Predator-Prey Equations – Modeling Food Chains

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Abstract. This report covers models for two and three-species food chains. The two-species food chain models covered by this report are made up of a prey that lives off an infinite food supply and gets eaten by a predator that exclusively eats this prey. The most well-known such model are the Lotka-Volterra differential equations, named after the mathematicians that discovered them. These equations can be extended to model a three-species food chain where the predator from the two-species system is now preyed on by an apex predator that exclusively eats that predator. This change makes the system of differential equations more interesting to analyze. For this analysis the mathematical software system SageMath will be used. Graphs and phase planes of the discussed systems will be provided.

MSC: 34A01

Contents

1. Introduction

Predator-Prey equations are differential equations describing the populations of predators and their prey. They describe the change in the number of organisms depending on certain parameters. The most famous predator-prey equations are the so-called Lotka-Volterra equations. They were derived independently by Vito Volterra (1860–1940) and Alfred James Lotka (1880–1949) in the 1920s [2].

Lotka (chemist, ecologist, mathematician) published his work on population dynamics in 1925 on the basis of his earlier work with oscillating chemical reactions in 1910 and 1920 where he derived the same equations [3]. Volterra (mathematician, physicist) based his work on the number of predator and prey fish in the Adriatic sea during WWI where he noticed a decrease in prey and increase in predator fish [2]. Both of their approaches lead them to the same system of differential equations because the processes they sought to describe are isomorphic – they are non-linear oscillators [3]. Thus the Lotka-Volterra equations describe any process of two things changing and influencing each other – plants getting eaten by herbivores, parasites living off their hosts, or oscillating chemical reactions [2].

1.1. Lotka-Volterra Equations.

Lotka-Volterra equations are the simplest predator prey equations [2]. They describe the development of two species over time using continuous functions [1], [2]. Following [1], equation (1) shows the Lotka-Volterra system of equations.

$$\begin{cases} \dfrac{dx}{dt} = ax - bxy & \text{Prey} \\ \dfrac{dy}{dt} = -cy + dxy & \text{Predator} \end{cases} \tag{1}$$

In (1), dx/dt is the change of the prey population, dy/dt the change of the predator population. The constants $a, b, c, d > 0$ in this system of equations represent

- a – growth rate of the prey if there are no predators,
- b – effect of predators killing prey,
- c – death rate of predators if there is no prey,
- d – growth rate of predators if there is prey [1].

1.2. **Expanded Lotka-Volterra Equations.** Equation (1) models a two-species food chain where x is the prey that gets eaten by y which is above it in the food chain. This model can be extended to a three-species system that describes the populations of three species part of the same food chain. Examples of these food chains are mouse–snake–owl and vegetation–hare–lynx [1]. This expansion requires a third equation to be added to our system. Again, following [1], we get equation (2).

$$\begin{cases} \dfrac{dx}{dt} = ax - bxy & \text{Prey} \\ \dfrac{dy}{dt} = -cy + dxy - eyz & \text{Intermediate Predator} \\ \dfrac{dz}{dt} = -fz + gyz & \text{Apex Predator} \end{cases} \tag{2}$$

The above equation models a food chain where prey x gets eaten by intermediate predator y, which in turn gets eaten by apex predator z. Of the constants $a, b, c, d, e, f, g > 0$, we have a, b, c, d from (1) which have the same functions. The remaining constants represent

- e – effect of predator z eating y,
- f – death rate of predator z in absence of y,
- g – growth rate of predator z if there is prey.

Equation (2) is a direct generalization of (1) which makes it both more interesting and more difficult to solve [1]. Both two-species and three-species food chains will be covered in this report.

1.3. **Phase Planes.** Phase planes are a special form of state space, the set of all possible states of a dynamic system. Every possible state of a system corresponds to a point in state space [5]. For two-dimensional systems of autonomous (independent of time [4]) ordinary differential equations, state space is called a phase plane. In this phase plane the points representing solutions to the system of equations move with time. Points moving over time trace trajectories in the phase plane. If a point does not move in a phase plane it is called equilibrium. If a point traces a closed trajectory the solution represented by that point is periodic

[5]. The movement of a system in phase space is represented by vectors that show the velocity of a system at that point.

In Figure 1 we see the phase plane for a system of differential equations describing a pendulum ($x' = y$ and $y' = -\sin(x)$) [5]. Every point on this plane is a state of that system, a combination of (angle, angular velocity). The points **A** and **B** are solutions of the pendulum equation. **A** moves on a clockwise trajectory very similar to the one it is next to in the figure. **A** is a periodic solution that represents a pendulum that swings forever with the same amplitude. **B** is an equilibrium of the pendulum equation that never moves. It represents a pendulum in its resting state where it hangs without any movement.

