

Modeling Population Dynamics with Volterra-Lotka Equations

by Jacob Schrum

in Partial Fulfillment of the Mathematics Capstone

December 6, 2005

Abstract

The purpose of this project is to model multi-species interactions using Volterra-Lotka equations in both two and three dimensions. Changes in population dynamics that arise as a result of modifying parameters are examined. The population dynamics of the resulting systems are analyzed in terms of stability around equilibrium points and within invariant surfaces. Of particular interest is periodic behavior and the initial conditions that lead to it. The two-dimensional system is found to exhibit stable periodic behavior for all initial conditions where neither population count is zero. The behavior of the three-dimensional system varies depending on the choice of constants used in the system definition. One case results in stable periodic behavior for all non-zero initial conditions, one case leads to the extinction of the top level predator and periodic stability for the remaining species, and the third case leads to unbounded growth for the bottom level prey and top level predator populations, and increasingly wild fluctuations in the population of the intermediate predator/prey population. The merits and flaws of these models are also discussed.

Introduction

This paper recreates much of the analysis and conclusions produced in “A Lotka-Volterra Three-species Food Chain” [2], and also incorporates knowledge from a course in both linear and non-linear dynamics taken in Germany called “Gewöhnliche Differentialgleichungen” [6] (Ordinary Differential Equations). It starts by presenting the basic exponential growth 2D Volterra-Lotka system of differential equations and analyzing it in terms of the stability of stationary points. This system is then extended into a 3D system and a similar analysis is carried out. Also important to the analysis of the 3D system are invariant surfaces, which are explained below.

The mathematical notation used to present some of the theorems and definitions below may be unfamiliar to some, so the following table of symbol definitions is provided:

Mathematical Symbol	Meaning
\dot{x}	The derivative of the function x with respect to time t , or $\frac{\partial x}{\partial t}$
$\mathcal{C}^1(\mathcal{U}, \mathcal{V})$	The set of all continuous functions from a set \mathcal{U} to a set \mathcal{V} whose derivatives exist and are continuous in \mathcal{U} .
\mathfrak{R}	The set of all real-numbers.
Re	The real part function, which returns the real number component of a complex number.
$\sigma(A)$	The spectrum of the matrix A , which is the set of all Eigenvalues of A .
$\nabla F(\vec{x})$	Gradient of the vector function F evaluated at the point \vec{x} .
$A \subseteq B$	The set A is a subset of B , possibly equal

Meanings of several mathematical symbols used in the paper.

This paper assumes some familiarity with differential equations. Volterra-Lotka equations are coupled first-order ordinary differential equations. It is impossible to solve these equations explicitly in terms of an independent variable, which is why an analysis of the stability of the system is so important.

In order to discuss the concept of stability, we first define *flow*. Flow is a way of representing the solutions to a differential equation for all possible times and initial conditions. The concept of flow is useful in that we can use it even if we do not know the solution to a differential equation.

Definition 1 (Flow [3, 6]) *Let there be a differential equation $\dot{\vec{x}} = F(\vec{x})$ where $F \in \mathcal{C}^1(\mathcal{U}, \mathfrak{R}^n)$ for $\mathcal{U} \subseteq \mathfrak{R}^n$. Define $\mathcal{J}(\vec{x}_0)$ to be the maximal existence interval for an initial condition $\vec{x}(0) = \vec{x}_0$ of the differential equation. Then we define the flow φ as follows:*

$$\varphi : \{(t, \vec{x}_0) \mid \vec{x}_0 \in \mathcal{U}, t \in \mathcal{J}(\vec{x}_0)\} \rightarrow \mathcal{U}$$

Such that $\varphi(0, \vec{x}_0) = \vec{x}_0$ and $\varphi(t, \vec{x}_0) = \vec{x}(t)$ for $\vec{x}(0) = \vec{x}_0$. By convention $\varphi(t, \vec{x}_0) = \varphi^t(\vec{x}_0)$.

For fixed t and \vec{x}_0 , the value of $\varphi^t(\vec{x}_0)$ is a single point. If we let t flow through all values in $\mathcal{J}(\vec{x}_0)$, then the result is a set $\{\varphi^t(\vec{x}_0) \mid t \in \mathcal{J}(\vec{x}_0)\}$, which we call a *trajectory*. A trajectory represents all points in the graph of a single solution to the differential equation. Geometrically, it represents the curve along which a solution flows as time changes. These trajectories are unique for each solution to the differential equation. Furthermore, different trajectories cannot intersect each other.

Trajectories are plotted within the *phase space* of a differential equation. This space depicts the path of one or more trajectories over time. Special points for which $\varphi^t(\vec{x}_0) = \vec{x}_0$ for all t are called fixed points, stationary points or equilibrium solutions. They appear as single points within phase space. These points play an important role in defining the stability of a system of differential equations.

Definition 2 (Stability [6]) Let \vec{p} be a fixed point of a differential equation with flow φ .

1. \vec{p} is stable \Leftrightarrow For every neighborhood \mathcal{U} of \vec{p} , there exists a neighborhood \mathcal{V} of \vec{p} such that

$$\varphi^t(\mathcal{U}) \subseteq \mathcal{V} \text{ for all } t \geq 0$$

2. \vec{p} is asymptotically stable $\Leftrightarrow \vec{p}$ is stable and there exists a neighborhood \mathcal{W} of \vec{p} such that

$$\lim_{t \rightarrow \infty} \varphi^t(\vec{x}) = \vec{p} \text{ for all } \vec{x} \in \mathcal{W}$$

3. \vec{p} is unstable $\Leftrightarrow \vec{p}$ is not stable.

Geometrically, a point is stable if all the trajectories around it stay within an area around it. This could mean that the trajectories keep moving along a closed path whose values repeat. This is called a periodic solution. A point could also be stable if the trajectories around it approach ever closer to a closed path around the point. Such a closed path is called a limit cycle, but is not particularly important to our analysis. A point is asymptotically stable if all trajectories in a neighborhood around the point *approach* the point. Our terminology is very important in this case, because we mentioned above that different trajectories do not intersect. This means that although all trajectories around an asymptotically stable point approach that point, they never actually reach that point. Therefore none of these trajectories intersect with each other, nor with the fixed point itself.

Armed with this knowledge, we now proceed to analyzing the two-dimensional Volterra-Lotka system. In the course of this analysis, theorems and definitions helpful to our analysis shall be stated. We will also make use of several diagrams, particularly those of the phase space for the system. All diagrams featured below were generated using Maple 9. The code for these diagrams is presented in an appendix at the end of this document.

2D Volterra-Lotka System

Volterra-Lotka equations are differential equations that can be used to model predator-prey interactions. The original system discovered by both Volterra and Lotka independently [1, pg. 504] consisted of two entities. Vito Volterra developed these equations in order to model a situation where one type of fish is the prey for another type of fish. The model was simplified by the following assumptions:

1. The prey population increases exponentially in the absence of predators.
2. The predator population decreases exponentially in the absence of prey.
3. The prey population decreases relative to the frequency with which predators meet prey as a result of predation.
4. The predator population increases relative to the frequency with which predators meet prey as a result of predation.

Using these assumptions, the Volterra-Lotka equations for the two-dimensional predator-prey system with exponential growth is defined by the following system of differential equations:

$$F(x(t), y(t)) = \begin{cases} \dot{x} &= Ax - Bxy &= x(A - By) \\ \dot{y} &= -Cy + Dxy &= y(-C + Dx) \end{cases} \quad (1)$$

In the above equations, x represents the size of the prey population and y represents the size of the predator population. The growth rate of each of these populations is defined in terms of x and y , both of which are functions of the time t , which is not present in the equations. The values A , B , C and D are positive constants. The Ax term models assumption #1, the $-Cy$ term models assumption #2, the $-Bxy$ term models assumption #3 and the Dxy term models assumption #4.

The assumptions made above describe a closed system in which the two given species are only affected by each other. There are no outside factors that can influence the system, such as another species or features of the environment. The exponential growth of the prey population in the absence of predation is an unrealistic assumption, but provides for a tractable model. Should one wish, one can extend the system to one with logistic growth [5].

The stationary points of the exponential growth system are $(x, y) = (0, 0), (C/D, A/B)$. The stationary point $(0, 0)$ is uninteresting because there are no organisms to observe in such a system. However, the second stationary point is of interest. We want to discover the dynamics of the system, which involves determining whether or not the stationary points are stable, or perhaps even asymptotically stable.

