Math 532H Project

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Abstract

This project is on the Lotka-Volterra model for ecological population dynamics, which is described by the following nonlinear system of differential equations:

$$\dot{x} = \alpha x - \beta xy$$

$$\dot{y} = \delta xy - \gamma y$$

where x is the prey population, y is the predator population, and $\alpha, \beta, \gamma, \delta > 0$ are parameters. The Lotka-Volterra model is well known and has been widely studied, although it is generally considered to be a poor model. However, it serves as a foundation for which to build other models that incorporate ideas of competition or predation. We will make a slight improvement to the base model, and then investigate a multi-dimensional variation that models a more complicated food chain. We will accomplish this by introducing a third dimension to our system and analyzing how the resulting dynamics change. This will allow us to examine more complex and realistic ecological relationships.

Goals

My main goal with this project is to become better acquainted with how models are built and analyzed. Starting from a simple base model, I want to alter certain aspects in order to create more complex models. Building a robust model is a daunting and time consuming task, so I will limit myself to small changes to the original model.

In particular, the two models I will construct are a logistic Lotka-Volterra variant, and a 3 dimensional food chain variant. The exact details and motivations of the models are explained in later sections. We wish to answer two main questions:

- How does a logistic growth constraint affect the dynamics of the Lotka-Volterra system (fixed points, stability)?
- How does introducing more species into the system affect the dynamics?

Methods

Our principal method of investigation will be linear analysis of systems of ODEs via the jacobian. This will allow us to classify the fixed points of the systems, which tells us a great deal about the dynamics of the system as a whole.

In terms of numerical methods, we will use numerical integration to plot both individual solutions and entire phase portraits for a range of parameters to confirm our analytic predictions. We will use matplotlib for plotting and numpy/scipy for computations. At one point, we will use Mathmatica's symbolic calculation to aid us in finding the eigenvalues of a jacobian.

Model 0 - Base Model

Before we can analyze the Lotka-Volterra variants, we must first understand the base model:

$$\dot{x} = \alpha x - \beta xy$$

$$\dot{y} = \delta xy - \gamma y$$

Note that all parameter values are strictly greater than 0. We can interpret the parameters like so:

- α - The natural population growth of the prey
- β - The effects of the predators hunting the prey
- δ - Growth in predator population as a result of hunting prey
- γ - Natural death rate of predators

The fixed points of this system are:

$$(0, 0)$$

$$\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$$

Linearization of this system using the jacobian yields:

$$J(x, y) = \begin{bmatrix} \alpha - \beta y & -\beta x \\ \delta y & \delta x - \gamma \end{bmatrix}$$

Origin: At the origin, we get:

$$J(0, 0) = \begin{bmatrix} \alpha & 0 \\ 0 & -\gamma \end{bmatrix}$$

The trace is $\tau = \alpha - \gamma$ and the determinant is $\Delta = -\alpha\gamma < 0$. Note that since the determinant is always less than 0, the origin will be an **saddle point** for all values in the parameter space.

Other: At our other fixed point, we get:

$$J\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right) = \begin{bmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ \dfrac{\alpha\delta}{\beta} & 0 \end{bmatrix}$$

The trace is $\tau = 0$ and the determinant is $\Delta = \alpha\gamma > 0$. This indicates the fixed point *may* be a center. It is not guaranteed at this point because our linear approximation introduces errors that may cause a center to become a spiral instead. We can confirm that this fixed point is in fact a center because of the existence of the following conserved quantity (Devaki, Swathi):

$$E = \delta x - \gamma \ln(x) + \beta\gamma - \alpha \ln(y)$$

Our fixed point is indeed a local extremum of this quantity:

$$\frac{\partial E}{\partial x} = \delta - \frac{\gamma}{x} = 0 \implies x = \frac{\gamma}{\delta}$$

$$\frac{\partial E}{\partial y} = \beta - \frac{\alpha}{y} = 0 \implies y = \frac{\alpha}{\beta}$$

Thus by Theorem 6.5.1 (Strogatz 163), the fixed point is a **center** for all values in the parameter space.