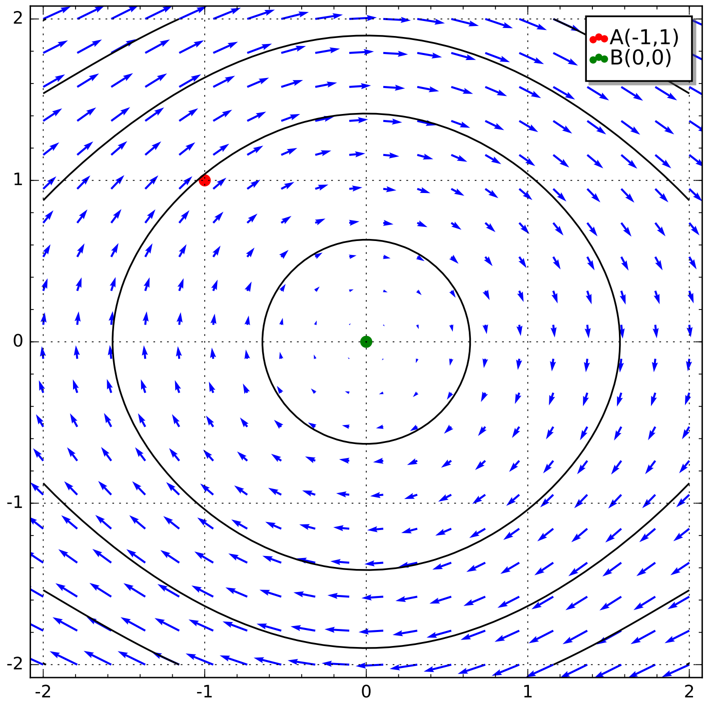


Figure 1. Phase plane of a pendulum with contour lines

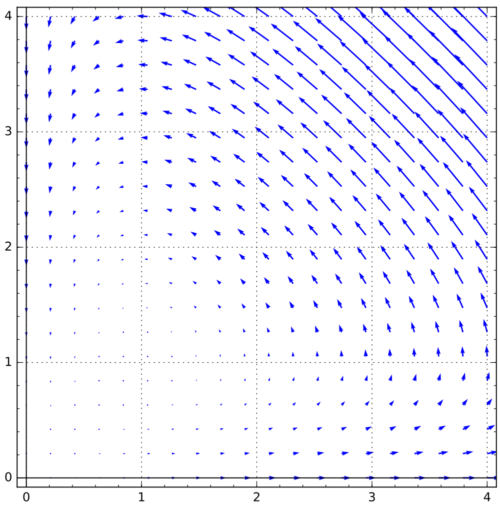
This example illustrates that phase planes are methods of qualitative solving differential equations, they provide solutions without the need to necessarily solve the system. They can also be used to make statements about families of solutions [4]. So with the phase plane in Figure 1 we can make statements about the pendulum equation without actually solving it, like predicting the behaviors of **A** and **B**. Another thing Figure 1 shows is that the points close to **A** will follow similar trajectories to the one of **A**. Phase planes will prove be useful to analyze two-species food chains.

2. Two-Species Food Chain

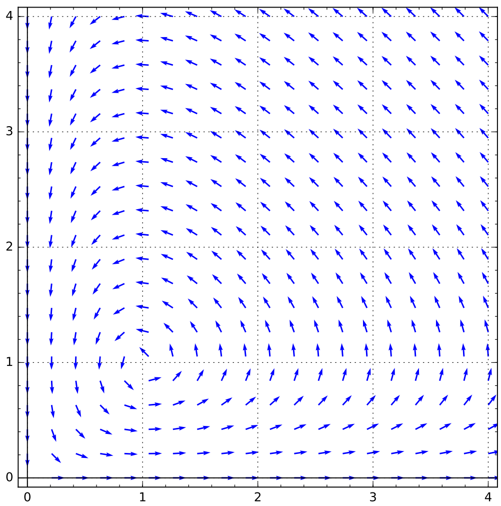
A two species food chain as described by the Lotka-Volterra equations in (1) is a system that has one prey that has an infinite food supply and one predator that exclusively eats the prey. The three-species food chain in (2) with 0 apex predators yields the same system as (1). For our example we chose the parameters $a = b = c = d = 1$ for simplicity. System (1) now becomes

$$\begin{cases} \dfrac{dx}{dt} = x(1-y) & \text{Prey,} \\ \dfrac{dy}{dt} = y(x-1) & \text{Predator.} \end{cases} \tag{3}$$

Two phase planes of (3) can be seen in Figure 2 below. The x-axis represents the number of prey and the y-axis represents the number of predators.



(A) Phase plane



(B) Normalized phase plane

Figure 2. Two-species system phase planes with $a = b = c = d = 1$

Part (A) gives insight into the speed of the system while the normalized (same-length) vectors in part (B) give more insight into the direction at a point. These two phase planes contain a lot of information about the system (3). We can see that (3) moves faster as the distance to the origin increases and moves slowly around the point $(1, 1)$. Furthermore, the system moves counterclockwise around a point approximately at $(1, 1)$ at all distances from it. From subsection 1.3 we know that a point that does not move in a phase plane is a equilibrium, thus we can suspect that $(1, 1)$ is an equilibrium of this system. Additionally, the counterclockwise movement could represent closed curves that are periodic solutions of (3).

The next graph in FIGURE 3 shows a normalized phase plane with contours. The contours are closed curves on the phase plane which means that they are periodic solutions to system (3). The contours in this graph are generated using the family of equations

$$C = a \ln y - by + c \ln x - dx \tag{4}$$

(C being a constant) that, according to [1], is a solution to (1). Using (4) with the parameters $a = b = c = d = 1$, we can draw these contours to show some possible periodic solutions of (3).

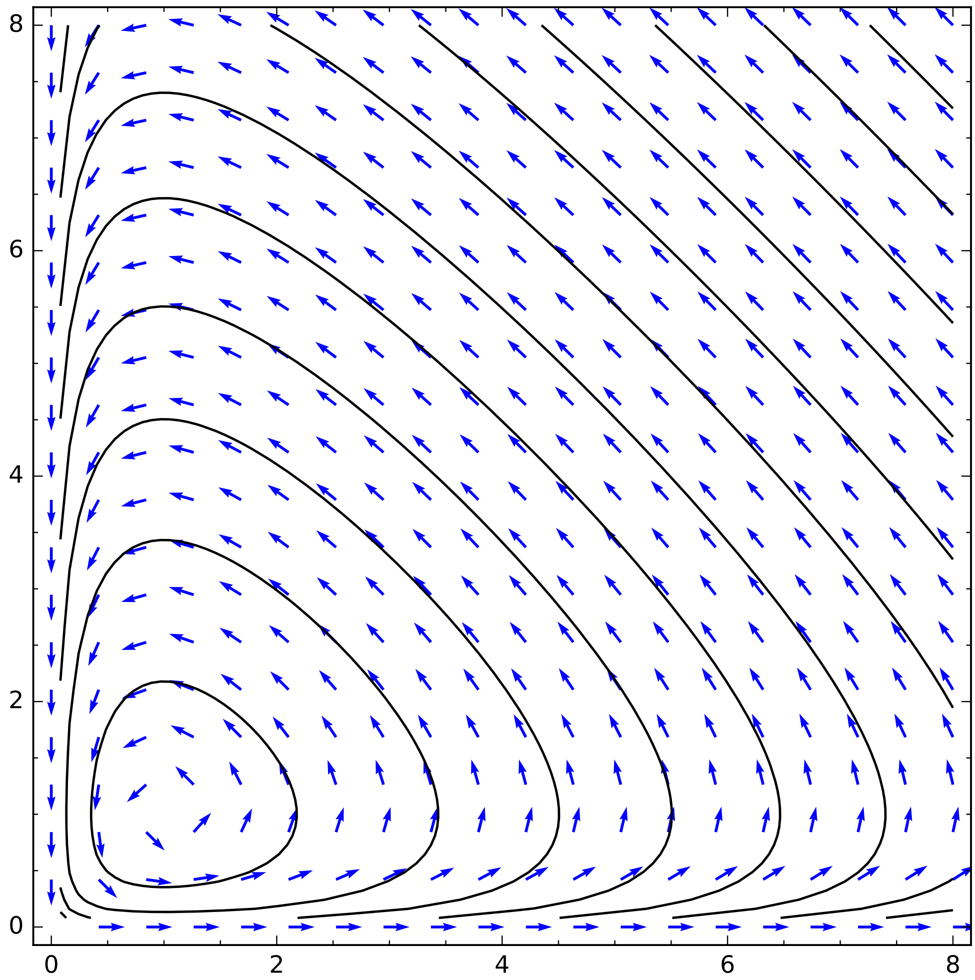


FIGURE 3. Two-species system phase plane with normalized vectors, contour lines, and $a = b = c = d = 1$

