Bifurcation theory:
When does extinction become a threat?

By Vibha Kumar

1. Introduction

I used to think that maths and biology mixed as well as oil and water. Why interweave logic and rigour with the unpredictable nature of living organisms? But through my (initially sceptical) exploration of mathematical biology, I have grown to appreciate the scope of modelling the behaviour of biological systems, which can help build predictions without conducting the relevant - and frankly quite expensive - experiments.

The formal definition of a bifurcation is a major change in the behaviour of a dynamic system in response to changing a parameter. But what does this really mean?

Parameter: this is a quantity that influences the behaviour of a system or object. Putting on our biologist hats for a minute, if we are investigating the sudden outbreak of a virus as our 'system', one of the main affecting 'parameters' could be a decrease in the temperature of our lab environment.

Dynamic system: a system where something (a given factor) changes with time. This could be the changing population of the virus, for example.

Solutions to problems can usually be achieved by just plugging in data available to us and evaluating an equation. Instead of this, I would like to focus this essay on the *understanding* of bifurcation models - rather than the computation itself - by using an example of population dynamics.

2. Thinking intuitively

When we begin to build an equation for our dynamic system, it's crucial to grasp the *how, what and why.* Bifurcation models use differential equations (specifically first-order, nonlinear differential equations, in this case) which may seem daunting, but are quite intuitive and can be understood without necessarily knowing the concept beforehand!

First order: The highest degree in a differential equation (D.E) is dy/dx.
Nonlinear D.E: The graph is not a straight line when plotted.

Going back to the 1840's, Belgian mathematician Pierre Francois Verhulst proposed the logistic function - and more relevant to us, the logistic differential equation. The latter was revolutionary when it came to modelling population dynamic systems. But how can we deduce the formula on our own?

Starting off by defining some variables:

N = population
t = time

$$\frac{dN}{dt} = kN$$

Shown above is a simple differential equation. dN/dt means 'the rate of change of population', and the equation suggests that this rate of change is proportional to the population itself (where k represents an arbitrary constant). Thinking about this in real life makes sense, because a pond filled with 10 fish will definitely reproduce at a lower rate compared to a pond filled with 500 fish. This would make the equation a suitable first guess for our formula.

$$\frac{dN}{N} = k\,dt$$

$$\int \frac{1}{N}\,dN = \int k\,dt$$

$$\ln|N| = kt + c$$

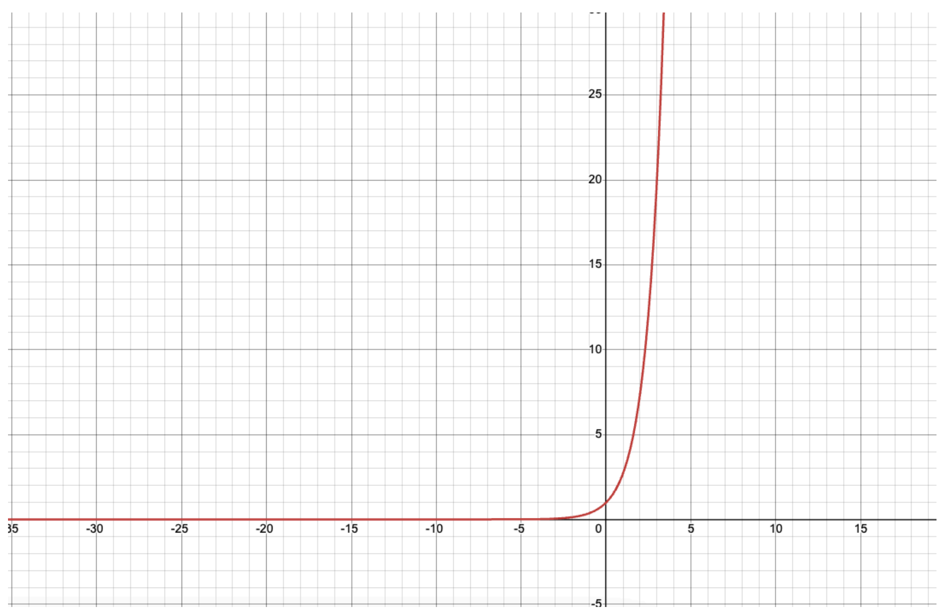
$$e^{\ln|N|} = e^{kt+c}$$

$$N = Ae^{kt}$$

(^solved using separation of variables, but don't worry if you don't know this)

When we solve this differential equation, we are left with the solution that the population is some form of an exponential function (differential equation solutions are a 'family of functions' rather than an individual value). The phrase 'exponential growth' is thrown around a lot, usually to explain a sudden and rapid increase. But is it the right descriptor in this context?