Our analysis on this system predicts somewhat simple behavior: one fixed point is always a saddle point, and the other is always a center. We can perform numerical computations to see what individual solutions and the whole phase plane look like:

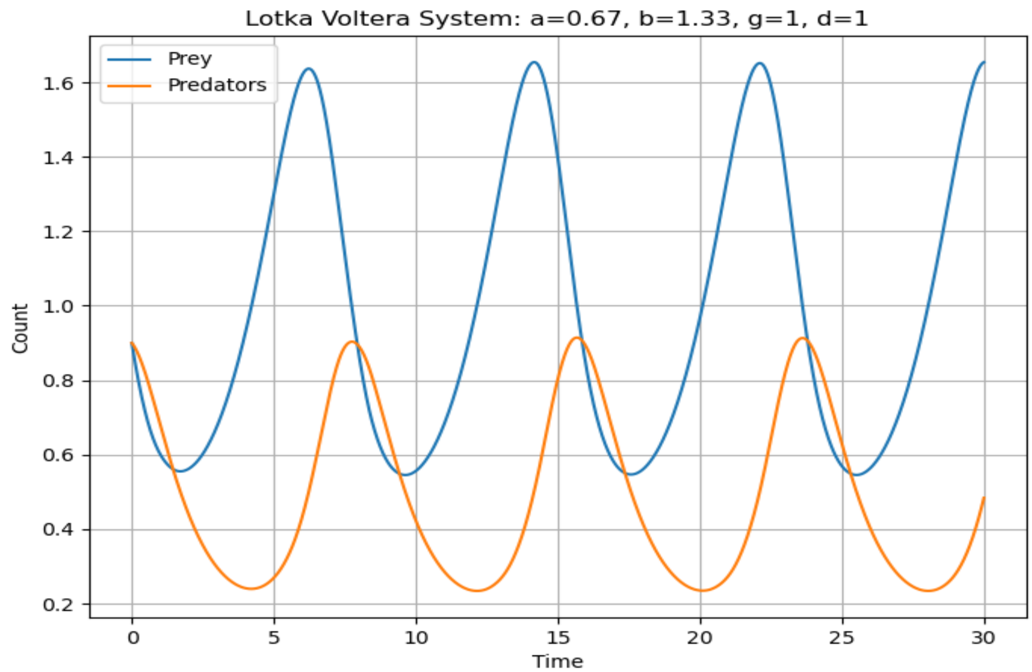

Figure 1: A specific solution to the Lotka-Volterra system.

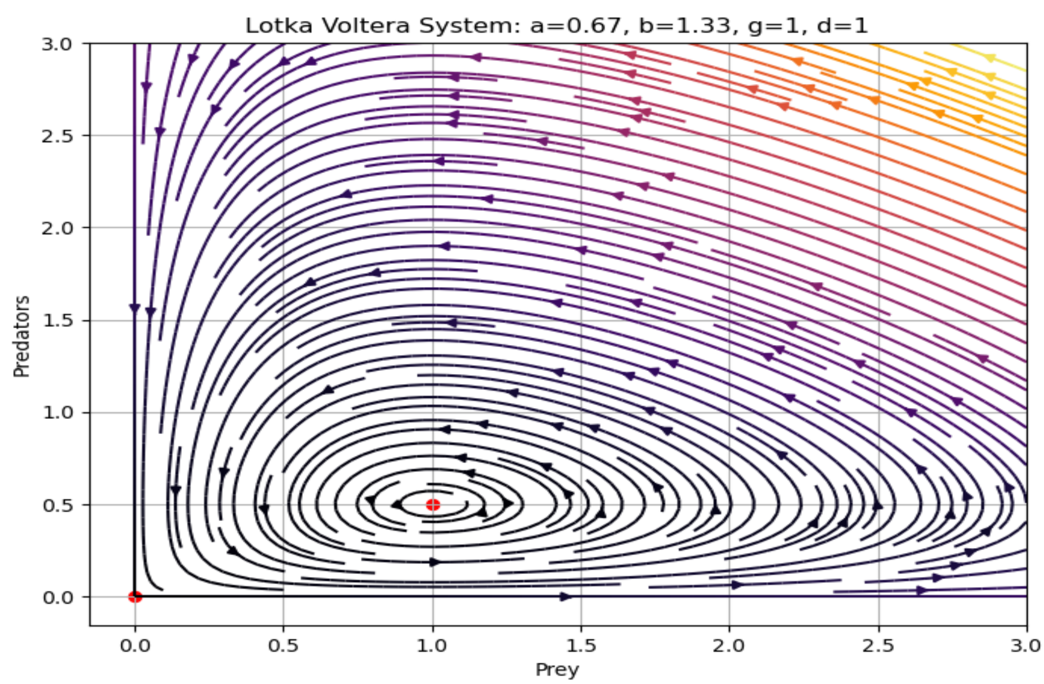

Figure 2: The phase plane of the Lotka-Volterra system (fixed points are in red).