We can say from the above figure that our prediction of periodic solutions using the phase planes was correct (this is supported by [1], [2], [6]). When it comes to $(1,1)$ as the equilibrium of the system, FIGURE 3 supports that assumption. The vectors close to it seem to rotate around it and all the contours revolve around it. The equilibrium of equation (1) can be found by considering the parameters. The equilibrium is $(c/d, a/b)$ [1], and because our example as $a = b = c = d = 1$, our equilibrium point is $(1,1)$. At this point the number of prey and predator are perfectly balanced and never change. The example has another equilibrium, the point $(0,0)$. At this point there are no predators or prey and thus nothing changes.

In FIGURE 3 we can see that at the coordinate axes where $x = 0$ or $y = 0$ the vectors all point in the same direction along one of the axes. At $x = 0$ all the vectors point towards the x-axis. $x = 0$ is analogous to there being zero prey, meaning that the predators will have no food. This will lead to exponential death seen in FIGURE 4. Taking the initial values of $x = 0$ and $y = 3$ and numerically solving (3), we can draw that figure.

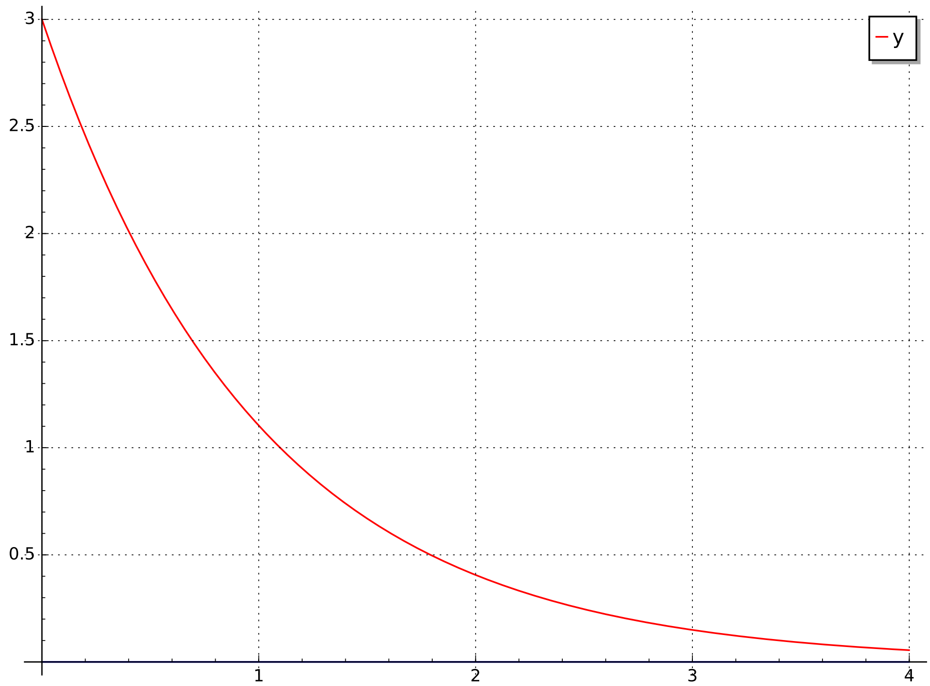


FIGURE 4. Two-species system graph for $x = 0$, $y = 3$, and $a = b = c = d = 1$

At $y = 0$ all the vectors point along the x-axis towards positive infinity. This case is analogous to a system with no predators so the prey will multiply unhindered and exponentially. In FIGURE 5 we see a numerical solution to this system with $x = 6$ and $y = 0$ as initial conditions.

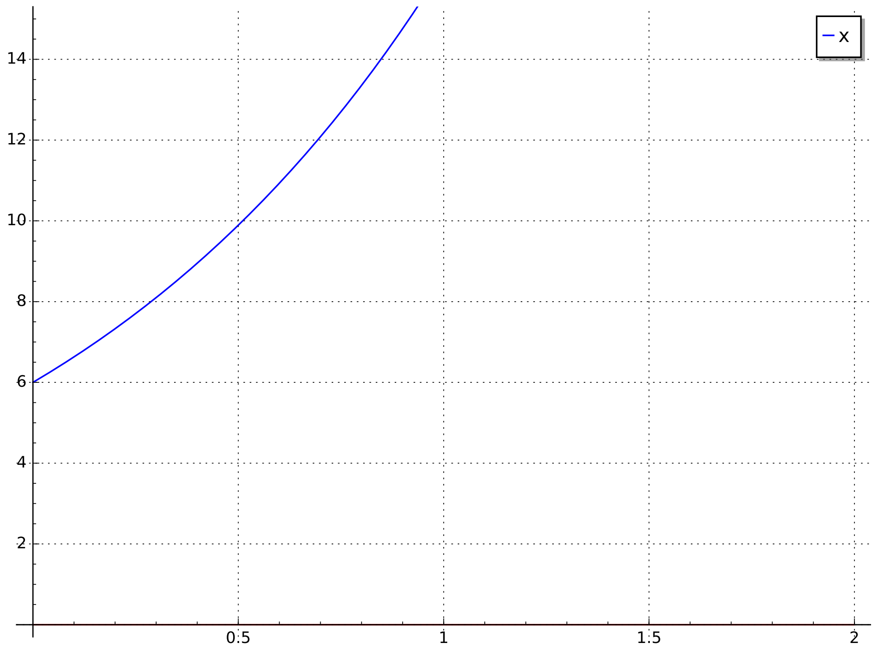


FIGURE 5. Two-species system graph for $x = 6$, $y = 0$, and $a = b = c = d = 1$

If neither x nor y are 0, this system has a periodic solution that can be numerically or analytically found. Taking the initial conditions $x = 6$ and $y = 3$ and graphing the result as a contour on a phase plane we get FIGURE 6. If the same result is graphed over time with both species' populations represented on the y-axis we get FIGURE 7. This figure shows that x and y continuously oscillate, with the prey population x peaking before the y population of predators. The reason for that is that if the prey is numerous, the predators have more to eat and their population grows. Then they eat more prey and reduce its numbers faster than they can multiply. The number of prey goes down and then the predators don't have enough food and their population shrinks. Then the prey population begins to grow again. This cycle repeats and the predators always lag behind the prey. Additionally, the cycles of predators and prey have the same period [1].

