://repositorio.ul.pt/bitstream/10451/26516/1/ulfc118901\\_tm\\_Pablo\\_Sommer.pdf](http://repositorio.ul.pt/bitstream/10451/26516/1/ulfc118901_tm_Pablo_Sommer.pdf)), and some others.

The critical points of the Lotka--Volterra system of equations are the solutions of the algebraic equations

$$x(a - \alpha y) = 0, \quad y(-\delta + bx) = 0,$$

namely (0,0) and ( $\delta/b$ ,  $a/\alpha$ ). Next we try to examine the local behavior of solutions near each critical point using linearization approach. Neglecting the nonlinear terms, we obtain the corresponding linear system near the origin:

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{bmatrix} a & 0 \\ 0 & -\delta \end{bmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

The eigenvalues of this system of equations are  $\lambda_1 = a > 0$  and  $\lambda_2 = -\delta < 0$ . So the origin is a saddle point, unstable. At another critical point, linearization yields

$$\frac{d}{dt} \begin{pmatrix} x - \delta/b \\ y - a/\alpha \end{pmatrix} = \begin{bmatrix} 0 & -\frac{\alpha\delta}{b} \\ \frac{ab}{\alpha} & 0 \end{bmatrix} \begin{pmatrix} x - \delta/b \\ y - a/\alpha \end{pmatrix}.$$

The eigenvalues of the above system of equations are pure complex conjugate:

$$\lambda = \pm j\sqrt{a\delta}.$$

Therefore, the Lotka--Volterra system of equation has not hyperbolic equilibrium point ( $\delta/b$ ,  $a/\alpha$ ) and linearization is inconclusive. So we need to find another approach. It is not hard to verify that the energy function

$$E = bx + \alpha y - \delta \ln x - a \ln y + \text{constant}$$

is a Lyapunov function for the predator-prey model. Indeed, its derivative with respect to the system of differential equation is

$$\dot{E} = b\dot{x} + \alpha\dot{y} - \frac{\delta}{x}\dot{x} - \frac{a}{y}\dot{y} = (a - \alpha y)(bx - \delta) + (-\delta + bx)(-a + \alpha y) \equiv 0.$$

Therefore, the stationary point  $(\delta/b, a/\alpha)$  is a stable critical point.

We may try to find the general solution of the Lotka--Volterra system of equations. From both equations, we get

$$\frac{\dot{x}}{x} = a - \alpha y \quad \text{and} \quad \frac{\dot{y}}{y} = -\delta + bx.$$

Multiplying the first relation by  $(-\delta + bx)$  and the second one by  $(a - \alpha y)$ , we obtain

$$\frac{\dot{x}}{x}(-\delta + bx) = (a - \alpha y)(-\delta + bx) = \frac{\dot{y}}{y}(a - \alpha y).$$

So we separated variables

$$\frac{\dot{x}}{x}(-\delta + bx) = \frac{\dot{y}}{y}(a - \alpha y),$$

which upon integration yields the energy integral.

Example 1: *Mathematica* solves Lotka--Volterra system of equations

Example 2: *Mathematica* solves another Lotka--Volterra equations

Example 3: competing predators

## Non Kolmogorov models

Though straightforward, the Lotka-Volterra model makes various assumptions regarding the environment and evolution of predator and prey populations, limiting its capabilities when applying it to real-world examples. Five key assumptions are as follows:

1. The population of prey is sustainable, as they are able to find and have ample food at all times.
2. The food supply of predators depends solely on the population of the prey, meaning that the predator eats nothing else but the prey.
3. The rate of change of population is proportional to its size.
4. The environment is static. It does not change in favor of one species over the other, nor does genetic adaptation play a role.
5. The predators' appetites are limitless.

Thus, we can see that the Lotka-Volterra model fails to impose restrictions on certain parameters, in turn failing to produce realistic projections for predator and prey population data from the field. Two main problems with the Lotka-Volterra model that deter accurate predictions are as follows:

1. In the absence of predators ( $y = 0$ ), the prey population grows exponentially; there is nothing to limit their growth.
2. The rate at which predators remove prey is  $\beta xy$ . By dividing this term by  $y$ , we see that the rate an individual predator consumes prey is  $\beta x$ . This rate increases as  $x$  increases, without any limit for  $x$ . Thus, in relation to assumption 5, this implies that an individual predator can never get full.

In order to address the limitations of the Lotka-Volterra model, Rosenzweig and MacArthur proposed their own model in 1963, which more realistically portrays predator-prey interactions.

Example 4: *Mathematica* solves Beddington--DeAngelis equations

Example 5: The Rosenzweig--MacArthur Model of Predator-Prey Interactions

## References

(<https://www.emis.de/journals/DM/vXI1/art1.pdf>)

Return to (<https://www.emis.de/journals/DM/vXI1/art1.pdf>) *Mathematica* ([../index.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) page

Return to the main page ([../index.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) (APMA0340)

Return to the Part 1 ([../ch1/part1.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Matrix Algebra

Return to the Part 2 ([../ch2/part2.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Linear Systems of Ordinary Differential Equations

Return to the Part 3 ([../ch3/part3.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Non-linear Systems of Ordinary Differential Equations

Return to the Part 4 ([../ch4/part4.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Numerical Methods

Return to the Part 5 ([../ch5/part5.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Fourier Series

Return to the Part 6 ([../ch6/part6.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Partial Differential Equations

Return to the Part 7 ([../ch7/part7.html](http://www.emis.de/journals/DM/vXI1/art1.pdf)) Special Functions