Math Exploration

Modelling Predator-Prey Relationships

Matthew Wang

Introduction

Many of the small ponds and lakes I lived beside when I was young were suspect to algal bloom: a situation when algae grow too quickly and overpopulate the body of water. Algal blooms have many bad effects on the ponds, including blocking out sunlight and leeching resources, so it's in the best interest of maintainers to stop algal blooms. One mechanism that Japanese pond maintainers will often use is releasing koi fish into the pond. Koi fish are popular in Japan, and are also omnivorous and eat algae; after they're released into the pond, they'll quickly eat the algae and reproduce quickly. Eventually though, there won't be any algae left, and the koi fish will die out (or be removed from the habitat), and the algae will start growing again. It's the circle of life!

I moved away from Japan when I was four, but I always remembered the koi fish and how they were used as a biological cleanup tool. Since then, I've learned in bits and pieces about feedback loops and modelling different systems through different kinds of media, but I never pieced together the entire puzzle until I discussed my interest with my math teacher. There, I realized that this modelling of a predator-prey dynamic, such as one between koi fish and algae, can be explored with math.

Introducing the Lotka-Volterra Model and Equations

One very simple and succinct way to model the relationship between predators and prey is the Lotka-Volterra model, consisting of two differential equations that model the changes in the population of the predators (y) and the prey (x) over periods of time (t). A Lotka-Volterra model features four constant parameters: the prey growth rate (α), the predation rate (β), the predator growth rate (δ), and the predator death rate (γ).

$$\frac{dx}{dt} = \alpha x - \beta xy$$

$$\frac{dy}{dt} = \delta xy - \gamma y$$

The pair of equations are relatively self-explanatory, though it is helpful to think of each equation as two separate terms – the total growth of a population subtracted by the total death of a population. The rate of change of prey is the total growth (rate of growth multiplied by number of prey) subtracted by total death (the rate of predation multiplied by the number of prey and the number of predators), and the rate of change of predators is the total growth (rate of growth multiplied by the number of prey and predators) subtracted by the predator death rate (predator death rate multiplied by the number of predators). Note that the prey growth rate and the predator death rate vary solely with the number of their respective populations, while the prey death rate and the predator growth rate rely on the population numbers for both prey and predator.

With these equations, there is one necessary mathematical limitation: none of the four parameters nor the number of predators or prey can go below 0, as that would be nonsensical data. However, we'll find that choosing the right parameters and using precise enough calculations will never yield this problem.

Model Assumptions

As with any mathematical model, there are key assumptions to make the model simpler. The majority of them ensure that the parameters are constant, which simplifies the model.

- The environment is unchanging – that is to say, the input parameters are unchanged by the surrounding environment.
- Prey and predators can only be added through reproduction and removed through death; the system is in a vacuum.
- The time elapsed is not long enough for evolution to have a significant impact.
- The prey have an infinite reservoir of food, or do not need it – that is to say, the supply of food for prey have no impact on their growth.
- The reproductive/growth capabilities of the predators are completely reliant on how many prey they eat.
- The predators' only food source is the prey.

In real life, none of these assumptions are wholly true. However, eliminating them makes analysis simpler, and doesn't detract from the overall idea of Lotka-Volterra equations (the idea of feedback loops).