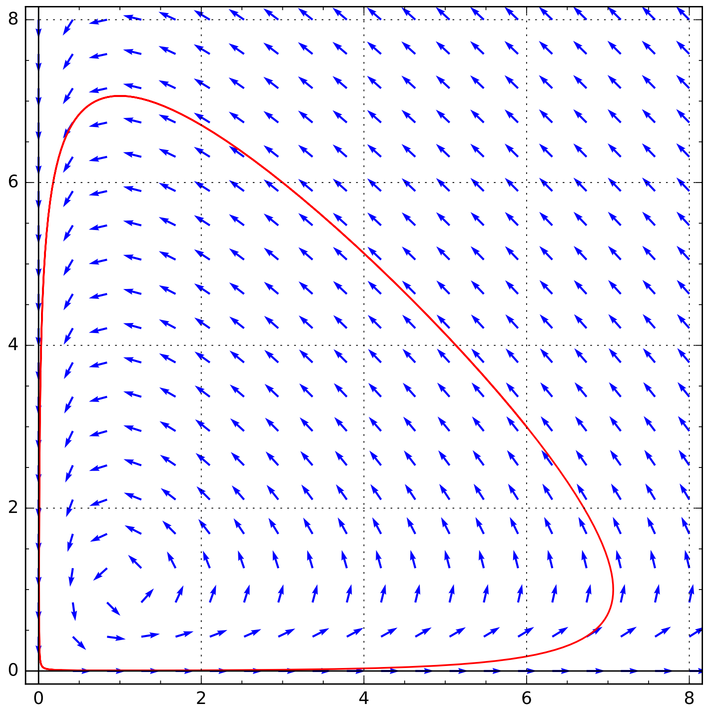


FIGURE 6. Two-species system contour for $x = 6$, $y = 3$, and $a = b = c = d = 1$

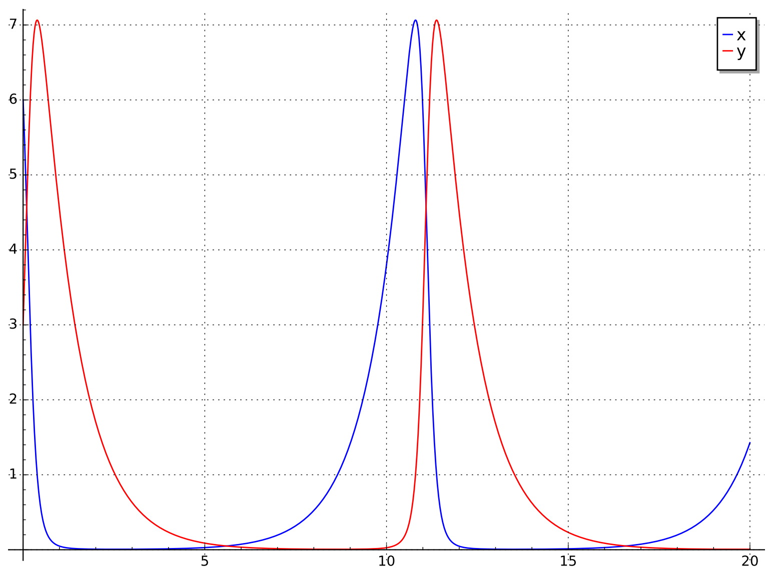


FIGURE 7. Two-species system graph for $x = 6$, $y = 3$, and $a = b = c = d = 1$

3. Three-Species Food Chain

A three-species food chain from equation (2) is a system that also has one prey with an infinite food supply, called x. This prey is being preyed on by intermediate predator y who exclusively eats x. Finally, apex predator z preys exclusively on y. Again, for this example we chose the parameters $a = b = c = d = e = f = g = 1$ because it is simpler. System (2) now becomes

$$\begin{cases} \dfrac{dx}{dt} = x(1-y) & \text{Prey} \\ \dfrac{dy}{dt} = y(x-z-1) & \text{Intermediate Predator} \\ \dfrac{dz}{dt} = z(y-1) & \text{Apex Predator} \end{cases} \tag{5}$$

Because we are now dealing with 3 species we can no longer use the phase planes that were so helpful for the two-species food chain. Now our system exists in 3 dimensions so it is a good start to look at the coordinate planes first (following [1]). The following examples are based on the initial conditions $x = 6$, $y = 3$, and $z = 1$.

If $z = 0$ (xy-plane), equation (5) becomes the same system as the example for two-species food chains in (3).

$$\begin{cases} \dfrac{dx}{dt} = x(1-y) & \text{Prey} \\ \dfrac{dy}{dt} = y(x-0-1) = y(x-1) & \text{Intermediate Predator} \\ \dfrac{dz}{dt} = 0(y-1) = 0 & \text{Apex Predator} \end{cases}$$

Using numerical solving to find the solution to the three-species system in (5) with the initial conditions $x = 6$, $y = 3$, and $z = 0$ yields the same system as can be seen in Figure 7 which is identical to Figure 9 below. Figure 8 shows the contour of the current system in three dimensions where it just lays in the xy-plane. This contour looks the same as the one obtained from the two-species equation in Figure 6, further supporting their sameness.