One means of determining the stability of stationary points is to linearize the system (by taking partial derivatives) and determine the stability of points in the linear system. The stability of points in a linear system can be determined by finding the Eigenvalues of the matrix for the linear system at those points and applying the following theorem:

Theorem 1 (Principle of Linearized Stability [6]) *Let $F \in C^1(\mathcal{U}, \mathfrak{R}^n)$ for $\mathcal{U} \subseteq \mathfrak{R}^n$ with $F(\vec{p}_0) = \vec{0}$. Then for the non-linear system $\dot{\vec{a}} = F(\vec{a})$ the following is true:*

1. $Re(\sigma(\nabla F(\vec{p}_0))) < 0 \Rightarrow \vec{p}_0$ is asymptotically stable
2. \vec{p}_0 is stable $\Rightarrow Re(\sigma(\nabla F(\vec{p}_0))) \leq 0$

The linearized 2D Volterra-Lotka system is shown below.

$$\nabla F(x, y) = \begin{pmatrix} A - By & -Bx \\ Dy & -C + Dx \end{pmatrix} \quad (2)$$

Plugging in the first stationary point $(0, 0)$ produces the matrix below, which has Eigenvalues A and $-C$, for $A > 0$ and $C > 0$. Therefore the matrix has a positive Eigenvalue A , meaning that the system is unstable at the point $(0, 0)$. This is not surprising given assumption #1, which states that the prey population increases in the absence of predators.

$$\nabla F(0, 0) = \begin{pmatrix} A & 0 \\ 0 & -C \end{pmatrix} \quad (3)$$

Plugging in the second stationary point $(C/D, A/B)$ produces the following matrix, whose Eigenvalues are $\pm i\sqrt{AC}$, which are complex numbers. Because the real part of these values is zero, the point could be either stable or instable. Another method of analysis is needed to find out more.

$$\nabla F(C/D, A/B) = \begin{pmatrix} 0 & -BC/D \\ DA/B & 0 \end{pmatrix} \quad (4)$$

A type of function that could be of help, should it exist, is an Integral. An Integral is defined as follows

Definition 3 (Integral [6]) *Given a system $\dot{\vec{a}} = F(\vec{a})$ where $F \in C^1(\mathcal{U}, \mathfrak{R}^n)$, a function $G \in C^1(\mathcal{U}, \mathfrak{R})$ is called an Integral of F provided:*

1. $G(\vec{a}(t)) = G(\vec{a}(0)) \forall t, \vec{a}$
2. $\nabla G(\vec{a}) \neq 0$ on open sets

A global Integral is one for which \mathcal{U} is equal to the entire area of interest within \mathfrak{R}^n , which in the case of the 2D Volterra-Lotka system is $\{(x, y) \in \mathfrak{R}^2 \mid x \geq 0, y \geq 0\}$. For any system, finding $n - 1$ linearly independent Integrals is equivalent to finding an implicit solution to the system. In the case of the 2D System, only one Integral needs to be found. A function G satisfying condition #1 of the definition of an Integral is found by setting the derivative of G with respect to time equal to zero. To further simplify the search, we will make the separation assumption, which means that we assume G is the sum of two separate functions of x and y .

$$G(x, y) = f(x) + g(y) \text{ such that } \dot{G} = 0 \quad (5)$$

This assumption is not guaranteed to hold, but if it does, we will be able to find an Integral for the system. Such a function is found as follows:

$$\dot{G} = \frac{\partial G}{\partial x} \dot{x} + \frac{\partial G}{\partial y} \dot{y} = 0 \quad \{\text{Multivariable Chain Rule}\}$$

$$0 = \frac{\partial G}{\partial x} x(A - By) + \frac{\partial G}{\partial y} y(-C + Dx) \quad \{\text{Definition of Volterra-Lotka System}\}$$

$$0 = f'(x)x(A - By) + g'(y)y(-C + Dx) \quad \{\text{Separation Assumption}\}$$

$$g'(y)y(C - Dx) = f'(x)x(A - By)$$

Should $(x, y) = (C/D, A/B)$, then both sides of the equation are zero and the equation is true for all f and g , but to find a solution that works in all cases we will assume that this is not the case, and thus avoid dividing by zero.

$$\frac{g'(y)y}{A - By} = \frac{f'(x)x}{C - Dx} \text{ for } (x, y) \neq (C/D, A/B)$$

Given that the left and right hand sides are functions of different variables, this implies that both sides are equal to the same constant value. According to #2 in the definition of an Integral, the gradient cannot equal zero, and this will be the case as long as the constant to which both sides of the equation are equal is not 0. We choose it to be 1, though other values would also work (Integrals are not unique).

$$g'(y) = \frac{A - By}{y} = \frac{A}{y} - B \quad \wedge \quad f'(x) = \frac{C - Dx}{x} = \frac{C}{x} - D$$

$$g(y) = \int g'(y)dy = A \ln |y| - By + K_1 \quad \wedge \quad f(x) = \int f'(x)dx = C \ln |x| - Dx + K_2$$

Where K_1 and K_2 are constants of integration. Combining these into one constant K results in the following definition for G

$$G(x, y) = C \ln |x| - Dx + A \ln |y| - By = K \quad (6)$$

This is an Integral because $\nabla G(x, y) = (C/x - D, A/y - B) \neq 0$. The other requirement of an Integral is satisfied by construction. It is worth noting that the same Integral could be derived using other simplifying assumptions besides the separation assumption. Having the derivative of G with respect to t identical to 0 means that solutions to the system of differential equations run along level planes of the function G . This can be seen by comparing the the graphs of G , the contours of G and the phase space portrait of the 2D Volterra-Lotka system, all of which are shown below for $A = B = C = D = 1$.

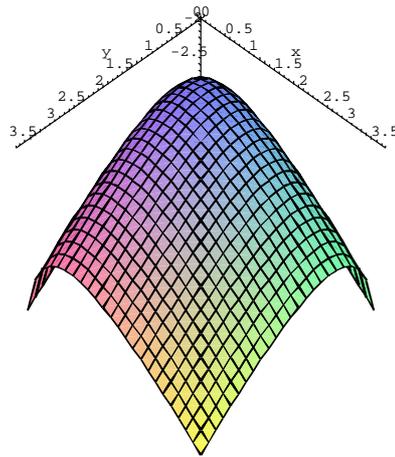
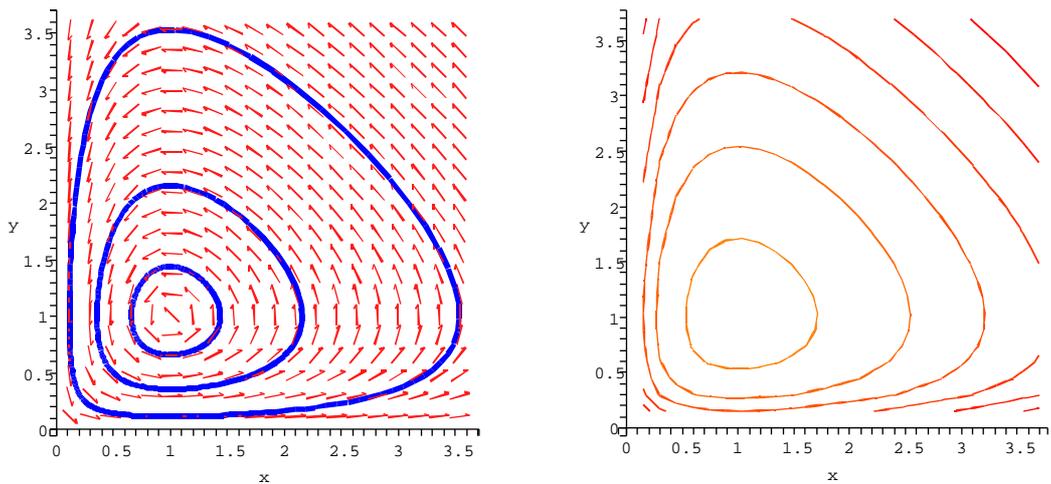


Figure 1: 3D graph of $G(x, y) = C \ln |x| - Dx + A \ln |y| - By$ for $A = B = C = D = 1$.



Figures 2 and 3: On the left is the phase space portrait of the Volterra-Lotka system for initial conditions $(x(0), y(0)) = (0.25, 0.25), (0.5, 0.5), (0.75, 0.75)$, listed in order from outermost trajectory to innermost trajectory, with stable fixed point $(1, 1)$. On the right is a plot of the contours of $G(x, y)$. Every contour of $G(x, y)$ is also a trajectory within the phase space of the system, and vice-versa.

Because the solutions to the system of differential equations run along level planes of the global Integral G , this implies that all solutions are stable with respect to the extrema of G . The maximum value of G is the fixed point $(C/D, A/B)$ of the system. Therefore this point is stable, but not asymptotically stable. This results in periodic behavior for all solutions not starting at either a fixed point or along one of the axes.

This behavior can be seen by plotting both x and y against time t . However, since x and y cannot be solved in terms of t , numerical methods must be used to plot x and y . Below is a plot made using the Runge-Kutta method as described in “Elementary Differential Equations and Boundary Value Problems” [1, pg. 456]. The plots use constant values $A = 0.5$ and $B = C = D = 1$ with initial condition $(x(0), y(0)) = (1, 1)$.