Model 1 - Improved Lotka-Volterra Model (ILV)

Now that we have analyzed the most basic model, we can move on to more complex models. The Lotka-Volterra model makes many implicit assumptions about the system that aren't necessarily reflected in reality. For example, it assumes that the prey's population can only decrease due to interactions with the predator, and that the predator depends solely on one species of prey for food. However, if we were to try to fix all of the poor assumptions, we would end up with an extremely complicated model with many parameters, making it very difficult to analyze analytically. Instead, we will focus on fixing one specific assumption, and seeing how it affects the population dynamics. The base model assumes that in the absence of predators($y = 0$), that the prey population will grow exponentially. This is not true, since resources in an ecosystem are limited. We will introduce a carrying capacity k for the prey, which will model their growth as logistic instead of exponential. Our new model will be:

$$\dot{x} = \alpha x\left(1 - \frac{x}{k}\right) - \beta xy$$

$$\dot{y} = \delta xy - \gamma y$$

ILV Analysis

We can analyze this 2D model using the standard tools of linear analysis, along with numerical algorithms.

The fixed points of this system can be found relatively easily. Clearly $(0, 0)$ is a fixed point, so suppose x and y are not both 0. We have two cases:

$y = 0$

If $y = 0$, then:

$$\dot{x} = \alpha x\left(1 - \frac{x}{k}\right) = 0$$

Thus $x = 0$ or $x = k$. We have already found the fixed point $(0, 0)$, so a new fixed point is $(k, 0)$.

$y \neq 0$

If $y \neq 0$, then we can divide out y from the predator equation to get:

$$\dot{y} = 0 = \delta x - \gamma$$

Therefore $x = \frac{\gamma}{\delta}$. We can substitute this back into the prey equation to get:

$$\alpha\frac{\gamma}{\delta}\left(1 - \frac{\gamma}{\delta k}\right) - \beta\frac{\gamma}{\delta}y = 0$$

$$\implies \alpha\frac{\gamma}{\delta}\left(1 - \frac{\gamma}{\delta k}\right) = \beta\frac{\gamma}{\delta}y$$

$$\implies \alpha\left(1 - \frac{\gamma}{\delta k}\right) = \beta y$$

$$\implies \frac{\alpha}{\beta}\left(1 - \frac{\gamma}{\delta k}\right) = y$$

Thus the final fixed point is:

$$\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\left[1 - \frac{\gamma}{\delta k}\right]\right)$$

Now that we have found all of the fixed points, we can compute their stability. The jacobian of the system is:

$$J(x, y) = \begin{bmatrix} a - \frac{2\alpha}{k}x - \beta y & -\beta x \\ \delta y & \delta x - \gamma \end{bmatrix}$$

Let us consider the value of the jacobian at each of the three fixed points:

Fixed Point 1

For the fixed point (0,0), we have:

$$J(0,0) = \begin{bmatrix} a & 0 \\ 0 & -\gamma \end{bmatrix}$$

which has trace $\tau = \alpha - \gamma$ and determinant $\Delta = -\alpha\gamma$. Since all parameters are greater than 0, this means $\Delta < 0$ always, making the origin a **saddle point** for all values in the parameter space.

Fixed Point 2

For the fixed point $(k, 0)$, we have:

$$J(k,0) = \begin{bmatrix} -\alpha & -\beta k \\ 0 & \delta k - \gamma \end{bmatrix}$$

which has trace $\tau = \delta k - \gamma - \alpha$ and determinant $\Delta = -\alpha(\delta k - \gamma)$. Note that since the jacobian is an upper-triangular matrix, its eigenvalues are the diagonal entries $-\alpha$ and $\delta k - \gamma$. We have three cases:

Case 1: $\delta k - \gamma < 0$

In this case both eigenvalues will be less than 0, so the fixed point will be some kind of nonlinear **stable node**.

Case 2: $\delta k - \gamma = 0$

In this case, one eigenvalue is negative and the other is 0. This predicts a borderline case, so the linear analysis is **inconclusive**. We will need to use numerical simulation to determine the true stability.

Case 3: $\delta k - \gamma > 0$

In this case there is one positive and one negative eigenvalue, so we have a **saddle point**.