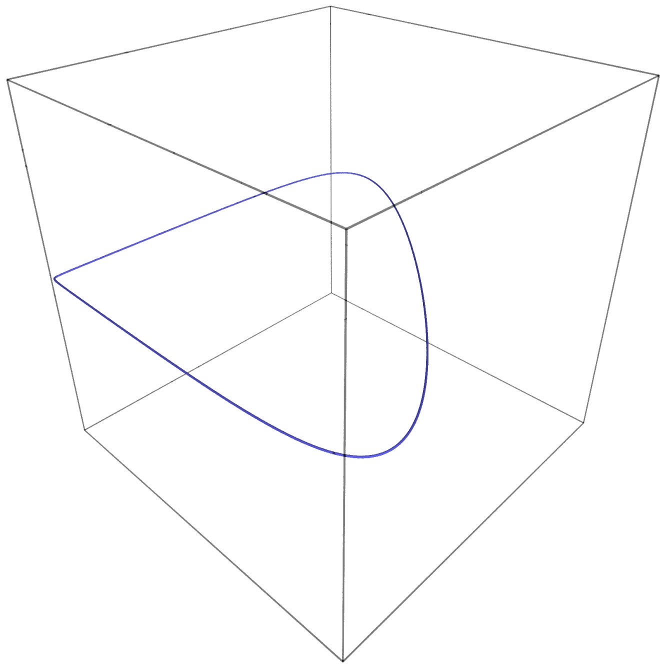


FIGURE 8. Three-species system contour for $x = 6$, $y = 3$, $z = 0$,
$a = b = c = d = e = f = g = 1$

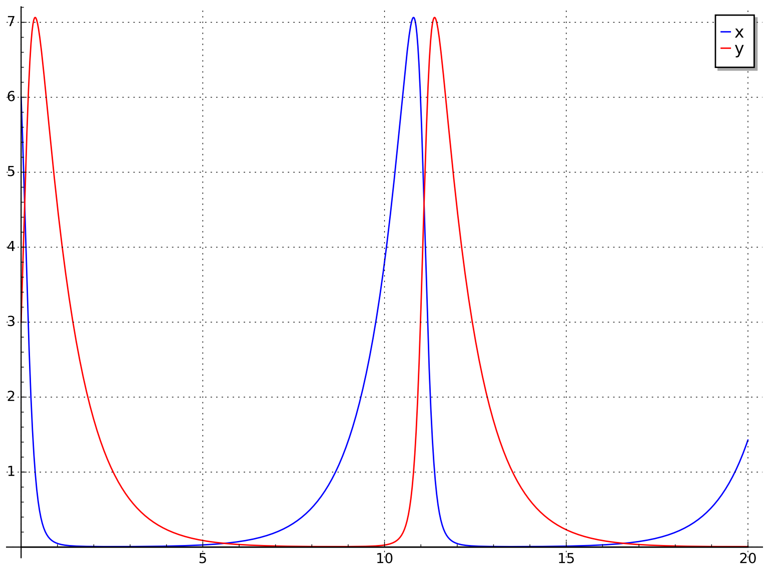


FIGURE 9. Three-species system graph for $x = 6$, $y = 3$, $z = 0$,
$a = b = c = d = e = f = g = 1$

The second coordinate plane is the zy-plane. Here $x = 0$ and thus intermediate predator y has so source of food and starves. Because y starves z will also eventually starve because their food runs out. In the equation below all factors of y are negative meaning that it will always decline. Accordingly, z will also decline.

$$\begin{cases} \dfrac{dx}{dt} = 0(1-y) = 0 & \text{Prey} \\ \dfrac{dy}{dt} = y(0-z-1) = y(-z-1) & \text{Intermediate Predator} \\ \dfrac{dz}{dt} = z(y-1) & \text{Apex Predator} \end{cases}$$

The population of y will start dropping exponentially immediately because of the lack of food but z may rise for a bit because they can prey on y until y dies out. The end result will be that all species eventually die out because neither of them have sustainable food sources. Taking $x = 0$, $y = 3$, and $z = 1$ and solving (5) numerically yields Figure 10.

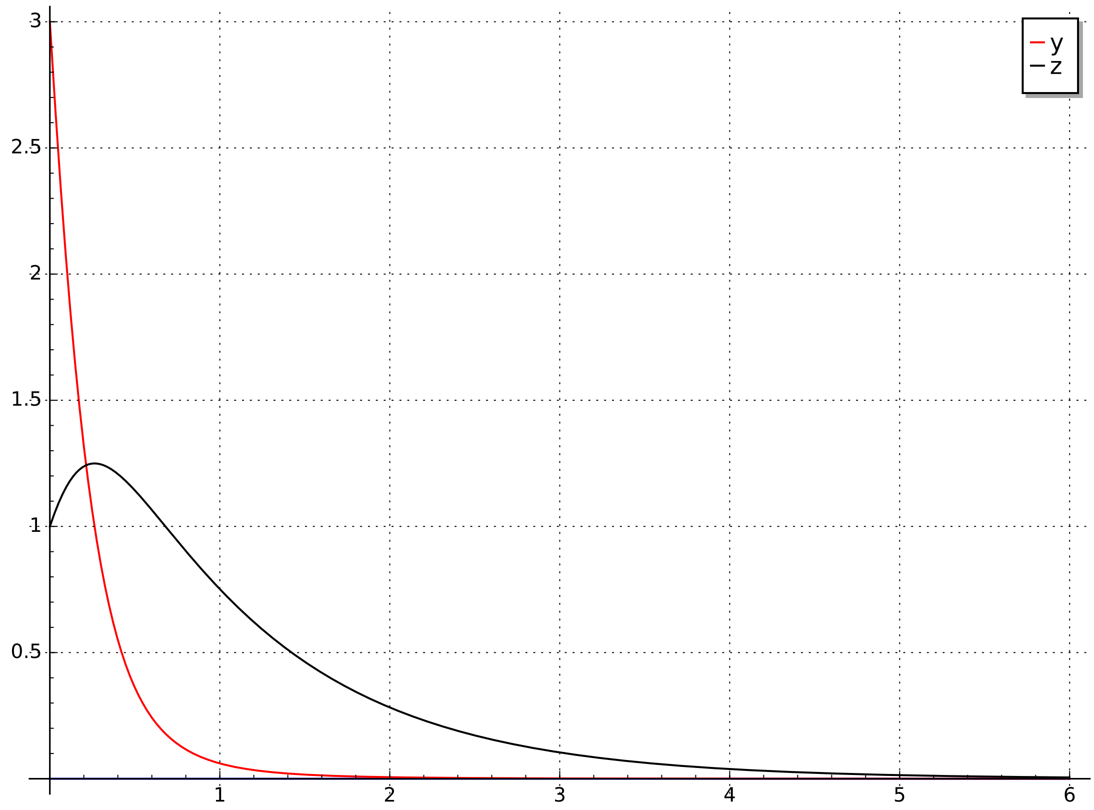


Figure 10. Three-species system graph for $x = 0$, $y = 3$, $z = 1$, $a = b = c = d = e = f = g = 1$

The third coordinate plane is the xz-plane where $y = 0$. In this plane the intermediate predator y does not exist and thus z always exponentially declines and starves because of lack of food. On the other hand, x is now free from predation and will exponentially grow in population size.

$$\begin{cases} \dfrac{dx}{dt} = x(1-0) = x & \text{Prey} \\ \dfrac{dy}{dt} = 0(x-z-1) = 0 & \text{Intermediate Predator} \\ \dfrac{dz}{dt} = z(0-1) = -z & \text{Apex Predator} \end{cases}$$

This system results in a exponentially and unboundedly growing prey population and a exponentially declining apex predator population that will die out. This results in only species x surviving.