Thinking back to our exponential graph, f(x) = e^x we can see that as x gets larger, f(x) increases at a very fast rate, for all positive values of x. We can ignore the negative values, as it's impossible to have a negative population.



Unfortunately, there are some flaws that arise with an exponential model. *Theoretically,* going back to our fish-in-pond example, the fish could reproduce continuously until the population tends towards ∞. But realistically, the pond has a **limited** amount of resources such as water, food, and space for all the fish to coexist happily. This gives us the idea that there must be some sort of ceiling, or cap, at the number of fish that can be present. Furthermore, the rate at which the fish reproduce must also reduce due to the shortage of resources.

Using this information, we can deduce that when N is small, (and resources are abundant) we want the graph to resemble the original D.E, but as N increases, we want the rate of population increase to *decrease.*

$$\frac{dN}{dt} = kN(\ldots)$$

We want to fill these brackets with a value which will allow the graph to meet our new requirements.

Low population: (...) —> close to 1
High population: (...) —-> close to 0

All that's left now is to come up with a suitable expression for our brackets.

$$\frac{dN}{dt} = kN\left(1 - \frac{N}{L}\right)$$

L = carrying capacity; the maximum population of a system

The fraction N/L basically represents the current population as a fraction of the maximum, so that when we evaluate the expression, dN/Dt decreases as population increases.

With this understanding, we can define logistic growth as a model where the growth rate gets smaller and smaller as we tend towards the carrying capacity.

3. Modelling rabbit populations

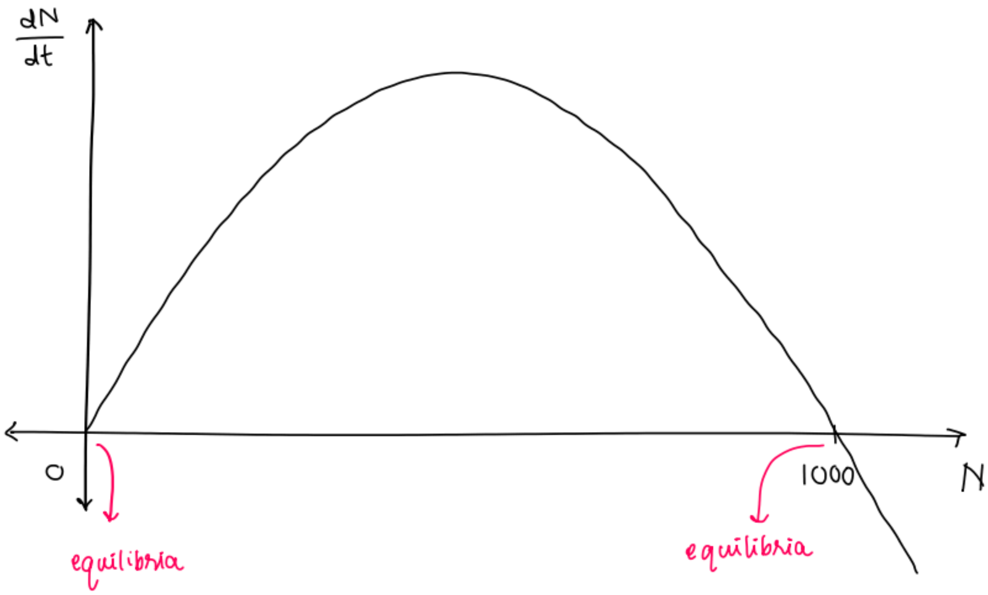
Okunoshima is a small island in Japan (and hopefully my next holiday destination!) which is known for its rabbit population.

If there are approximately 1000 rabbits on the island, we can model the population using the logistic differential equation that we deduced above.

In order to sketch this equation, there are a few steps we can follow:

$$\frac{dN}{dt} = \frac{1}{10} N \left(1 - \frac{N}{1000} \right)$$

If this is our equation, then we can start off by finding some critical values, such as the roots of this equation. When we substitute the values N = 0 and N = 1000, we see that dN/dt becomes 0. These are the equilibria points of our equation. Plotting a couple more points, we can see that the shape of the graph resembles a quadratic.