Fixed Point 3

Since we are dealing with populations, we are only interested in fixed points where both coordinates are positive. Thus for the fixed point $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}(1 - \frac{\gamma}{\delta k}))$, we require:

$$\frac{\alpha}{\beta}(1 - \frac{\gamma}{\delta k}) > 0$$

$$\implies \delta k > \gamma$$

Computing the jacobian, we get:

$$J\left(\frac{\gamma}{\delta},\ \frac{\alpha}{\beta}(1 - \frac{\gamma}{\delta k})\right) = \begin{bmatrix} -\frac{\alpha\gamma}{\delta k} & -\frac{\beta\gamma}{\delta} \\ \frac{\alpha\delta}{\beta}(1 - \frac{\gamma}{\delta k}) & 0 \end{bmatrix}$$

which has trace $\tau = -\frac{\alpha\gamma}{\delta k}$ and determinant $\Delta = \alpha\gamma(1 - \frac{\gamma}{\delta k})$. Again, since all parameters have positive values, we have $\tau < 0$. For the specific classification, we must look to the sign of Δ:

Case 1: $\Delta < 0$

In this case, since $\Delta < 0$ we have a saddle point. Δ is only negative when $1 - \frac{\gamma}{\delta k} < 0$, which implies that $\gamma > \delta k$. However, as stated earlier we require $\gamma < \delta k$ in order for the fixed point to have positive coordinates. Thus when $\delta k - \gamma < 0$ the fixed point is **nonphysical**.

Case 2: $\Delta = 0$

In this case, we must have $\gamma = \delta k \implies \frac{\gamma}{\delta} = k$. This forces the the fixed point to become:

$$\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}(1 - \frac{\gamma}{\delta k})\right) = \left(k, \frac{\alpha}{\beta}(1 - \frac{k}{k})\right)$$
$$= (k, 0)$$

which is just the previous fixed point we discussed. Therefore this fixed point **collapses** into the fixed point $(k, 0)$ when $\delta k - \gamma = 0$.

Case 3: $\Delta > 0$

In this case, we must have $1 - \frac{\gamma}{\delta k} > 0$, which means $\delta k > \gamma$. Thus when $\delta k - \gamma > 0$ the fixed point is **stable**. However, depending on the particular values of δ, k, and γ we may get a node or spiral. We can examine the sign of $\tau^2 - 4\Delta$ to determine what we get:

$$\tau^2 - 4\Delta = \left(-\frac{\alpha\gamma}{\delta k}\right)^2 - 4\alpha\gamma\left(1 - \frac{\gamma}{\delta k}\right) = 0$$
$$\implies \left(\frac{\alpha\gamma}{\delta k}\right)^2 - 4\alpha\gamma\left(1 - \frac{\gamma}{\delta k}\right) = 0$$
$$\implies \frac{\alpha\gamma}{(\delta k)^2} - 4\left(1 - \frac{\gamma}{\delta k}\right) = 0$$
$$\implies \frac{\alpha\gamma}{(\delta k)^2} = 4\left(\frac{\delta k - \gamma}{\delta k}\right)$$
$$\implies \alpha\gamma = 4\delta k(\delta k - \gamma)$$
$$\implies \alpha = \frac{4\delta k(\delta k - \gamma)}{\gamma}$$

This gives us the following three cases:

- $\alpha < \dfrac{4\delta k(\delta k - \gamma)}{\gamma}$: In this case $\tau^2 - 4\Delta < 0$ as well, so the fixed point will be a **stable spiral**.
- $\alpha = \dfrac{4\delta k(\delta k - \gamma)}{\gamma}$: In this case $\tau^2 - 4\Delta = 0$, so the fixed point is predicted to be a degenerate node. This is a borderline case, so we cannot know for sure if this is accurate. Thus the results are **inconclusive**.
- $\alpha > \dfrac{4\delta k(\delta k - \gamma)}{\gamma}$: In this case $\tau^2 - 4\Delta > 0$, so the fixed point is predicted to be a **stable node**.