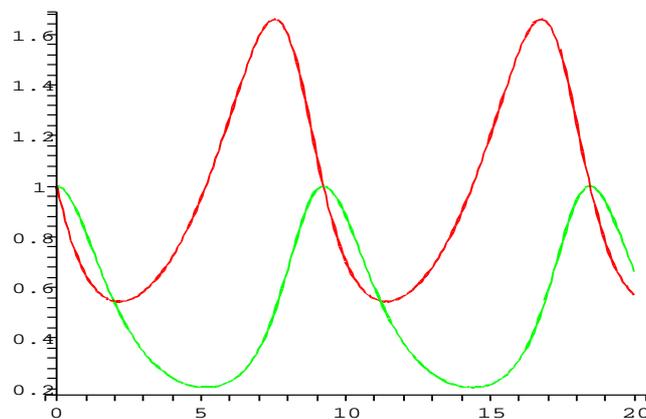


Figure 4: Plot of prey and predator populations over time. The line with the lower peak value is the predator population, and the other line is the prey population.

Notice how the predator population begins to decline shortly after the prey population starts to decrease. Then when the prey population begins to recover, the predator population also starts to recover. This is what one would expect to see in nature: the predator population grows as the prey population grows, until the point where the number of predators becomes restrictive for the prey population. This causes the prey population to decrease, and without enough prey to eat the predator population soon follows suit. This repeats for both populations. They share a common period. We would like to know if such periodic behavior also occurs in a system of three organisms.

3D Volterra-Lotka System

In order to extend the 2D system above into a 3D system, we will add a third species z to the system. Species z is a population of predators that feeds exclusively on the other predator population y . The new system makes the following assumptions in addition to those of the original system.

1. The new predator population z decreases exponentially in the absence of the other predator species y , which is its prey.
2. The original predator population y decreases relative to the frequency with which its members meet members of the new predator population z as a result of predation.
3. The new predator population z increases relative to the frequency with which its members meet members of the original predator population y as a result of predation.

Therefore the 3D Volterra-Lotka System is:

$$H(x(t), y(t), z(t)) = \begin{cases} \dot{x} &= Ax - Bxy &= x(A - By) \\ \dot{y} &= -Cy + Dxy - Eyz &= y(-C + Dx - Ez) \\ \dot{z} &= -Fz + Gzy &= z(-F + Gy) \end{cases} \quad (7)$$

All constants A, B, C, D, E, F and G are positive. The $-Fz$ term models assumption #1, $-Eyz$ models assumption #2 and Gzy models #3. This system suffers from the same shortcomings of the original system, in that it maintains an unrealistic exponential growth assumption, but it also shares the advantage of being a more tractable model.

The stationary points of the new system are similar to those of the original system. These points are $(x, y, z) = (0, 0, 0), (C/D, A/B, 0)$. We will once again use the Principle of Linearized Stability in an attempt to determine the stability of these points. Here is the linearized version of the 3D system.

$$\nabla H(x, y, z) = \begin{pmatrix} A - By & -Bx & 0 \\ Dy & -C + Dx - Ez & -Ey \\ 0 & Gz & -F + Gy \end{pmatrix} \quad (8)$$

Plugging in the point $(0, 0, 0)$ gives the matrix below, whose Eigenvalues are $A, -C$ and $-F$. Because A is positive and real, the point $(0, 0, 0)$ is unstable. Once again, this is not surprising given the assumption of exponential growth for x in the absence of predators. This point is not particularly interesting because there are no organisms to observe at the point $(0, 0, 0)$.

$$\nabla H(0, 0, 0) = \begin{pmatrix} A & 0 & 0 \\ 0 & -C & 0 \\ 0 & 0 & -F \end{pmatrix} \quad (9)$$

Plugging the point $(C/D, A/B, 0)$ in to the linearized system produces the matrix below. Its Eigenvalues are $(GA/B) - F$ and $\pm i\sqrt{AC}$. The Eigenvalue $(GA/B) - F$ could be negative, positive or zero depending on the choice of constants. If it is positive then the system is unstable around the point. Otherwise the Principle of Linearized Stability tells us nothing about the stability of the system around this point. The analysis of these various cases is carried out below.

$$\nabla H(C/D, A/B, 0) = \begin{pmatrix} 0 & -BC/D & 0 \\ DA/B & 0 & -EA/B \\ 0 & 0 & -F + GA/B \end{pmatrix} \quad (10)$$

Before going into further analysis of these stationary points, we will first perform an analysis of invariant surfaces within the model. An invariant surface is one which the solutions of a system do not escape, provided they start on it. One way of determining if this is the case is to use the following theorem [2].

Theorem 2 Let S be a smooth closed surface in \mathbb{R}^3 and

$$H(x, y, z) = \begin{cases} \dot{x} &= f(x, y, z) \\ \dot{y} &= g(x, y, z) \\ \dot{z} &= h(x, y, z) \end{cases} \quad (11)$$

where f , g and h are continuously differentiable. Suppose that for all $(x, y, z) \in S$, \vec{n} is a normal vector to the surface S at (x, y, z) and $\vec{n} \cdot \langle \dot{x}, \dot{y}, \dot{z} \rangle = 0$. Then S is invariant with respect to the system H .

Given that a population of organisms cannot reproduce when there are none left, it is reasonable to assume that the xy , yz and xz coordinate planes are invariant with respect to the system. We will prove this one plane at a time.

If $z = 0$ then we are in the xy coordinate plane, and the system becomes:

$$H(x(t), y(t), z(t)) = \begin{cases} \dot{x} &= Ax - Bxy \\ \dot{y} &= -Cy + Dxy \\ \dot{z} &= 0 \end{cases} \quad (12)$$

This is the same as the original 2D system. Therefore $\langle \dot{x}, \dot{y}, \dot{z} \rangle = \langle Ax - Bxy, -Cy + Dxy, 0 \rangle$. A vector normal to the xy plane at all points is $\langle 0, 0, 1 \rangle$. Since $\langle 0, 0, 1 \rangle \cdot \langle Ax - Bxy, -Cy + Dxy, 0 \rangle = 0$, the xy plane is invariant with respect to the system. The trajectories within this plane are the same as those for the 2D Volterra-Lotka system analyzed above.

The yz plane is defined by $x = 0$, which transforms the system into

$$H(x(t), y(t), z(t)) = \begin{cases} \dot{x} &= 0 \\ \dot{y} &= -Cy - Eyz \\ \dot{z} &= -Fz + Gzy \end{cases} \quad (13)$$

Proving that this plane is invariant is done in the same way as the previous plane. This time the normal vector is $\langle 1, 0, 0 \rangle$, and $\langle 1, 0, 0 \rangle \cdot \langle 0, -Cy - Eyz, -Fz + Gzy \rangle = 0$. Because y and z are both predator species they cannot survive without prey. The species y dies out because it feeds on x , and once y dies out z follows soon after, because it feeds on y . The z population may grow slightly at first, but as the y population nears extinction, the z population cannot help but follow. This can be seen on the resulting phase space portrait.

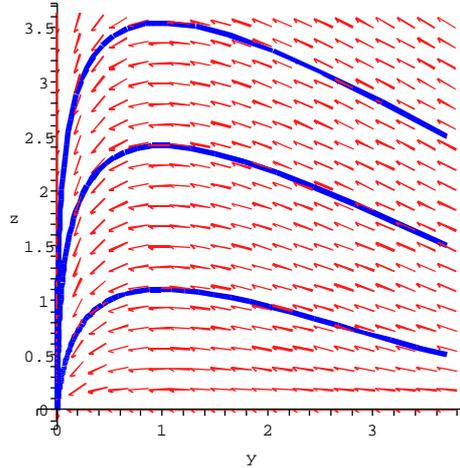


Figure 5: Phase space portrait of the yz plane for the 3D Volterra-Lotka system with three solutions shown, whose initial conditions are $(y(0), z(0)) = (3.7, 2.5), (3.7, 1.5), (3.7, 0.5)$.

It is also easy to show that the xz plane is invariant. The system resulting from $y = 0$ is

$$H(x(t), y(t), z(t)) = \begin{cases} \dot{x} &= Ax \\ \dot{y} &= 0 \\ \dot{z} &= -Fz \end{cases} \quad (14)$$

The vector $\langle 0, 1, 0 \rangle$ is normal to this plane and $\langle 0, 1, 0 \rangle \cdot \langle Ax, 0, -Fz \rangle = 0$. Therefore the xz plane is also invariant. In this plane, the x population grows without bound and the z population dies out. The two populations do not interact with each other at all. The z population dies due to lack of food, and the x population grows due to lack of predators. This exponential growth of the x population is illogical, and therefore a shortcoming of the model. Here is the resulting phase space portrait:

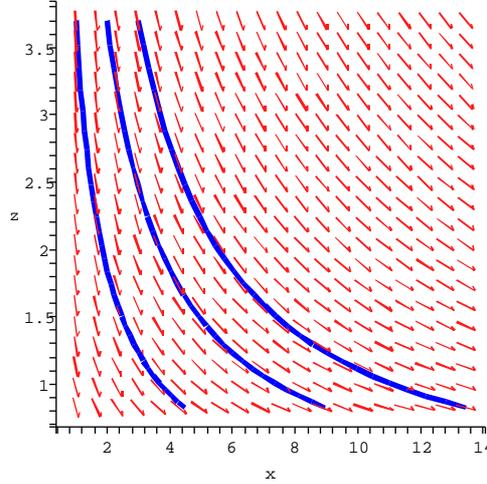


Figure 6: Phase space portrait of the xz plane for the 3D Volterra-Lotka system with three solutions shown.