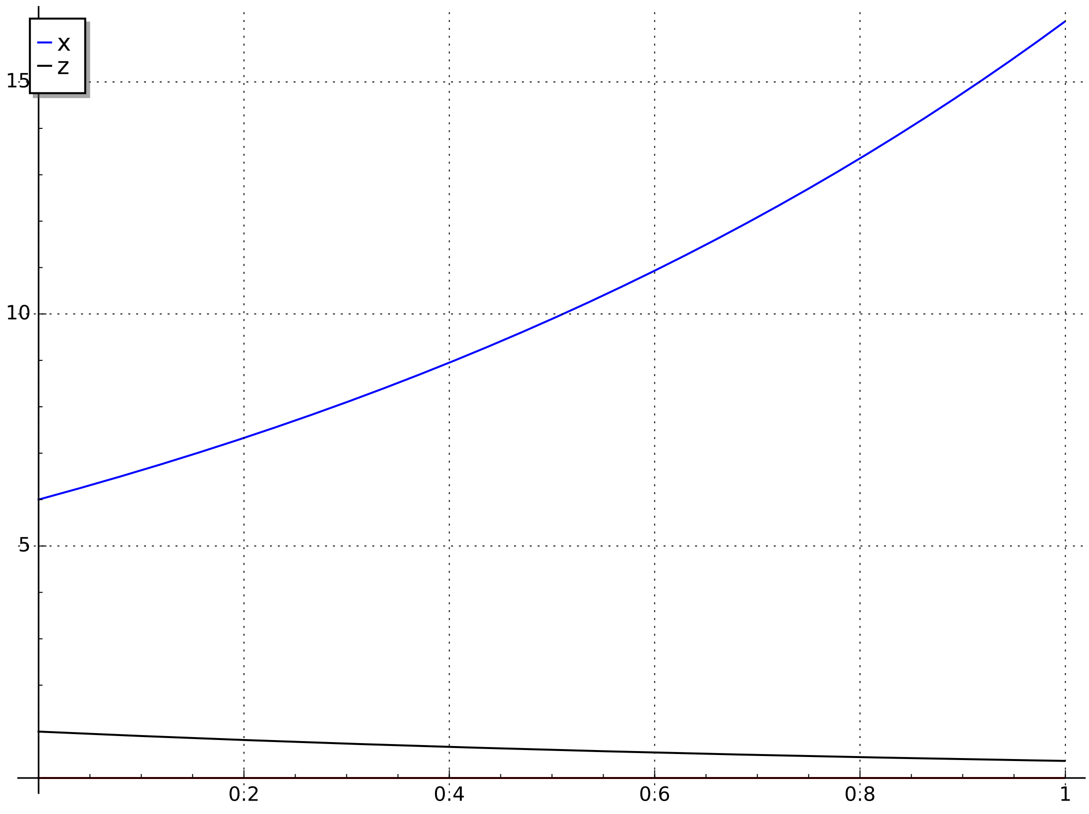


Figure 11. Three-species system graph for $x = 6$, $y = 0$, $z = 1$,
$a = b = c = d = e = f = g = 1$

All coordinate planes of this system are invariant, meaning a system never escapes from a coordinate plane. This makes sense because on a coordinate plane one species does not exist and it cannot just come back [1]. One point of this system that is obvious is $(0,0,0)$ where it never changes and thus has a equilibrium. When it comes to the coordinate axes, two of the values must be zero. As established above, if $x = 0$ all species eventually die out. This means that for the y- and z-axis both species will eventually die out. If our system starts on the x-axis species x will grow unboundedly and the other species will remain at 0.

In their analysis in [1] the authors use further criteria to analyze system (2). They use the equations and inequalities below to describe the systems' behaviors not already mentioned. These classifications are purely based on the constants a, b, f, g [1]

$$ga > fb, \qquad ga < gb, \qquad ga = fb.$$

If $ga > fb$, for example $a = g = 1.1$ and all other constants equal to 1, equation (2) becomes

$$\begin{cases} \dfrac{dx}{dt} = 1.1x - xy & \text{Prey,} \\ \dfrac{dy}{dt} = -y + xy - yz & \text{Intermediate Predator,} \\ \dfrac{dz}{dt} = -z + 1.1yz & \text{Apex Predator.} \end{cases}$$

This equation suggests that species x is now growing quicker than before while the predation by y has remained the same. The change of species y remain unchanged and species z now grows more from eating species y than before. All these observations combined would suggest that the populations of both x and z increase over time while y could remain the same. When the above equation is numerically solved for the mentioned constants and the initial conditions $x = 6$, $y = 3$, and $z = 1$ and then graphed Figure 12 is created.

This graph confirms the prediction as it shows that z and especially x increase over time but that y remains the same. The analysis in [1] showed that the populations of both x and z approach infinity, but not monotonically because of the oscillations. For y the peaks will become taller and skinnier but at a much