The analysis of the fixed points is somewhat lengthy, so the information will be condensed into the following table for ease:

Condition	Subcase	$(0, 0)$	$(k, 0)$	$(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}(1 - \frac{\gamma}{\delta k}))$
$\delta k - \gamma < 0$		saddle	stable node	nonphysical
$\delta k - \gamma = 0$		saddle	inconclusive	N/A
$\delta k - \gamma > 0$	$\alpha < \frac{4\delta k(\delta k - \gamma)}{\gamma}$	saddle	saddle	stable spiral
	$\alpha = \frac{4\delta k(\delta k - \gamma)}{\gamma}$	saddle	saddle	inconclusive
	$\alpha > \frac{4\delta k(\delta k - \gamma)}{\gamma}$	saddle	saddle	stable node

The type of behavior seen in this model is more varied than that of the base model, which had two fixed points with the same stability for all parameter values. The following plots will verify numerically the results we have found here:

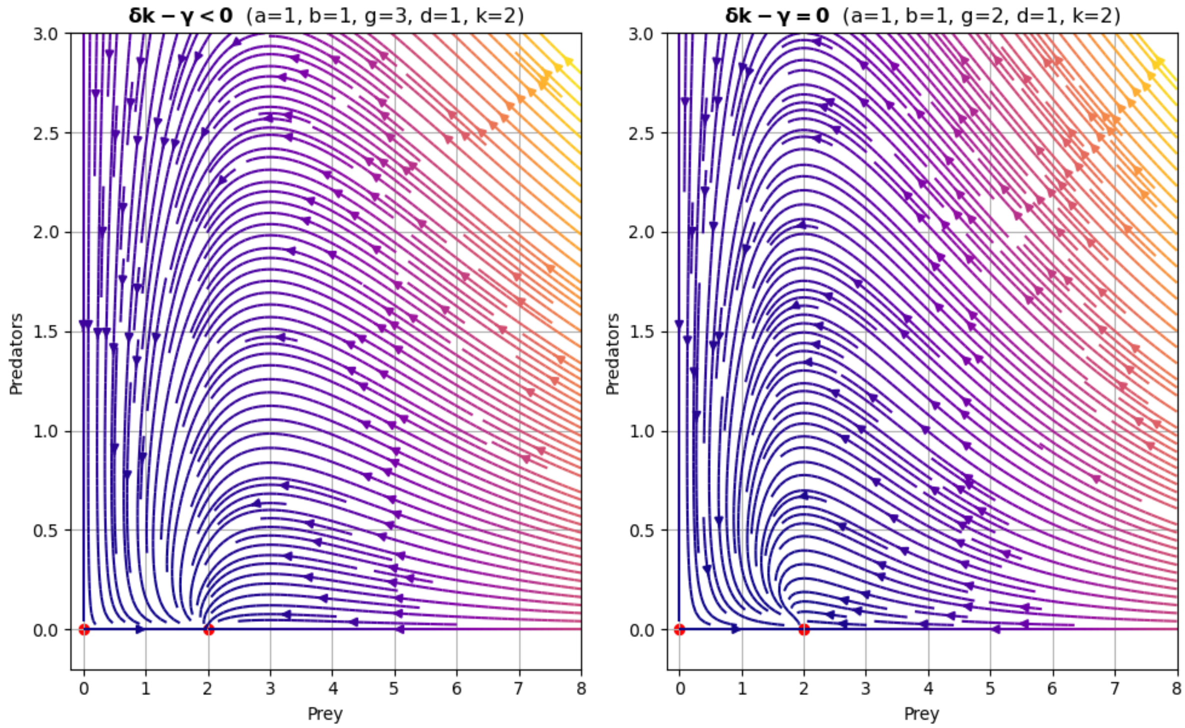

Figure 3: Phase Plane for the ILV model when $\delta k - \gamma \leq 0$

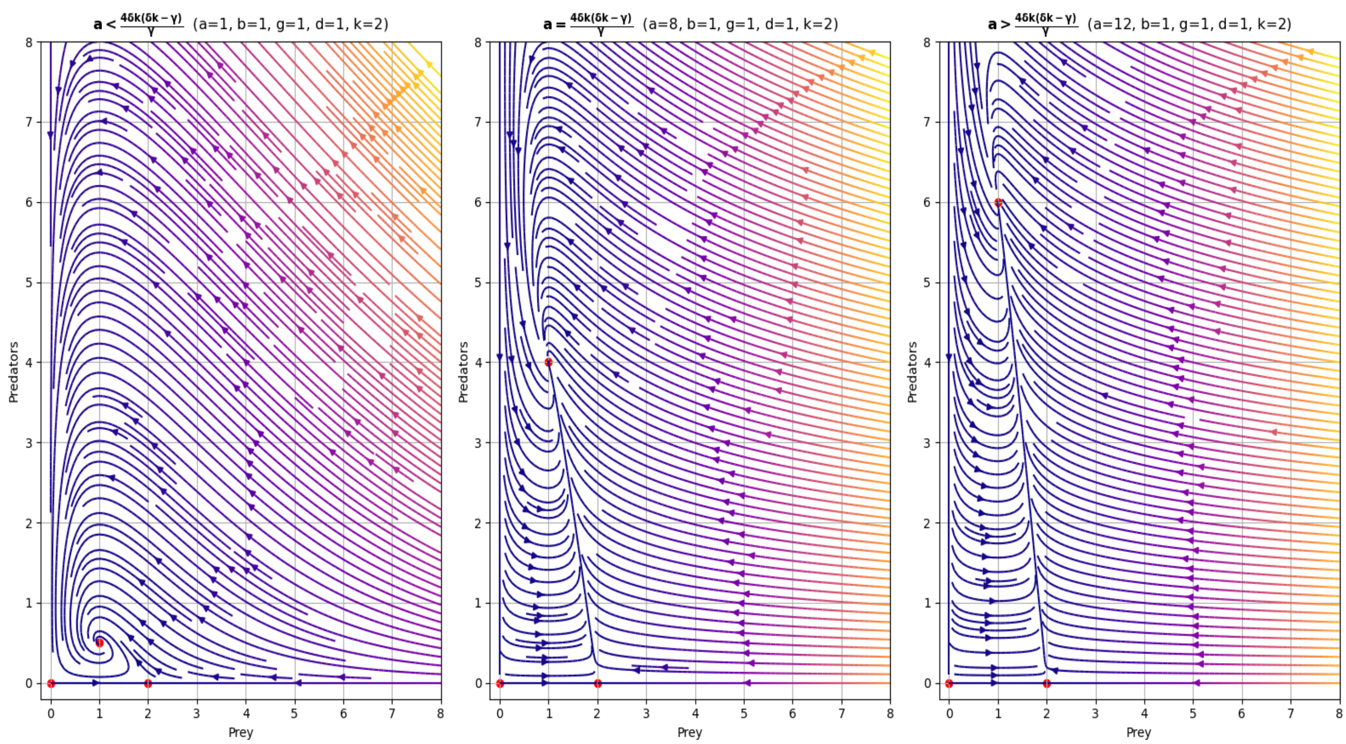

Figure 4: Phase Plane for the ILV model for each subcase of $\delta k - \gamma > 0$

As we can see, the numerical simulations agree with our predictions. In the first two plots we see an unstable origin (saddle) and a stable fixed point at $(k, 0)$. In the lower three plots we see the third fixed point emerge, which is stable in each case. An interesting property of this model is that unlike the base Lotka-Volterra model, which has exclusively periodic solutions, this model has **no** periodic solutions for any parameter values. Solutions either tend towards extinction of the predators, or they converge to a steady state of coexistence between predators and prey. The constraint of logistic growth on the population of prey seems to propagate to the predators and constraints them as well. We see this in real ecological systems: limited resources for a species of prey that predators heavily rely on for food will force the predator numbers down as well.