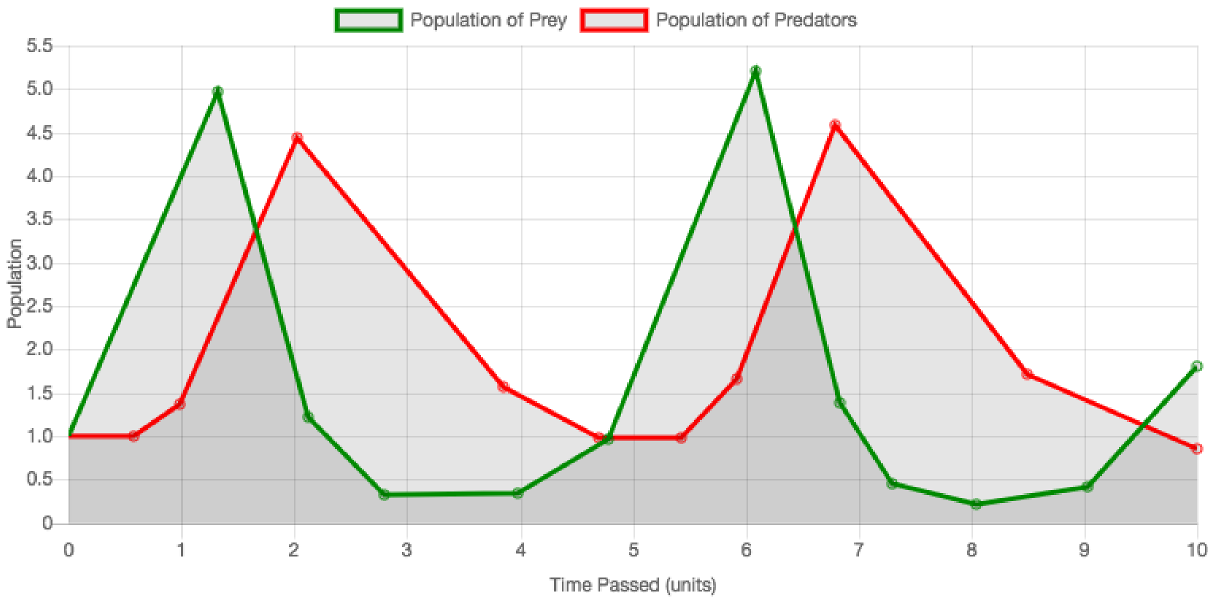
General Pattern of Model

The model usually has four phases:

1. There are little predators and prey.
2. As a result of the lack of predators, the prey population grows.
3. As a result of the large amount of food, the predator population grows; the prey population collapses as it is eaten.
4. As a result of the lack of food, the predator population dies out very quickly.

Every phase of this cycle can be easily shown with a graph, by plotting the populations of prey and predators against an arbitrary passage of time. I did this using the Euler step method, which is discussed in-depth later.

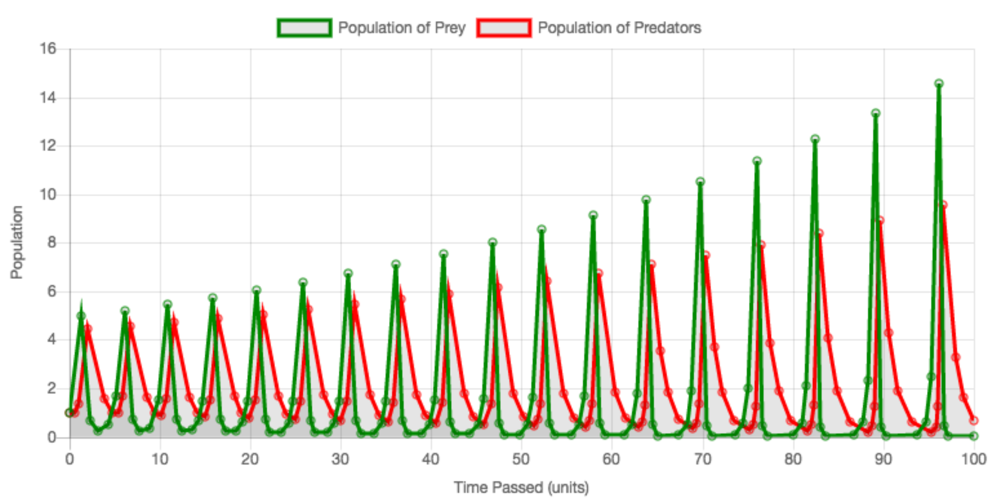
Figure 1: Population of Prey vs. Population of Predators, Short-Term



At $t = 0$, there are little predators and prey. Naturally, the prey start growing quickly. At $t = 1$, the predator population also starts growing quickly. While the prey population peaks at around $t = 1.3$, it quickly plummets as the predators continue eating the prey. By $t = 2$, the predator population peaks, but due to the lack of food it also decreases. By $t = 4.5$, there are little predators and prey, and the cycle starts all over again.

This cyclical nature continues on forever – in Figure 2, the time passed is significantly increased. Notice how the pattern of an initial prey spike, a following predator spike, and a crash of both populations always occurs.