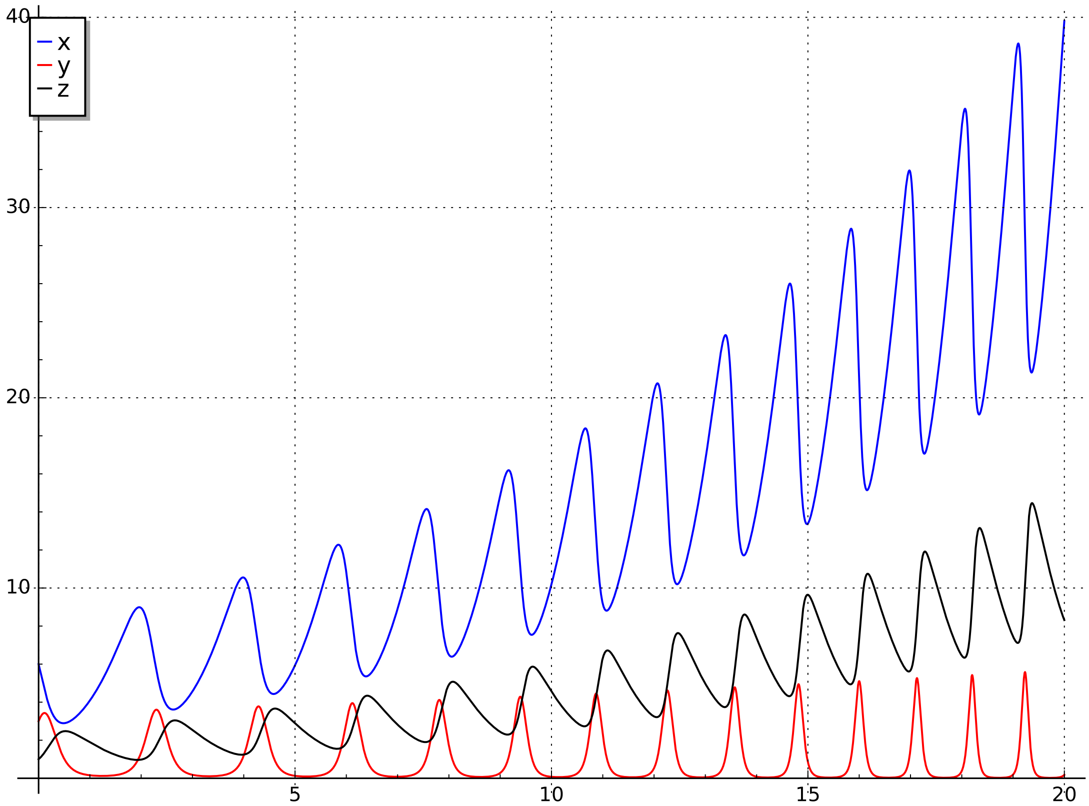


Figure 12. Three-species system graph for $x = 6$, $y = 3$, $z = 1$, $b = c = d = e = f = 1$, and $a = g = 1.1$

slower rate. Overall, no species will die out and two of them will increase without bound.

If $ga < fb$, e.g. $b = f = 1.1$ and all other constant equal 1, the general three-species system (2) turns into

$$\begin{cases} \dfrac{dx}{dt} = x - 1.1xy & \text{Prey,} \\ \dfrac{dy}{dt} = -y + xy - yz & \text{Intermediate Predator,} \\ \dfrac{dz}{dt} = -1.1z + yz & \text{Apex Predator.} \end{cases}$$

The system above suggests that now the predation effect of y on x will be stronger and that the natural death rate of z increased. The increase in death rate of z could lead to a drastic reduction in population size or even extinction while the increased effect of predation of y on x might decrease the population size of x and subsequently of y because there is now less prey. Figure 13 is the result of numerical solving of (2) with the above mentioned constants and the initial conditions $x = 6$, $y = 3$, $z = 1$. The figure supports the hypothesis that z

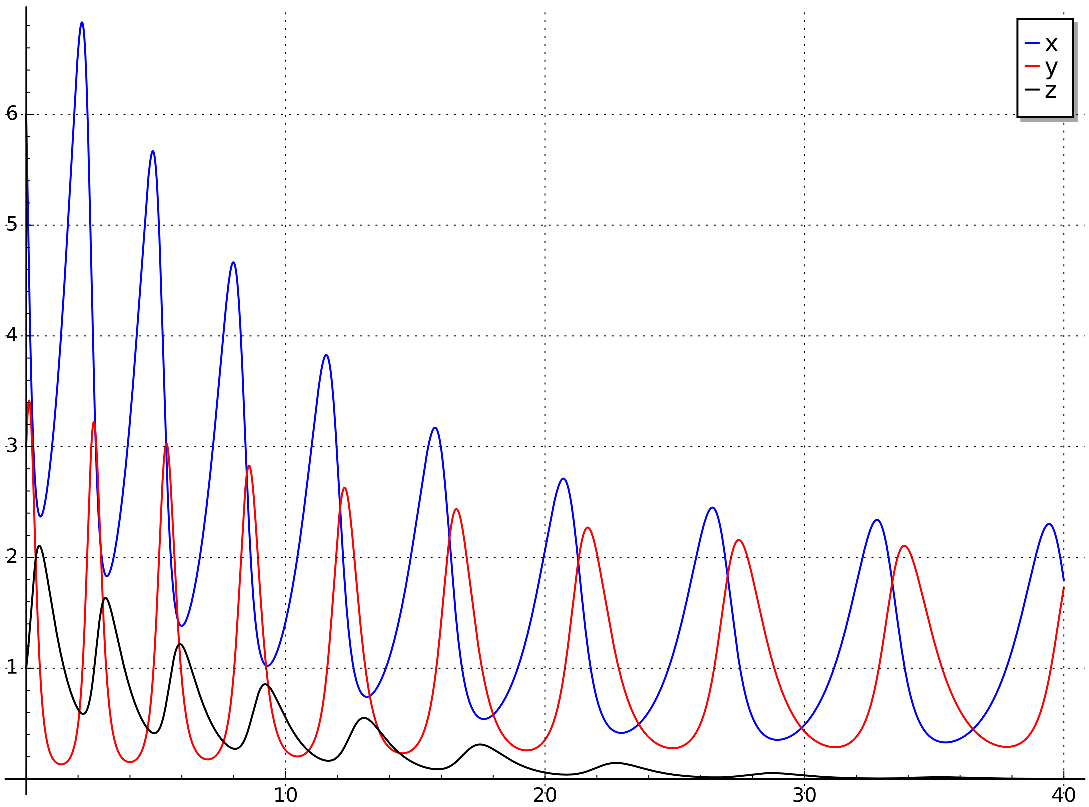


Figure 13. Three-species system graph for $x = 6$, $y = 3$, $z = 1$, $a = c = d = e = g = 1$, and $b = f = 1.1$

might go extinct and in fact shows that that happens. As expected, the increased predation effect of y on x causes its population to shrink and then subsequently to make the population of y shrink. When z goes extinct the system has been reduced to a two-species system of equations as in (1). This system will then periodically oscillate like a normal two-species food chain. In Figure 14 the three-dimensional contour of the system is shows and one can see that the system spirals downwards towards the xy-plane.