Model 2 - Food Chain System

Predator and prey is not necessarily black and white - sometimes a species falls somewhere in between. For example, field mice are often eaten by snakes, who are often hunted by large birds. In this case, the mice are the prey, the snakes the intermediate predator, and the bird the top predator. Such a system represents a **food chain**. We will ignore interactions between the top level predator and the bottom level prey for simplicity. We can model such a system like so:

$$\dot{x} = \alpha x - \beta xy$$

$$\dot{y} = \delta xy - \gamma y - \mu zy$$

$$\dot{z} = nyz - pz$$

This is very similar to the original Lotka-Volterra system, but with one extra term in the $\dot{y}$ equation and an extra variable z, which represents the top level predator population. The extra term in the $\dot{y}$ equation $-\mu zy$ represents species Y being eaten by predator Z. The new $\dot{z}$ equation has a term nyz to represent the increase in the population of Z due to eating species Y, and a term $-pz$ to account for the natural death rate of species Z.

Food Chain Analysis

Of course, our first order of business is to find the fixed points of the system. This system is nonlinear in 3 dimensions, so there is no standard method. Through some experimentation, one can obtain as fixed points:

$$(0, 0, 0)$$

$$(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}, 0)$$

$$(0, \frac{p}{n}, -\frac{\gamma}{\mu})$$

Note that the last fixed point has a negative coordinate and is thus non-physical (negative populations are nonsense!). Under certain parameter conditions, we can also find non-isolated fixed points. It can be shown that if $\alpha n = \beta p$, then any point satisfying:

$$\left(x, \frac{p}{n}, \frac{1}{\mu}(\delta x - \gamma)\right)$$

will be a fixed point. It turns out that whether or not $\alpha n = \beta p$ is true plays a large role in the behavior of the system.