Because the trajectories of solutions in this plane do not cross each other within open sets, which excludes the x and z axes, one would assume that an Integral exists for this plane. Once again making the separation assumption, we will seek a function $V(x, y) = f(x) + h(z)$ such that $\dot{V} = 0$.

$$\begin{aligned} \dot{V} &= \frac{\partial V}{\partial x} \dot{x} + \frac{\partial V}{\partial z} \dot{z} = 0 && \{\text{Multivariable Chain Rule}\} \\ 0 &= \frac{\partial V}{\partial x} Ax - \frac{\partial V}{\partial z} Fz && \{\text{Definition of System } H \text{ within } xz \text{ Plane}\} \\ 0 &= f'(x)Ax - h'(z)Fz && \{\text{Separation Assumption}\} \end{aligned}$$

$$h'(z)Fz = f'(x)Ax$$

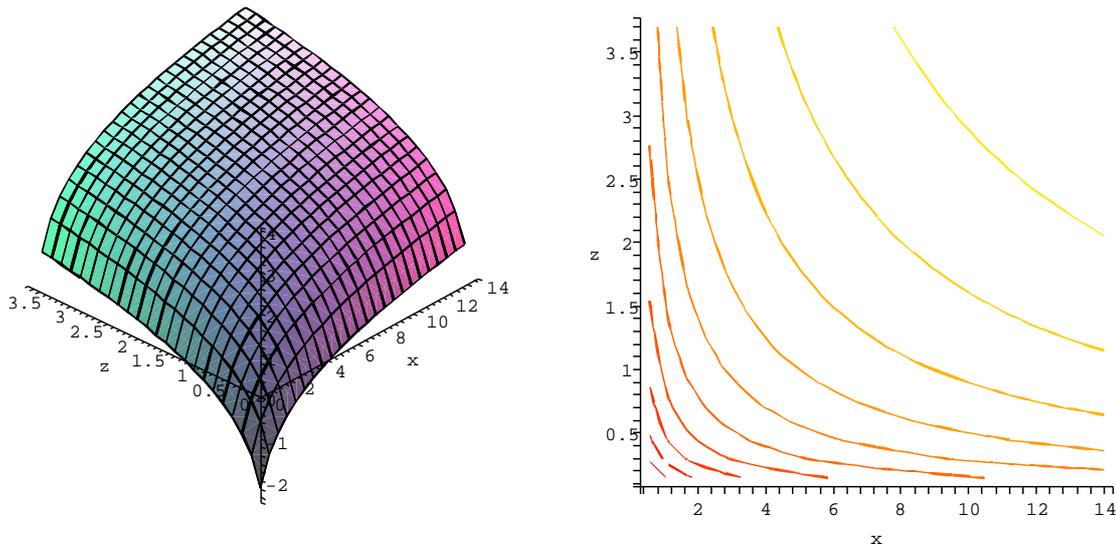
Since both sides of the equation are functions of different variables, both sides are equal to a constant, which we choose to be 1.

$$\begin{aligned} h'(z)Fz = 1 &\quad \wedge \quad f'(x)Ax = 1 \\ h'(z) = 1/Fz &\quad \wedge \quad f'(x) = 1/Ax \\ \int h'(z)dz = \int (1/Fz)dz &\quad \wedge \quad \int f'(x)dx = \int (1/Ax)dx \\ h(z) = \frac{\ln |z|}{F} + K_1 &\quad \wedge \quad \frac{\ln |x|}{A} + K_2 \end{aligned}$$

where K_1 and K_2 are constants of integration. Combining them into a single constant provides the following definition for the Integral V .

$$V(x, z) = \frac{\ln |x|}{A} + \frac{\ln |z|}{F} = K \tag{15}$$

As with the previous Integral, we can look at the graph of V and the graph of its contours to see the relationship between it and the phase space portrait of the system in the xz plane.



Figures 7 and 8: On the left is the graph of $V(x, z)$ and on the right is the graph of the contours of V . Notice the correspondence between these contours and the trajectories within the xz plane shown earlier.

Furthermore, this equation can be solved in terms of a single variable, so we choose to solve it for z . We then graph the resulting function $z(x)$ for $F = A = 1$ and several values of K to show that it is in fact the same as the plot of the contours of V .

$$z(x) = Kx^{-F/A} \quad (16)$$

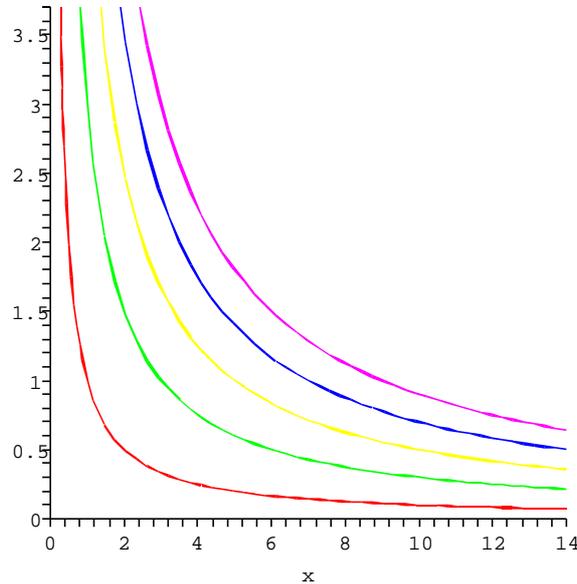


Figure 9: The function $z(x)$ for $F = A = 1$ and $K = 1, 3, 5, 7, 9$.

It turns out that the surfaces generated by this function in \mathbb{R}^3 are themselves invariant surfaces provided that $(GA/B) - F = 0$, or rather, $GA = BF$. Remember from above that this makes all Eigenvalues of the linear system around the fixed point $(C/D, A/B, 0)$ equal to zero, which allows for the possibility of stability around this point. By demonstrating the existence of invariant surfaces, we prove that this is in fact the case. The invariant surfaces are shown below, followed by a proof of their invariance.

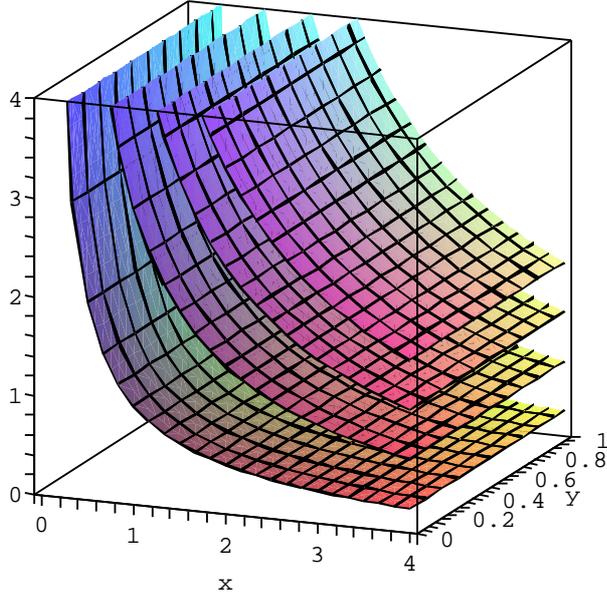


Figure 10: The surfaces $z(x) = Kx^{-F/A}$ in \mathfrak{R}^3 for $F = A = 1$ and $K = 1, 3, 5, 7$.

Let $W(x, y, z) = z - Kx^{-F/A} = 0$. These surfaces are the same as those shown above, and there is a vector \vec{n} normal to these surfaces such that

$$\vec{n} = \nabla W(x, y, z) = \left\langle \frac{FK}{A}x^{-(1+F/A)}, 0, 1 \right\rangle \quad (17)$$

which we use to show that all W are invariant in the 3D Volterra-Lotka system H .

$$\begin{aligned} & \vec{n} \cdot \langle \dot{x}, \dot{y}, \dot{z} \rangle \\ &= \left\langle \frac{FK}{A}x^{-(1+F/A)}, 0, 1 \right\rangle \cdot \langle Ax - Bxy, -Cy + Dxy - Eyz, -Fz + Gzy \rangle \quad \{\text{Def. of } \vec{n} \text{ and system } H\} \\ &= (Ax - Bxy) \frac{FK}{A} x^{-(1+F/A)} - Fz + Gzy \\ &= FKx^{-F/A} - \frac{BFKy}{A} x^{-F/A} - FKx^{-F/A} + GKyx^{-F/A} \quad \{\text{Definition of } z\} \\ &= -\frac{BFKy}{A} x^{-F/A} + \frac{BFKy}{A} x^{-F/A} = 0 \quad \{GA = BF \equiv G = BF/A\} \end{aligned}$$

Therefore W is invariant in H for all x, y, z , provided $GA = BF$.