Figure 2: Population of Prey vs. Population of Predators, Long-Term



Approximating the Lotka-Volterra Equations: Euler's Step Method

As I noted earlier, the pair of Lotka-Volterra equations are differential equations. But, they are nonlinear differential equations, which means they aren't explicitly solvable. However, they can be approximated using the Euler Step Method: starting at a certain point, and then calculating the derivative of each variable with intervals of the independent variable. In this case, the independent variable (or the "y" value, not to be confused with the quantity of predators) is time. Therefore, I can increment time by a certain interval, plug in values for the equation, and plot it.

In order to perform Euler's Step Method throughout this exploration, I used a computer program written in Javascript, to allow for thousands of steps to be calculated with ease – I've attached the code for the function in the Appendix.

Interval Value

In Euler's Step Method, there is a specific constant value used for every increment of the independent variable (time). A smaller step value means that the approximation will be closer to the real value of the function. Throughout this entire exploration, I'll use a step value of 0.01, which is precise enough that the general trends are very clear.

Looking for Equilibrium

The idea of equilibrium in a system is very interesting: is it possible for the number of predators and prey to never change? If the number of predators and prey don't change, then the derivative of each function needs to be consistently zero. Let's see what conditions need to be possible for the derivatives of each variable ($x \text{ and } y$) to be zero.

Prey Equation

$$0 = \alpha x - \beta xy$$

$$\alpha x = \beta xy$$

There are two conditions that make this equation true: either $x = 0$ or $y = \frac{\alpha}{\beta}$

Predator Equation

$$0 = \delta xy - \gamma y$$

$$\gamma y = \delta xy$$

There are two conditions that make this equation true: either $y = 0$ or $x = \frac{\gamma}{\delta}$

Equilibrium

For there to be an equilibrium in the system, the rate of change of both the prey and the predators needs to be zero. There are only two possibilities where this happens: either, $x = 0 \; and \; y = 0$, or $x = \frac{\gamma}{\delta} \; and \; y = \frac{\alpha}{\beta}$. Not having any prey and predators is technically and equilibrium, but isn't particularly useful in an analysis perspective. However, the second set, $x = \frac{\gamma}{\delta} \; and \; y = \frac{\alpha}{\beta}$, is a non-zero equilibrium – therefore it is possible, within the model, to have a perfect equilibrium.

Real-Life Application: Koi Fish and Algae

I can now apply my knowledge of Lotka-Volterra equations to the real world, tying back to my real-life example of Koi fish and algae. While Koi fish aren't the typical predator, and algae aren't the typical prey, the both fit the biological definitions of predator and prey, and almost entirely obey the model.

In the hypothetical situation, there is a lake that is only populated by Koi fish and algae. I can arbitrarily set the starting number of fish and algae, and look for real-life data on the four parameters. Then, I can create graphs of different scenarios, and set an optimal starting point for creating a perfect equilibrium.

Gathering Parameter Values

Gathering real-life parameter values is tough, especially due to the constraints of the model: while the model assumes that total prey growth is directly proportional to the previous population, algae (and other real-life organisms) rarely behave in this way. Specifically, algal growth rates are affected by the availability of light and its wavelengths, water salt content, and temperature. This is further complicated by the different kinds of algae that exist, as algae is an informal term with no clear definition.

Since I had to choose one type of algae, I chose *Porphyra tenera*, a type of seaweed that is often used to make sushi and naturally occurs in Japan. Not only does it relate back to my personal experience in Japan, but it also has some data on its growth; in a paper titled "Observation on the Ecology and Reproduction of Free-Living Conchocelis of Porphyra tenera", Hideo Iwasaki and Chikayoshi Matsudaira analyze the growth of *Porphyra tenera* in its natural environment. Importantly, the paper cites that it took about 16 days for a culture of *Porphyra tenera* to produce its seeds and have those seeds germinate into more cultures.

Predation rate was slightly easier to approximate, for two reasons. Firstly, predation rate is dependent on how often the fish interact with the prey – mobile prey can make predation rate calculations hard. However, seaweed isn't mobile – therefore, I can assume that the predators have infinite ability to access prey, which makes logical sense. Secondly, the data on how much food Koi fish typically eat is publicly available, as Koi are a popular pet. At typical pond temperatures, Koi eat 3 or 4 times a day; the predation rate can be set to 3.5 per day.