Now that we have found all fixed points, we will compute the jacobian for our linear analysis:

$$J(x, y, z) = \begin{bmatrix} \alpha - \beta y & -\beta x & 0 \\ \delta y & \delta x - \gamma - \mu z & -\mu y \\ 0 & nz & ny - p \end{bmatrix}$$

Just as with the ILV model, we will calculate the value of the jacobian at each of the fixed points to determine their stability.

For the origin, we have:

$$J(0,0,0) = \begin{bmatrix} \alpha & 0 & 0 \\ 0 & -\gamma & 0 \\ 0 & 0 & -p \end{bmatrix}$$

The jacobian has simplified nicely to a diagonal matrix, so we can compute its eigenvalues easily: they are $\alpha, -\gamma$, and $-p$. Since one of the eigenvalues is positive and two are negative, the origin will be a sort of 3D **saddle point**.

For the second fixed point, we have:

$$J\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}, 0\right) = \begin{bmatrix} 0 & -\frac{\beta\gamma}{\delta} & 0 \\ \frac{\alpha\delta}{\beta} & 0 & -\frac{\alpha\mu}{\beta} \\ 0 & 0 & \frac{\alpha n}{\beta} - p \end{bmatrix}$$

Using Mathematica, we can symbolically calculate the eigenvalues of the jacobian. They are:

$$\pm i\sqrt{\alpha\gamma} \quad \text{and} \quad \frac{\alpha n - \beta p}{\beta}$$

So there are two purely imaginary eigenvalues and one real eigenvalue. Note that if $\alpha n = \beta p$ then the third eigenvalue is zero.

The existence of non-isolated fixed points complicates the linear analysis, so we will need to rely on numerical methods more heavily to examine the structure of the system. We will plot solutions for various parameter regimes to exhibit the behavior of the system (next page):