By looking at the phase space of the system generated for $GA = BF$ we can see that the solutions are closed trajectories within the invariant surfaces defined by W .

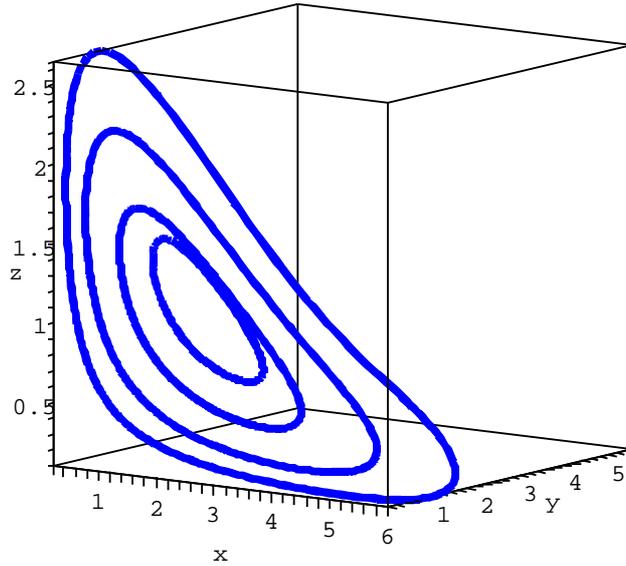


Figure 11: Phase space for the system H for $A = B = C = D = E = F = G = 1$ for solutions with initial conditions $(x(0), y(0), z(0)) = (0.25, 0.5, 2.5), (0.5, 0.5, 2), (1, 0.5, 1.5), (1.7, 0.5, 1.2)$.

Once again using the Runge-Kutta method, we can display a graph of x , y and z across time t . This graph demonstrates the periodic behavior of the system, which is non-asymptotically stable around the point $(C/D, A/B, 0)$.

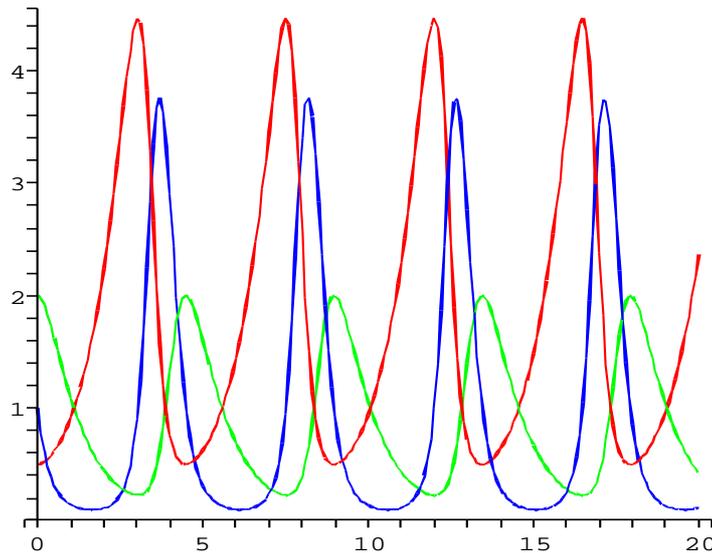
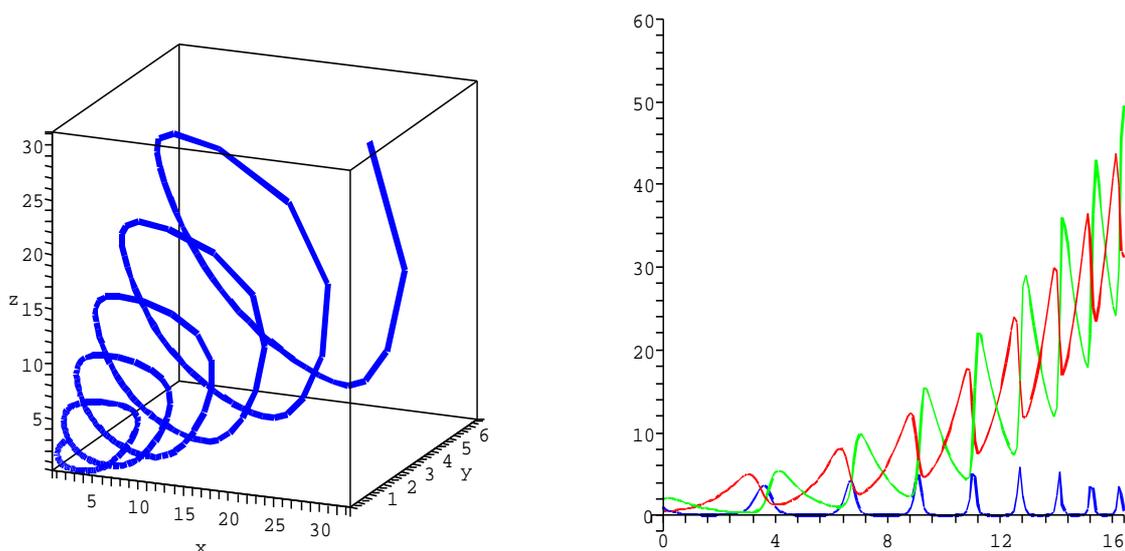


Figure 12: Plot of populations x , y and z over time with constants $A = B = C = D = E = F = G = 1$ and initial conditions $(x(0), y(0), z(0)) = (0.5, 1, 2)$. Notice that for the given constants, $GA = BF$. The species with the highest peak population is x , followed by y and z .

Once again an equilibrium is achieved within the system, such that each predator population increases as the population of its respective prey increases. Each predator population also peaks and then begins to decrease shortly after its respective prey population peaks and begins to decrease. The plots of populations x and y are essentially the same as they were in the 2D system, and the new predator population z behaves similarly with respect to y as y behaves with respect to x . All three populations share a common period.

The two cases left to study are for $GA < BF$ and $GA > BF$. We already know that if $GA > BF$ then the Eigenvalue $(GA/B) - F$ is positive, and the system is therefore instable around the point $(C/D, A/B, 0)$. This can be easily seen in both the phase space of the system and in the plots of x , y and z over time t .



Figures 13 and 14: In the two plots above, $A = B = C = D = E = F = 1$ and $G = 1.6$, thus corresponding to the case where $GA > BF$. Each graph is for the solution with initial condition $(x(0), y(0), z(0)) = (0.5, 1, 2)$. The graph on the left depicts that phase space of the system, in which one can see how the solution spirals endlessly upward and away from $(C/D, A/B, 0)$. The plots on the right are of x , y and z over time. Populations x and z approach infinity non-monotonically as time goes to infinity. The y population fluctuates more and more wildly as time increases.

Biologically, this solution makes no sense. Unbounded growth of a population does not occur in nature, because environmental factors and intraspecies competition restrict population growth. We expect a maximum sustainable population for each species, but the exponential growth model does not impose such a restriction.

The last case to consider is for $GA < BF$. In this case the Eigenvalue $(GA/B) - F$ is negative, and because the real parts of the other two Eigenvalues are zero, we cannot be sure of the behavior of the system. However, the phase space of the system in this case suggests that the solutions approach the xy plane and are stable around the point $(C/D, A/B, 0)$.

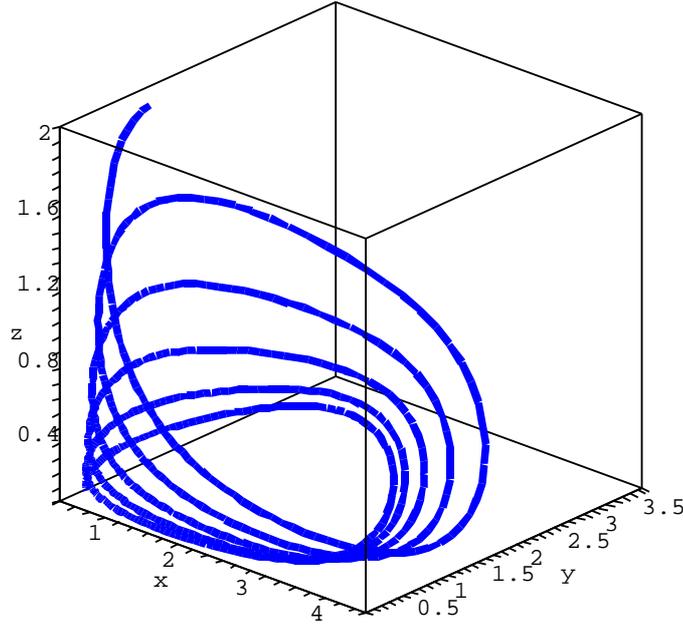


Figure 15: Phase space for constants $A = B = C = D = E = F = 1$ and $G = 0.88$ with initial condition $(x(0), y(0), z(0)) = (0.5, 1, 2)$. The solution spirals downwards, getting ever closer to the xy coordinate plane.