The predator growth rate is a little hard to understand – as it is dependent on how much the predator eats. However, I can assume that an algal diet is the most efficient diet they can consume, and then look at their fertility rates. Unfortunately, data on fertility rates for most fish, including Koi, is quite inconclusive – minor changes in variables such as temperature or mineral content can drastically change output. One paper, "Natural Reproduction and Survival of Carp in Small Ponds", has the best data to approximate the Koi's growth rate (Koi fish are a type of carp). In their paper, Mraz and Cooper measure the output of carp after 1 year, and combing through their data it seems the reproduction rate after 1 year is approximately 25 young fish per adult fish.

In this context, the death rate of the predators is synonymous with their natural life expectancy, as there are no environmental interferences. The life expectancies of Koi fish are also well-documented, averaging around 15-20 years; therefore, a safe estimate is 17.5 years.

In order for the parameters to make sense, the time frame must be standardized. For this to work, I make two key assumptions: first, that the variables are time-scalable (if a Koi eats 4 algae cultures a day, it eats 8 in two days), and secondly, that time-sensitive variables are equally distributed (if the life expectancy of a Koi fish is 17.5 years, then at any given year it has a 1/17.5 chance of dying). Again, both of these assumptions aren't entirely realistic, but they are required for any real-life data to work with the model.

With that in mind, we'll standardize all of the variables to one year. Therefore, $\alpha = 22.8, \beta = 1227.5, \delta = 25, \gamma = 0.0\overline{571428}$.

Using Parameter Values to Find Equilibrium

Now that I have parameter values, I can find the equilibrium value. This is just some very basic division!

$$x = \frac{\gamma}{\delta}$$

$$x = \frac{0.0\overline{571428}}{25} \cong 0.00228$$

$$y = \frac{\alpha}{\beta}$$

$$y = \frac{22.8}{1227.5} \cong 0.01857$$

Unfortunately, these values aren't large enough – you can't have 0.01857 of a Koi fish! These values actually indicate that, with these parameters, it's impossible for there to ever be an equilibrium – as soon as there is one whole algae colony or Koi fish, the system will immediately fall into disarray.

There is a simple explanation for this, assuming that the parameters are good (which they very well may not be). On orders of magnitude, the Koi fish is too strong of a predator, and out competes the algae. They are very hungry and have a very high predation rate, eating multiple cultures a day and therefore thousands per year, and also have an extremely low natural death rate with a life expectancy of 17.5 years (when compared to the algae, which is instantly eaten after 16 days). Because of the Koi's hyper-predator characteristics, any combination of Koi and algae would very quickly lead to the Koi becoming overpopulated and overeating the algae, and then the extinction of the Koi from the body of water.

This is easily demonstrable. In a pond, assume that there is a ridiculously large number of algae (which is the definition of algal blooms), such as 10 000 algae cultures. Then, introduce just 1 Koi fish (assuming a Koi fish can reproduce asexually, which they cannot – this is just to demonstrate the nature of the Koi fish). Using Euler's Step Method, the resulting numbers of algae and Koi can be easily analyzed, and show the rapid growth of the Koi and its subsequent over-predation.

Table 1: Sample Euler Step Method Calculations (Step Value of 0.01)

Step (steps of 0.01)	Number of Prey	Number of Predators
0	10000	1
1	9780	6.75
2	0	44.67
3	0	33.50
4	0	25.13
5	0	18.85
6	0	14.13
7	0	10.60
8	0	5.96

These values were calculated using Euler's step method, by plugging in all the values into the prey and predator equations for each step value, and repeating this for a set period of intervals to approximate what the functions would look like. Here is a sample calculation, that goes from step 0 to step 1.

$$new\ x = step * (\alpha x - \beta xy)$$

$$new\ x = 0.01 * (22.8 * 10000 - 1227.5 * \ 10000 * 1)$$

$$new\ x \approx 9780$$

$$new\ y = step * (\delta xy - \gamma y)$$

$$new\ y = 0.01 * (25 * 10000 * 1 - 0.0\overline{571428} * 1)$$

$$new\ y \approx 6.75$$

The values in Table 1 show just how voracious a predator the Koi fish are. By step 2 (which is just about 6 days), the Koi fish have eaten all of the algae in our hypothetical habitat – and when that happens, there is no recovery possible for the algae. Then, for the next few days (and for the rest of the habitat's lifecycle), the Koi will slowly die away. Even in extreme scenarios such as this one, the natural characteristics of Koi fish make it too strong of a predator, and make maintaining an equilibrium impossible.