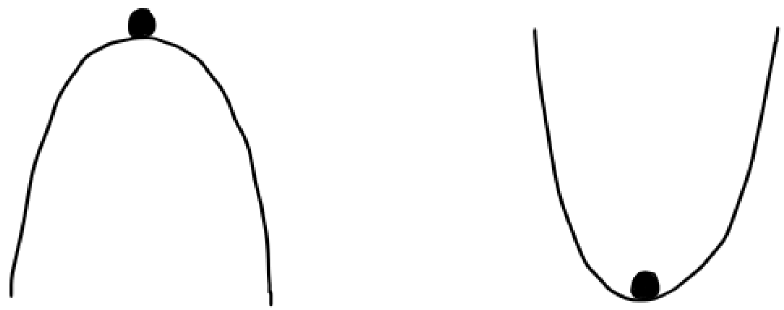


The second and third quadrants have not been drawn because there cannot be a negative population. Another misconception would be to think that from roughly halfway (around N = 500) the population starts to decrease. Keep in mind that the y-axis shows the *rate of change of population* - so while it does show a downwards slope, the population is still increasing, albeit, more slowly! The population only decreases in the 4th quadrant.

3.1 Stability

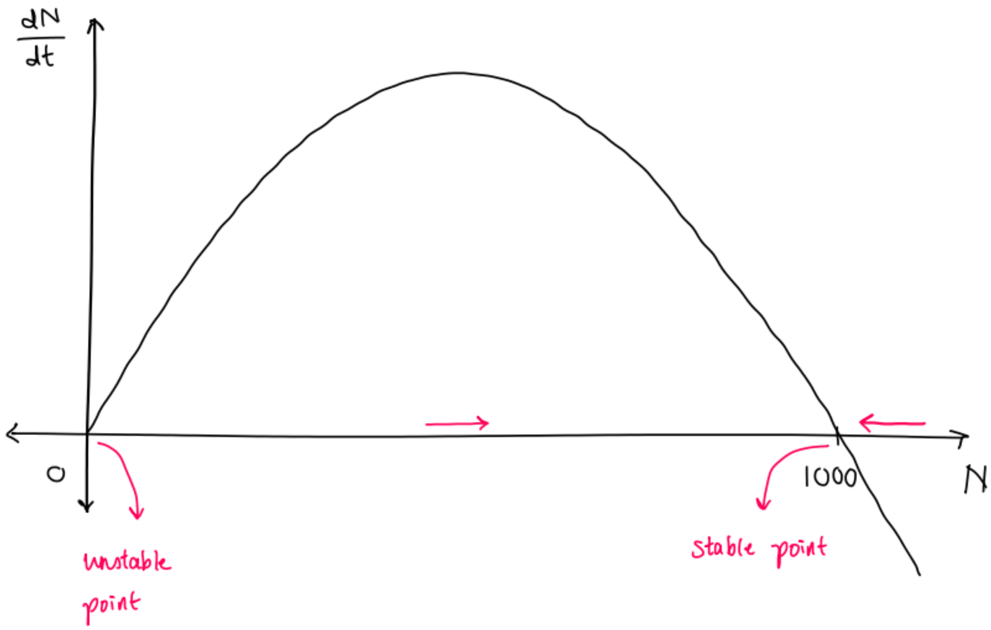
Stability of equilibria refers to which state the system would prefer to be in. The system usually tends towards a stable equilibrium (if there is one) in the long run.

Stability can be thought of using this diagram:



The diagram on the left represents instability. A small push of the ball from either side leads to it moving away drastically from the point it was previously on. The diagram on the right (stability) shows that the ball tends back towards the button of the curve.

To determine stability, look at the N values right before and after the equilibria.



At the point N = 0, the population values immediately after have a positive dN/dt which means the population tends away from the equilibrium. At N = 1000, the N values immediately before are increasing towards the equilibrium, and immediately after are decreasing (because dN/dt is negative), showing that it tends back towards 1000. This is shown by the arrows on the graph. Applying this to the rabbit scenario, the stability explains why in the long run, the rabbit population tends towards its maximum carrying capacity of 1000.