In order to prove this, we will first make use of the surfaces $z = Kx^{-F/A}$ defined earlier. These surfaces are no longer invariant, but we can show that the trajectories in the case of $GA < BF$ travel downward along these surfaces for decreasing values of K . First we redefine the surface as the function $K(x, y, z) = zx^{F/A}$. Then we show that the derivative of the function with respect to time t is always negative.

$$\begin{aligned}
& \frac{\partial}{\partial t} K(x(t), y(t), z(t)) \\
&= \frac{\partial}{\partial t} (zx^{F/A}) && \{\text{Definition of } K\} \\
&= \dot{z}x^{F/A} + (F/A)z\dot{x}x^{(F/A)-1} && \{\text{Product rule}\} \\
&= z(-F + Gy)x^{F/A} + (F/A)zx(A - By)x^{(F/A)-1} && \{\text{Definition of system } H\} \\
&= zx^{F/A}(-F + Gy + F - (FB/A)y) \\
&= yzx^{F/A}(G - (FB/A)) < 0 && \{x, y, z > 0 \wedge GA < BF \equiv G - (FB/A) < 0\}
\end{aligned}$$

Therefore $\dot{K} < 0$. This means that as time increases, the surfaces upon which the solutions are found have lower K values, meaning that the trajectories in phase space move along these surfaces from higher to lower values of K . Unfortunately, the surface defined for the limit of K approaching zero is not the xy plane, but rather the union of the xy and yz planes. This leaves open the possibility of trajectories approaching the plane $x = 0$ as time goes to infinity. Therefore we must do some further analysis to assure that all trajectories go only to the xy plane.

To do this we will define trapping regions. A trapping region is one which a trajectory will never leave once it has entered it. By making these trapping regions neighborhoods of the point $(C/D, A/B, 0)$, we directly prove the stability of the point using our definition of stability. We also want to assure that all trajectories move towards the xy plane, therefore the surfaces defining our trapping regions will need to intersect the xy plane in such a way that the region between the surfaces and the xy plane is completely enclosed.

Hill shaped surfaces meet these requirements, and in going back to the analysis of the 2D system we recall the Integral $G(x, y) = C \ln |x| - Dx + A \ln |y| - By$, whose graph is hill shaped. First we convert this Integral function to an equation of three variables: $z - C \ln |x| + Dx - A \ln |y| + By = 0$. For fixed constants A, B, C, D , the graph of this equation is a single surface in \mathfrak{R}^3 . By replacing the 0 with a constant M , we get a different surface for each M . Furthermore, surfaces with smaller M values are nested inside surfaces with higher M values, much like Russian nesting dolls. Our goal is then to prove that as time increases, the trajectories burrow down along these surfaces from surfaces with higher M values to surfaces with lower M values. In other words, we wish to prove that

$$\dot{M}(x(t), y(t), z(t)) < 0 \text{ for } M(x(t), y(t), z(t)) = z - C \ln |x| + Dx - A \ln |y| + By \quad (18)$$

$$\begin{aligned} & \frac{\partial}{\partial t} M(x(t), y(t), z(t)) \\ = & \frac{\partial}{\partial t} (z - C \ln |x| + Dx - A \ln |y| + By) \quad \{\text{Definition of M}\} \\ = & \dot{z} - C \frac{\dot{x}}{x} + D\dot{x} - A \frac{\dot{y}}{y} + B\dot{y} \\ = & \{\text{Definition of System H}\} \\ & -Fz + Gzy - C \frac{x(A - By)}{x} + D(Ax - Bxy) - A \frac{y(-C + Dx - Ez)}{y} + B(-Cy + Dxy - Eyz) \\ = & -Fz + Gzy - AC + BCy + ADx - BDxy + AC - ADx + AEz - BCy + BDxy - BEyz \\ = & -Fz + Gzy + AEz - BEyz \\ = & z(-F + AE) + yz(G - BE) \end{aligned}$$

Now we have a problem. We are unable to prove that the expression $z(-F + AE) + yz(G - BE)$ is negative. Because y and z are positive, it would suffice to show that of $(-F + AE)$ and $(G - BE)$, at least one is less than zero and the other is at most zero. However, we will have to modify our surface function M to accomplish this. Looking at the expressions $(-F + AE)$ and $(G - BE)$, we remember that we are at the moment concerned with the case where $GA < BF$. If the constants F and G were both multiplied by AE/F , then our expressions would be changed to $(-AE + AE) = 0$ and $((AEG/F) - BE) = E((GA/F) - B) < 0$. Both F and G entered our expressions from \dot{z} , and because constants remain after taking the derivative, our function M will satisfy our requirements if we modify it such that:

$$M(x, y, z) = z(AE/F) - C \ln |x| + Dx - A \ln |y| + By \quad (19)$$

Given this function, we know that $\dot{M} < 0$ by construction, which proves that trajectories of the system spiral down along the surfaces defined by M for decreasing values of M . These layered surfaces appear as follows:

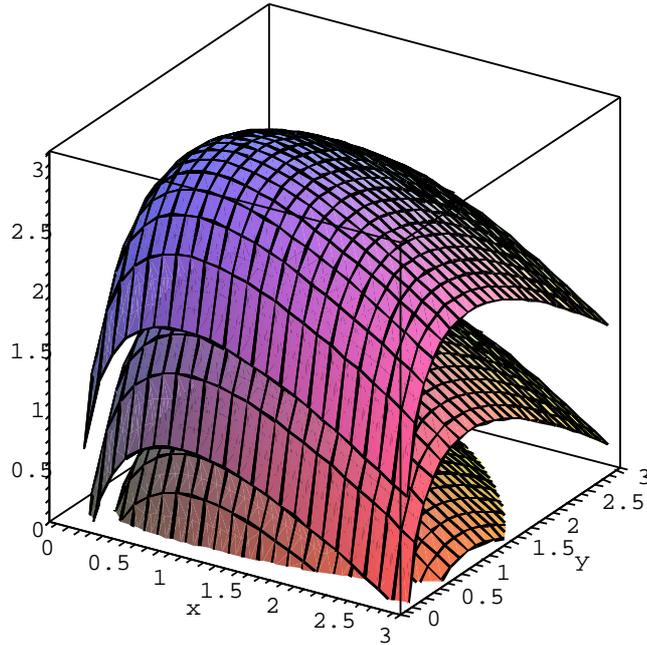


Figure 16: Plots of $z(AE/F) - C \ln|x| + Dx - A \ln|y| + By = M$ for $A = B = C = D = E = F = 1$ and $M = 3, 4, 5$. The trajectories of the 3D Volterra-Lotka system for the case $GA < BF$ burrow downward from surfaces with higher M values to surfaces with lower M values.

This proves that all trajectories for the case where $GA < BF$ spiral downward towards the the xy plane by travelling through the surfaces $z(AE/F) - C \ln|x| + Dx - A \ln|y| + By = M$ and $z = Kx^{-F/A}$ for decreasing values of M and K . Because the trajectories become trapped within neighborhoods of $(C/D, A/B, 0)$, this fixed point is stable. By once again using the Runge-Kutta method of numerical approximation we get the following plots of populations x , y and z over time.

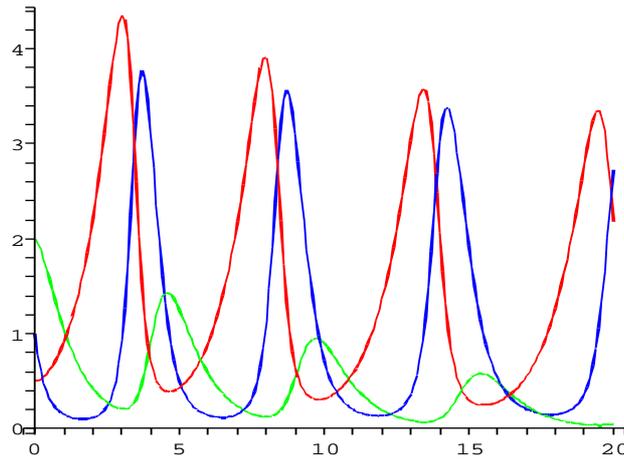


Figure 17: Plots of x , y and z over time t for $A = B = C = D = E = F = 1$ and $G = 0.88$ with initial condition $(x(0), y(0), z(0)) = (0.5, 1, 2)$. This behavior matches the phase space plot shown earlier, and demonstrates how the population of z approaches 0 as time goes to infinity.

This is biologically realistic behavior. Because of the choice of constants, the z population tends towards extinction and the x and y populations tend towards the same equilibrium they establish in the 2D system.