Limitations and Extensions

As with most high school analyses, there are several limitations to this analysis. The most obvious ones to point out are the structural limitations of this model. As I've noted earlier, many of the assumptions that I have to make for this model aren't true in real-life, and the assumptions I made to process the data often warps its value. With a greater knowledge of math (and biology), it might be possible to solve more complex multivariable differential equations involving more variables (such as the availability of the prey's food source, or a predator to the predator). In addition, there are other assumptions that change the structure of the problem: for example, Koi fish eat more than just algae in real life, and more things than just Koi fish eat algae.

With that in mind, a cool extension would be to examine the effect that a growth in one predator population has on the population of another predator that eats the same resource. This is more applicable to real-life, but would also require a more complex set of equations.

There's also the classical limitation of less data and bad data. This is hard to remedy, as the reproduction rates of Koi fish are hard to document (as other scientists have shown), but also isn't a particularly interesting topic, which means there's a lack of analysis on the subject. This is also combined with how hard it is to isolate for one specific characteristic (such as population) – since carp are very hard to maintain in a laboratory, carp can only be raised outside, where controlling for variables becomes extremely hard. In addition, the data we're looking for (directly proportional growth rates for organisms) just doesn't exist!

There is a creative way to remedy this problem, which is to examine other non-traditional predator-prey relationships. For example, there are many types of bacteria that sustain themselves off of other bacteria – and bacterial growth rates are much more well-documented than algae or Koi. In addition, predator and prey don't necessarily have to be living organisms: they could model the spread of a virus, or the deadliness of lead poisoning.

Another interesting line of extension is to examine how intervention can be used to maintain an equilibrium. While I am greatly disappointed that I can't just have a Koi pond in my house and rely on natural equilibriums, I can attempt to figure out what I'll need to do to maintain that Koi pond. For example, we can look for an "interventionist" equilibrium – if the net growth of the algae is exactly 0 per time frame, and the net growth of the Koi is exactly 5 per time frame, I could simply remove 5 Koi fish from the system every time frame, thereby keeping the system in a low-intervention equilibrium. This method, if solvable, is easily applicable to real-life.

Conclusion

Looking at my results, I now understand exactly why the Koi fish were used as natural algal bloom cleaners: their inherent traits as hungry eaters and long-living predators mean that they will outgrow and devour any algal bloom. Eventually, they'll overeat the algal blooms, and without intervention, they'll die out too, leaving their pond or lake a barren waste water. Furthermore, by examining scientific data, I recognized that the traits of algae and Koi mean that an equilibrium where the number of Koi and algae stay the same over an extended period of time is impossible.

Throughout this process, I learned more about the idea of a Lotka-Volterra model and how it's applicable to real life situations. More broadly, I learned about a real-life application of non-linear differential equations. In addition, I learned how to implement Euler's Step Method using a programming language, which is one of the primary ways that computers solve and plot differential equations. And, I destroyed my lifelong dream of having a Koi pond. But, with scientific progress, there are always sacrifices.

Appendix

1.1 Basic Euler Step Method Code

Here is the code for a very basic implementation of Euler's Step Method, written in Javascript. I adapted this code for the interactive website listed in 1.2.

```
"use strict";

let a; // the rate of growth
let b; // the rate of predation
let c; // predator growth rate
let d; // the natural death rate
let step = 0.01; // each step for the Euler step method
let time; // time units passed

function preyEq(x, y) {
  return x * (a - (b * y));
}

function predatorEq(x, y) {
  return -y * (c - (d * x));
}

function doEuler(prey0, predator0) {
  let prey = prey0;
  let predator = predator0;
  let preyArr = [];
  let predatorArr = [];

  for (let i = 0; i < time; i += step) {
    preyArr.push({x: i/step, y: prey0})
    predatorArr.push({x: i/step, y: predator0})

    prey0 = prey;
    predator0 = predator;

    prey += step * preyEq(prey0, predator0);
    predator += step * predatorEq(prey0, predator0);
  }
  return [preyArr, predatorArr]
}
```

1.2 Interactive Web Application

As part of writing this exploration, I created a web application that graphs out the Lotka-Volterra equations and allows the users to fiddle around with any of the variables, and plots out the changes. It is accessible at https://matthewwang.me/lotka-volterra/

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