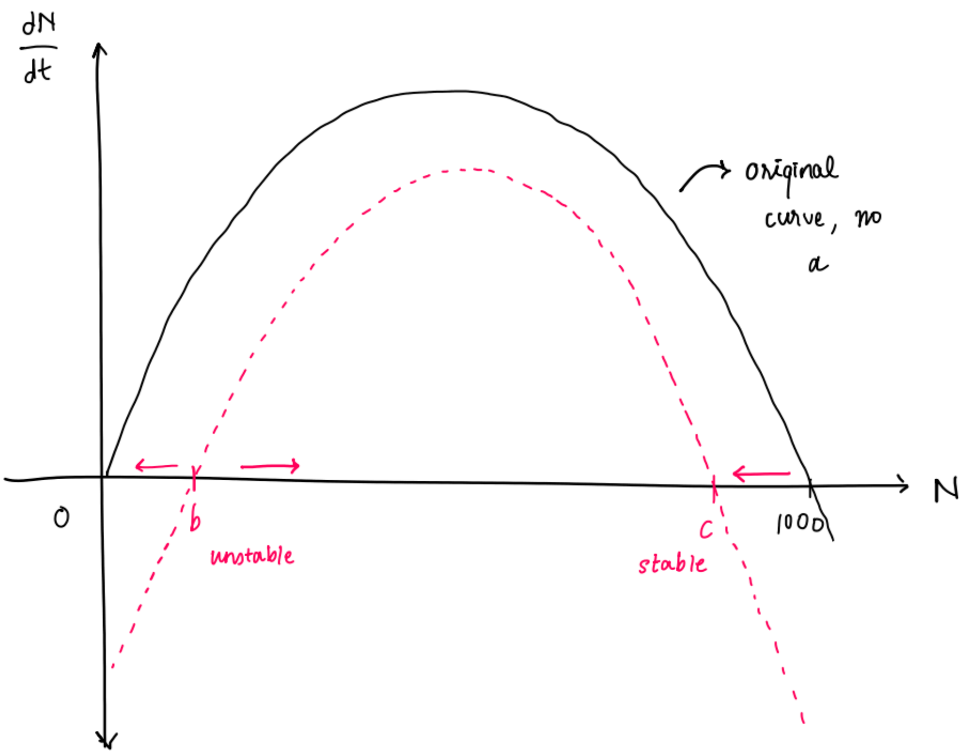
4. Introducing predators

Let’s say that some snakes find their way to the rabbit island. At what number of snakes does extinction of rabbits become a possibility? How does this affect our graph? When is extinction guaranteed? We can take a stab at these questions through some remodelling of our equation: by introducing the **constant** a, the number of snakes.

$$\frac{dN}{dt} = \frac{1}{10} N \left(1 - \frac{N}{1000} \right) - \alpha$$

We know that from graph transformations, $y = f(x) - a$ results in a downwards shift of the graph.

4.1 - Small a



For a small value of a, we can observe two new equilibria points, b and c. You can attempt this yourself by:

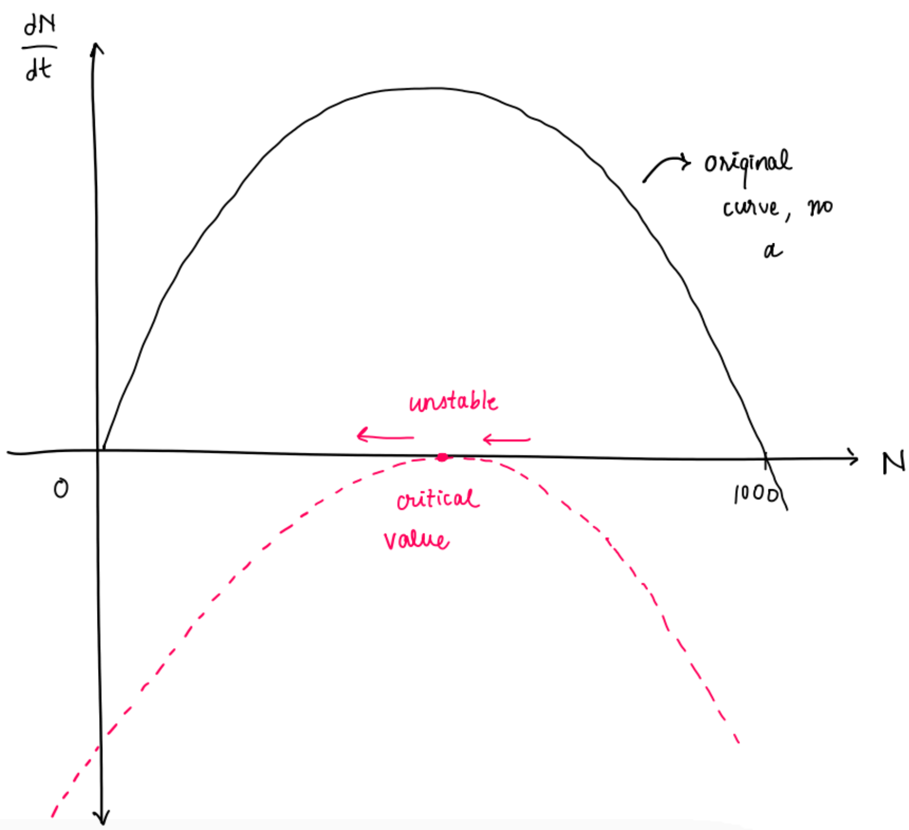
1. Replacing a with a relatively small value