Conclusion

The two-dimensional Volterra-Lotka system exhibits stable periodic behavior for all non-zero initial conditions. These trajectories run along closed paths around the stationary point $(C/D, A/B)$, which is non-asymptotically stable. The other stationary point is at $(0, 0)$, for which both populations are extinct. This point is instable. If only the predator population y is extinct, then the prey population x grows without bound. If only the prey population x is extinct, then the predator population y approaches extinction. Constants A, B, C, D are positive by definition, so no alteration of the constants changes this behavior. Periodic stability is present for all possible combinations of variables.

The main weakness of this model is the exponential growth assumption. The unbounded growth of the prey species in the absence of predators is biologically unrealistic. The fact that the model does not allow for the extinction of either species (provided both species were present at the start) is also unrealistic. The introduction to each equation of a *social stress* term would convert the system to a logistic growth model, and solve these problems. Social stress is a way of representing the restrictions imposed on a population by intraspecies competition and environmental factors.

Another problem with this system is that it is completely closed. Organisms can neither leave these populations nor enter them from outside. This means that no migration is possible. This model also assumes that the predator has one and only one prey, and that the prey has one and only one predator. This is rarely the case in nature.

The three-dimensional system shares many of the same problems. Although it models three populations, the system is still closed. These populations cannot change as a result of migration, nor can they interact with other populations that are not modeled. The x and z species do not even interact with each other directly, but rather through the intermediate species y .

In the three-dimensional Volterra-Lotka system, the three coordinate planes are invariant with respect to the system. The xy plane is identical to the 2D Volterra-Lotka system. In the yz plane, there is no bottom level prey, and as a result both populations tend towards extinction. In the xz plane, the z population dies out because it cannot eat species x , but the x population grows unbounded.

Outside of these planes, there are three cases for how the system behaves. If $GA = BF$, then solutions are periodic. All trajectories run along invariant surfaces $z = Kx^{-F/A}$, and the stationary point $(C/D, A/B, 0)$ is stable. This is biologically realistic behavior. The system maintains an equilibrium similar to the one established in the 2D system. Prey populations increase until the respective predator populations get too large, and the predator populations begin to drop soon after their respective prey populations begin to drop. Once the predator populations are small again, the prey populations grow anew, repeating the process.

In the case where $GA > BF$, both the x and z populations grow without bound, while the y population fluctuates ever more wildly. The trajectories spiral away from the xy plane indefinitely. This is unrealistic behavior, and as with the 2D system could be fixed by switching to a logistic growth model. Because all trajectories spiral away from the xy plane, $(C/D, A/B, 0)$ is unstable.

The case $GA < BF$ is the opposite of this case. The trajectories for these two cases are the same except that they flow in opposite directions. In this case all trajectories spiral towards the xy plane. As they near the xy plane the z population approaches extinction, and populations x and y approach the equilibrium exhibited in the 2D system. The point $(C/D, A/B, 0)$ is therefore stable. The fact that z can only *approach* zero but not reach it is a weakness of the model.

In the 3D model the behavior of the system depends on the constants A, B, G and F . The x and y populations survive in all three cases, but the survival of species z hinges upon these parameters. Increasing G or A , or decreasing B or F , both tend towards the case $GA > BF$ in which the z population approaches infinity. Alternatively, decreasing G or A , or increasing B or F , both tend towards the case $GA < BF$, in which the z population becomes extinct. Only in the case $GA = BF$ does z survive in a biologically realistic fashion. It is surprising that C, D and E , the parameters directly affecting the z population's only food source, namely population y , do not affect the qualitative behavior of the system.

Of course, the very fact that the parameters are constants is another weakness of the model. Each constant represents either a growth rate or the frequency with which one species comes into contact with another. In the real world, these values would certainly not remain constant. The time of day and the current season often affect these values. Certain animals only mate during certain seasons. Some animals hibernate or migrate when the seasons change. Some animals hunt by day, and others are nocturnal. This means that A, B, C, D, E, F and G should be functions of t rather than constants, but the complexity of

such a model is daunting. The Volterra-Lotka model remains tractable by letting these values be constants rather than functions.

In general, the Volterra-Lotka model can be useful in studying real world behavior. Excluding the cases in which unbounded growth of any population occurs, this model is applicable in the real world [4]. By first understanding the exponential growth model, one can better understand why a logistic growth model would be more realistic. The Volterra-Lotka equations serve as a useful teaching tool, and by studying the 2D and 3D systems, one learns of several useful techniques for studying the stability of non-linear dynamic systems.

Maple Code for 2D System

The 2D Volterra-Lotka System with exponential growth.

```
> prey := D(x)(t) = x(t)*(a-b*y(t));
> pred := D(y)(t) = y(t)*(-c+d*x(t));
```

A specific system in which $a = b = c = d = 1$.

```
> prey1 := subs(a=1,b=1,prey);
> pred1 := subs(c=1,d=1,pred);
```

```
> with(DEtools):
```

(Figure 2) The phase space portrait of the system with initial conditions $(x(0),y(0)) = (0.25,0.25), (0.5,0.5), (0.75,0.75)$.

```
> phaseportrait([prey1,pred1], [x(t),y(t)], t=0..10,
> [[x(0)=0.25,y(0)=0.25],[x(0)=0.5,y(0)=0.5],[x(0)=0.75,y(0)=0.75]],
> stepsize=.05, linecolour=blue);
```

An Integral for the system.

```
> G := (x,y) -> c*ln(x) - d*x + a*ln(y) - b*y;
```

Integral with $a = b = c = d = 1$.

```
> G1 := subs(a=1,b=1,c=1,d=1,G(x,y));
```

(Figure 1) Graph of the Integral with $a = b = c = d = 1$.

```
> plot3d(G1,y=0..3.7,x=0..3.7);
```

```
> with(plots):
```

(Figure 3) Contour plot of the Integral.

```
> contourplot(G1,x=0..3.7,y=0..3.7,contours=10);
```

Numerical solution with Runge-Kutta method

```
> f := (x,y) -> (0.5*x - x*y, -y + x*y);
```

```
> t[0] := 0;
```

```
> x[0] := 1;
```

```
> y[0] := 1;
```

```
> h := 0.1;
```

```
> k1 := (x,y) -> f(x,y);
```

```
> k2 := (x,y) -> f((x,y)+(h/2)*k1(x,y));
```

```
> k3 := (x,y) -> f((x,y)+(h/2)*k2(x,y));
```

```
> k4 := (x,y) -> f((x,y)+h*k3(x,y));
```

```
> xy := (x,y) -> (x,y)+(h/6)*(k1(x,y)+2*k2(x,y)+2*k3(x,y)+k4(x,y));
```

```

> N := 200;
> for n from 0 to N do
>   nextpoint := xy(x[n],y[n]);
>   x[n+1] := nextpoint[1];
>   y[n+1] := nextpoint[2];
>   t[n+1] := t[n] + h;
> end do;

> xrun := seq([t[i],x[i]],i=0..N);
> yrun := seq([t[i],y[i]],i=0..N);

```

(Figure 4) Plot for x and y with Runge-Kutta, time step 0.1, initial conditions $(x(0),y(0)) = (1,1)$ and constants $a = 0.5$ and $b = c = d = 1$.

```

> plot([[xrun],[yrun]]);

```

Maple Code for 3D System

The 3D Volterra-Lotka System with exponential growth.

```

> prey := D(x)(t) = x(t)*(a-b*y(t));
> prpr := D(y)(t) = y(t)*(-c+d*x(t)-E*z(t));
> pred := D(z)(t) = z(t)*(-f+g*y(t));

```

A specific system in which $a = b = c = d = E = f = g = 1$.

```

> prey1 := subs(a=1,b=1,prey);
> prpr1 := subs(c=1,d=1,E=1,prpr);
> pred1 := subs(f=1,g=1,pred);

```

```

> with(DEtools):

```

(Figure 11) Phase space of the system for $a = b = c = d = E = f = g = 1$.

```

> DEplot3d(preyl,prpr1,pred1,x(t),y(t),z(t),t=0..10,
> [[x(0)=0.25,y(0)=0.5,z(0)=2.5],[x(0)=0.5,y(0)=0.5,z(0)=2],
> [x(0)=1,y(0)=0.5,z(0)=1.5],[x(0)=1.7,y(0)=0.5,z(0)=1.2]],
> stepsize=.05,lincolour=blue);

```

(Figure 15) Phase space of the system for $a = b = c = d = E = f = 1$ and $g = 0.88$, initial condition $(x(0),y(0),z(0)) = (0.5,1,2)$.

```

> DEplot3d(preyl,prpr1,subs(f=1,g=0.88,pred),x(t),y(t),z(t),t=0..30,
> [[x(0)=0.5,y(0)=1,z(0)=2]], stepsize=.05,lincolour=blue);