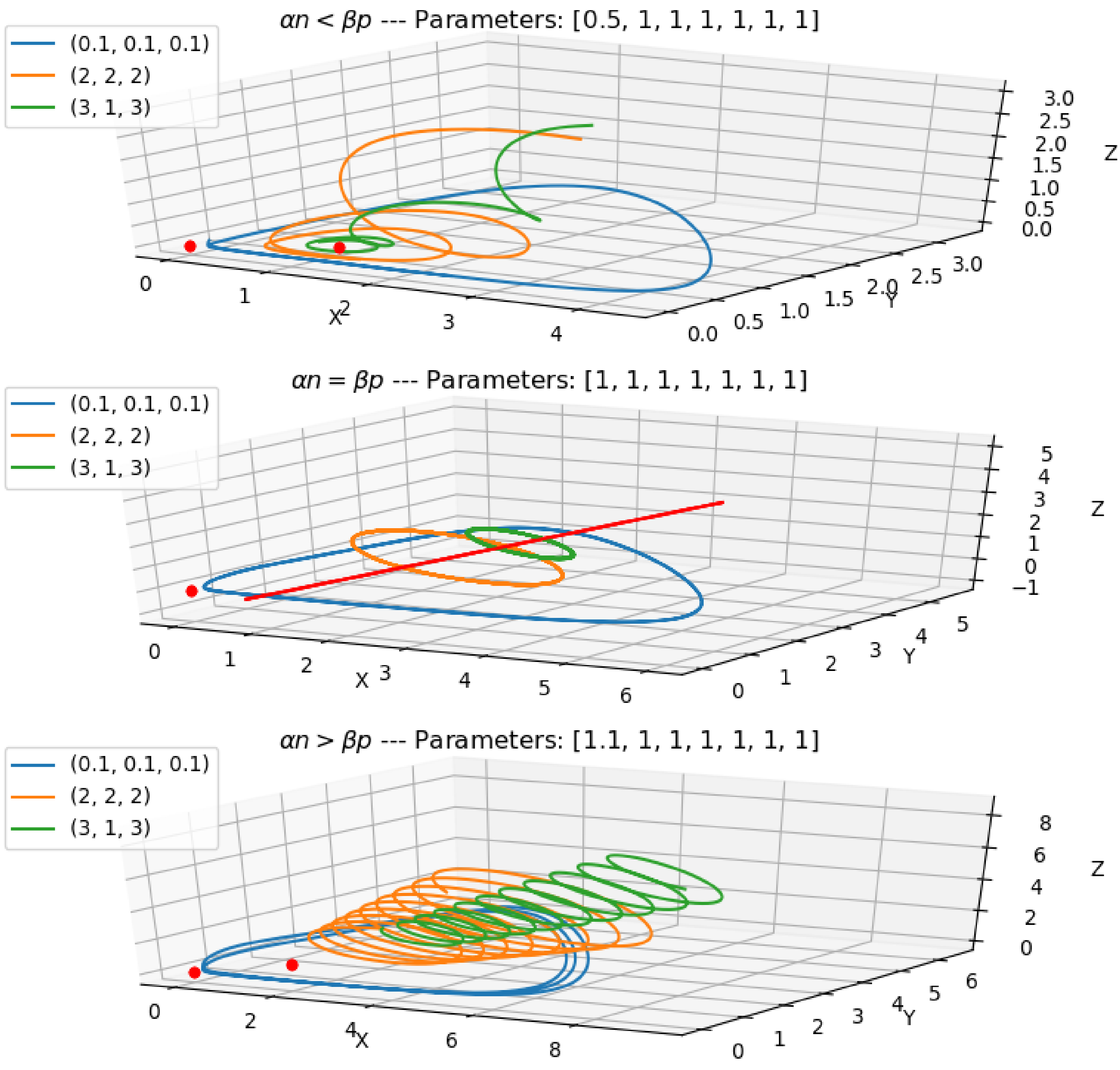

Figure 5: Individual solutions for different parameters of Food Chain System

The dynamics exhibited by this system are quite strange looking. In the first graph, we have $\alpha n < \beta p$. The jacobian at the non-origin fixed point has two imaginary eigenvalues and one negative real eigenvalue, which results in a stable spiral. It appears that species Z dies out for any initial condition, after which the trajectories form closed orbits around the fixed point, much like the standard Lotka-Volterra system.

In the second graph we have $\alpha n = \beta p$. Every solution appears to be a closed orbit. In fact, every solution forms a closed orbit around a line of non-isolated fixed points defined by the line in $\mathbb{R}^3$:

$$\left\langle x,\ \frac{p}{n},\ \frac{1}{\mu}(\delta x - \gamma) \right\rangle$$

In the graph, this is the represented by the red line. Initial conditions very close to the line will have tight orbits, while initial conditions that are farther away have wider orbits.

In the last graph, we have $\alpha n > \beta p$. The jacobian at the non-origin fixed point has two imaginary eigenvalues and one positive real eigenvalue. Solutions tend to spiral out towards infinity and are therefore unstable. These solutions spiral around the same line present in the previous graph (although this line is not composed of fixed points in this case).

Conclusions

We have now analyzed three models for population dynamics. The main takeaway we have is that relatively small changes to the underlying model can result in drastically different dynamics. We started with a simple model which exhibited simple behavior. Then we changed only one assumption and created a new model, which behaved entirely different than the original. Furthermore, the analysis of the new ILV model was much more involved than that of the standard Lotka-Volterra system. This demonstrates one of the primary difficulties in mathematical modelling: over-**complicating** the model. Trying to account for too many assumptions will lead to a messy model that can quickly become intractable to analyze. Instead, a better approach is to start with an over-**simplified**, and then use that as a starting point to build off of.

Another important aspect of these findings is showing the interplay between analysis and computation. Analysis is our primary means of explanation and study, but where analysis fails we can use computation to explore further. Having both at our disposal allows us to perform more versatile research and tackle more problems than either one can do alone.

We have only examined a few models here, but there are a plethora of potential models. The question of predator-prey dynamics could also be modelled by partial differential equations, stochastic differential equations. and machine learning, to name a few. If I were to continue this project, one thing I would like to explore would be using real ecological data in combination with our model to predict species counts. We have explored the use of PINNs in class, and the predator-prey system is a perfect example of something that would benefit from it. Data can be somewhat hard to collect on animal populations because it requires fieldwork. But by combining a limited amount of data with a model in a PINN, we could obtain new insight and potentially better predictive power.

References

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- Adamu, Hamid. "Mathematical analysis of predator-prey model with two preys and one predator". International Journal of Engineering and Applied Sciences (IJEAS). Accessed December 5th, 2021. https://www.ijeas.org/download_data/IJEAS0511014.pdf
- All code can be found on my github.