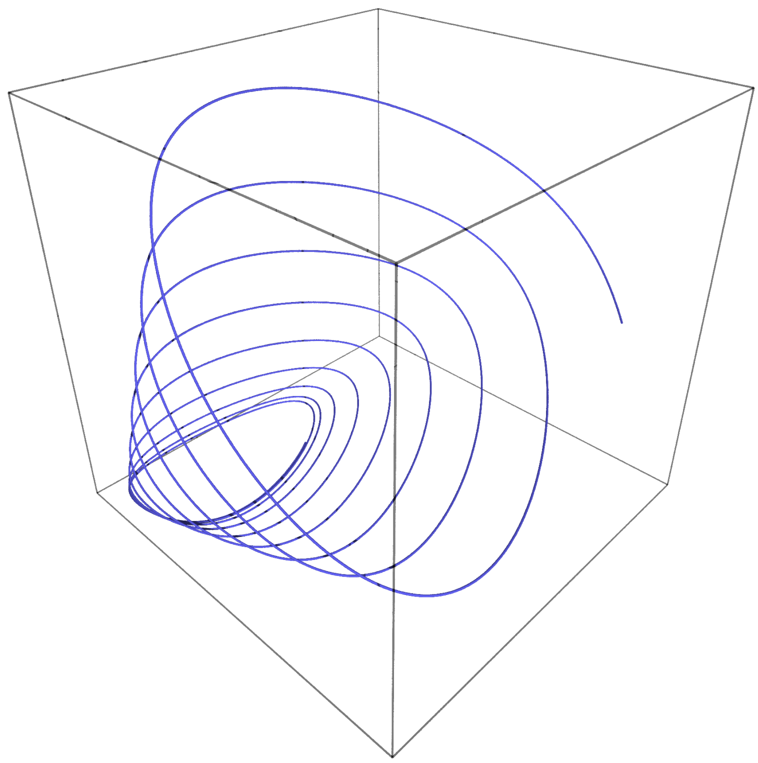


FIGURE 14. Three-species system contour for $x = 6$, $y = 3$, $z = 1$, $a = c = d = e = g = 1$, and $b = f = 1.1$

The last of the three options is that $ga = fb$. In this case we can keep our simple setup of $a = b = c = d = e = f = g = 1$ and the original example equation (5) does not change. In this particular system all the constants are equal so one could maybe expect the system to oscillate indefinitely like a two-species system. Using numerical solving and the initial conditions $x = 6$, $y = 3$, and $z = 1$ we get the graph in FIGURE 15.

In said figure we see three continuously oscillating graphs that have the same period. The highest peaks are the prey x, followed by intermediate predator y and then by apex predator z. The peaks are also shifted in time, with the graphs lagging behind each other in the same fashion, first x, then y, and then z. This has the same cause as the lag in the two-species system – it takes the species a while to react to increased or decreased numbers of predators and prey. In this system no species dies out and they all continue to exist. Figure 16 shows the contour of this system in three-dimensional space where it looks similar to a contour in two-dimensional space.

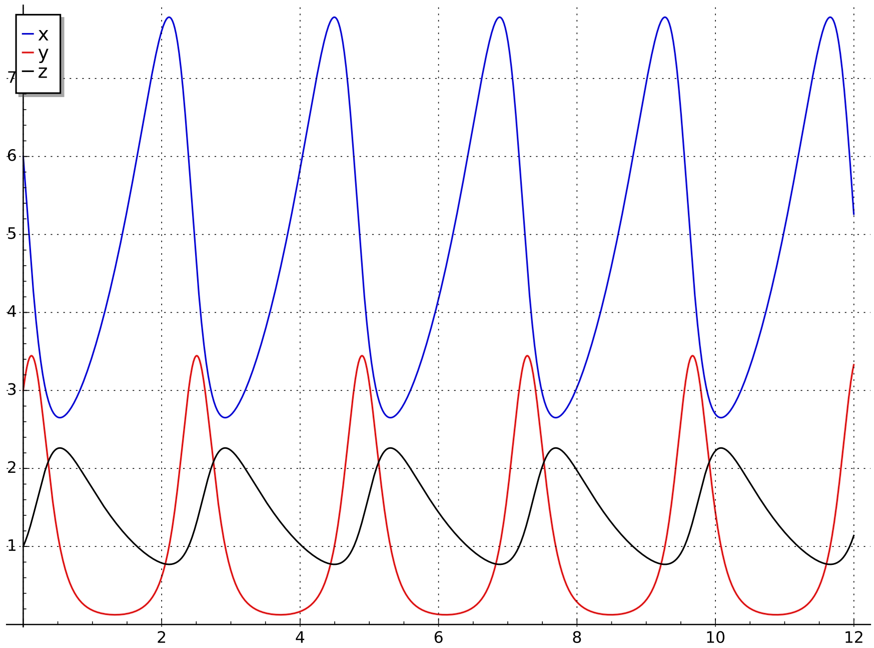


Figure 15. Three-species system graph for $x = 6$, $y = 3$, $z = 1$, and $a = b = c = d = e = f = g = 1$

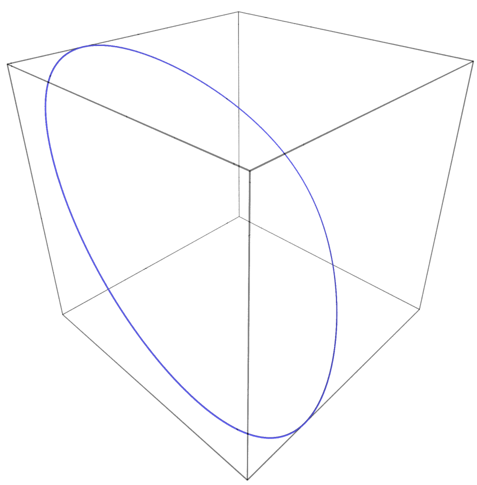


Figure 16. Three-species system contour for $x = 6$, $y = 3$, $z = 1$, and $a = b = c = d = e = f = g = 1$

4. Conclusion

The systems covered in this report are models for two and three-species food chains. As models, they fit most of the intuitions one has about what should happen to biological systems in certain situations. If there are no predators, they prey multiply greatly; if there is no prey the predators starve.

Some inaccuracies of these models are the restricted behavior of predator and prey when they only live off one thing and the fact that the prey has an infinite supply of food. Another aspect is the exponential and unbounded growth of prey populations if there are no predators. In many more accurate and complicated systems use logistic equations to get around this issue and make the equations more accurate.

To conclude, the two and three-species models covered in this report are relatively accurate in spite of their simplicity and can be analyzed using numerical solution methods and, for the two-species model, phase planes. The Lotka-Volterra equations (1) had a great impact on biology and ecology [6] and can, especially with modifications, still be relevant today.

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