```

(Figure 16) Trapping Regions

```

> L := -y+ln(y) -x +ln(x);
> plot3d([L+0,L+3,L+4,L+5], x=0..3, y=0..3);

```

(Figure 13) Phase space of the system for $a = b = c = d = E = f = 1$ and $g = 1.6$, initial condition $(x(0),y(0),z(0)) = (0.5,1,2)$.

```

> DEplot3d(preyl,prpr1,subs(f=1,g=1.6,pred),x(t),y(t),z(t),t=0..14.2,
> [[x(0)=0.5,y(0)=1,z(0)=2]], stepsize=.05,lincolour=blue);

```

(Figure 5) The phase space portrait of the yz plane (let $x = 0$) with initial conditions $(y(0),z(0)) = (3.7,2.5), (3.7,1.5), (3.7,0.5)$.

```

> phaseportrait([subs(x(t)=0,prpr1),pred1],[y(t),z(t)],t=0..10,
> [[y(0)=3.7,z(0)=2.5],[y(0)=3.7,z(0)=1.5],[y(0)=3.7,z(0)=0.5]],
> stepsize=.05,lincolour=blue);

```

(Figure 6) The phase space portrait of the xz plane (let $y = 0$) with initial conditions $(x(0),z(0)) = (3.7,2.5), (3.7,1.5), (3.7,0.5)$.

```
> phaseportrait([subs(y(t)=0,prey1),subs(y(t)=0,pred1)],[x(t),z(t)],
> t=0..1.5,[x(0)=1,z(0)=3.7],[x(0)=2,z(0)=3.7],[x(0)=3,z(0)=3.7]],
> stepsize=.05,linecolour=blue);
```

An Integral for the xz plane.

```
> V := (x,z) -> ln(x)/A + ln(z)/F;
```

Specific Integral with $A = F = 1$.

```
> V1 := subs(A=1,F=1,V(x,z));
```

(Figure 7) Graph of V1.

```
> plot3d(V1,x=0..14,z=0..3.7);
```

```
> with(plots):
```

(Figure 8) Contour plot of the Integral.

```
> contourplot(V1,x=0..14,z=0..3.7,contours=10);
```

Transform Integral into function z of x.

```
> Z := x -> K*x^(-F/A);
```

Let $F/A = 1$.

```
> Z1 := subs(F/A=1, Z(x));
```

(Figure 9) Graphs of several Z1 for different K.

```
> plot([subs(K=1,Z1),subs(K=3,Z1),subs(K=5,Z1),subs(K=7,Z1),subs(K=9,Z1)], x=0..14);
```

(Figure 10) Invariant surfaces in 3D System for $ga = fb$.

```
> plot3d([subs(K=1,Z1),subs(K=3,Z1),subs(K=5,Z1),subs(K=7,Z1)], x=0..4,y=0..2.5);
```

Numerical solution with Runge-Kutta method for $ga = fb$.

```
> f := (x,y,z) -> (x - x*y, -y + x*y - y*z, -z + y*z);
```

```
> t[0] := 0;
```

```
> x[0] := 0.5;
```

```
> y[0] := 1;
```

```
> z[0] := 2;
```

```
> h := 0.1;
```

```
> k1 := (x,y,z) -> f(x,y,z);
```

```
> k2 := (x,y,z) -> f((x,y,z)+(h/2)*k1(x,y,z));
```

```
> k3 := (x,y,z) -> f((x,y,z)+(h/2)*k2(x,y,z));
```

```
> k4 := (x,y,z) -> f((x,y,z)+h*k3(x,y,z));
```

```
> xyz := (x,y,z) -> (x,y,z)+(h/6)*(k1(x,y,z)+2*k2(x,y,z)+2*k3(x,y,z)+k4(x,y,z));
```

```
> N := 200;
```

```
> for n from 0 to N do
```

```
>   nextpoint := xyz(x[n],y[n],z[n]);
```

```
>   x[n+1] := nextpoint[1];
```

```
>   y[n+1] := nextpoint[2];
```

```
>   z[n+1] := nextpoint[3];
```

```
>   t[n+1] := t[n] + h;
```

```
> end do;
```

```

> xrun := seq([t[i],x[i]],i=0..N);
> yrun := seq([t[i],y[i]],i=0..N);
> zrun := seq([t[i],z[i]],i=0..N);

```

(Figure 12) Plot for x, y and z with Runge-Kutta, time step 0.1, initial conditions $(x(0),y(0),z(0)) = (0.5,1,2)$ and constants $a = b = c = d = e = f = g = 1$.

```

> plot([[xrun],[yrun],[zrun]],color=[red,blue,green]);

```

Numerical solution with Runge-Kutta method for ga i fb.

```

> g := (x,y,z) -> (x - x*y, -y + x*y - y*z, -z + 0.88*y*z);
> t[0] := 0;
> x[0] := 0.5;
> y[0] := 1;
> z[0] := 2;
> h := 0.1;

```

```

> k1 := (x,y,z) -> g(x,y,z);
> k2 := (x,y,z) -> g((x,y,z)+(h/2)*k1(x,y,z));
> k3 := (x,y,z) -> g((x,y,z)+(h/2)*k2(x,y,z));
> k4 := (x,y,z) -> g((x,y,z)+h*k3(x,y,z));
> xyz := (x,y,z) -> (x,y,z)+(h/6)*(k1(x,y,z)+2*k2(x,y,z)+2*k3(x,y,z)+k4(x,y,z));

```

```

> N := 200;
> for n from 0 to N do
>   nextpoint := xyz(x[n],y[n],z[n]);
>   x[n+1] := nextpoint[1];
>   y[n+1] := nextpoint[2];
>   z[n+1] := nextpoint[3];
>   t[n+1] := t[n] + h;
> end do;

```

```

> xrun := seq([t[i],x[i]],i=0..N);
> yrun := seq([t[i],y[i]],i=0..N);
> zrun := seq([t[i],z[i]],i=0..N);

```

(Figure 17) Plot for x, y and z with Runge-Kutta, time step 0.1, initial conditions $(x(0),y(0),z(0)) = (0.5,1,2)$ and constants $a = b = c = d = e = f = 1, g = 0.88$.

```

> plot([[xrun],[yrun],[zrun]],color=[red,blue,green]);

```

Numerical solution with Runge-Kutta method for ga i fb.

```

> j := (x,y,z) -> (x - x*y, -y + x*y - y*z, -z + 1.6*y*z);
> t[0] := 0;
> x[0] := 0.5;
> y[0] := 1;
> z[0] := 2;
> h := 0.1;

```

```

> k1 := (x,y,z) -> j(x,y,z);
> k2 := (x,y,z) -> j((x,y,z)+(h/2)*k1(x,y,z));
> k3 := (x,y,z) -> j((x,y,z)+(h/2)*k2(x,y,z));
> k4 := (x,y,z) -> j((x,y,z)+h*k3(x,y,z));
> xyz := (x,y,z) -> (x,y,z)+(h/6)*(k1(x,y,z)+2*k2(x,y,z)+2*k3(x,y,z)+k4(x,y,z));

```

```

> N := 200;
> for n from 0 to N do
>   nextpoint := xyz(x[n],y[n],z[n]);
>   x[n+1] := nextpoint[1];
>   y[n+1] := nextpoint[2];
>   z[n+1] := nextpoint[3];
>   t[n+1] := t[n] + h;
> end do;

> xrun := seq([t[i],x[i]],i=0..N);
> yrun := seq([t[i],y[i]],i=0..N);
> zrun := seq([t[i],z[i]],i=0..N);

```

(Figure 14) Plot for x, y and z with Runge-Kutta, time step 0.1, initial conditions $(x(0),y(0),z(0)) = (0.5,1,2)$ and constants $a = b = c = d = e = f = 1, g = 1.6$.

```

> plot([[xrun],[yrun],[zrun]],color=[red,blue,green]);

```

Bibliography

- [1] William E. Boyce and Richard C. DiPrima. *Elementary Differential Equations and Boundary Value Problems*. John Wiley & Sons, Inc., 2001.
- [2] Erica Chauvet, Joseph E. Paultet, Joseph P. Previte, and Zac Walls. A Lotka-Volterra Three-species Food Chain. *Mathematics Magazine*, 75(4):243–255, October 2002.
- [3] Koro. flow, September 2003. <http://planetmath.org/encyclopedia/Flow2.html>, Accessed 11/12/05.
- [4] Lawrence C. Moore and David A. Smith. Predator-prey models, 2003. <http://www.math.duke.edu/education/ccp/materials/diffeq/predprey/pred1.html>, Accessed 11/12/05.
- [5] Nardin Patrizia. The lotka-volterra equation, March 2001. <http://www.gris.uni-tuebingen.de/projects/dynsys/latex/dissp/node16.html>, Accessed 11/12/05.
- [6] Karl Friedrich Siburg. *Gewöhnliche Differentialgleichungen*, 2005. Lecture at the University of Dortmund, Germany. Spring-Summer Semester. Notes available upon request.