2. Replacing dN/dt with 0 (rate is 0 at the roots)
3. Expanding the brackets
4. Solving the equation the same way as you would a quadratic.

When b < N < c, the population will tend towards the stable equilibrium c, which implies that the rate of population growth of the rabbits is greater than the consumption of the snakes. However, as b is an unstable equilibrium, any values N < b will result in extinction, as dN/dt is negative, and the population tends towards 0.

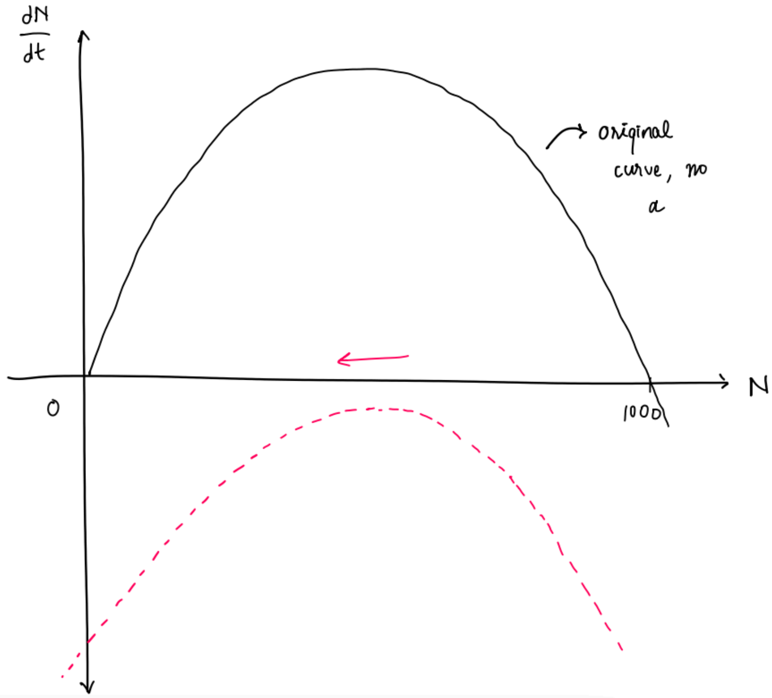
4.2 - Bifurcation!

As a increases, the graph moves even lower, until there is only one equilibrium point remaining.



This is a critical value of a, and its instability makes it a very precarious point. It also represents a bifurcation, because an a value any greater than this will result in the definite extinction of the rabbits. In other words, a small change in the parameter, a, results in a dramatic change in our system's behaviour.

4.3 - Extinction

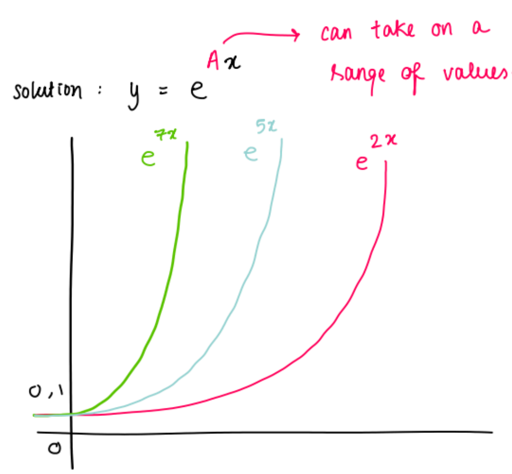


After increasing a past the critical point, there are no equilibrium points anymore, which implies that the rate of reproduction is lesser than the rate of the snakes catching the rabbits for all values of N. This will eventually lead to extinction.

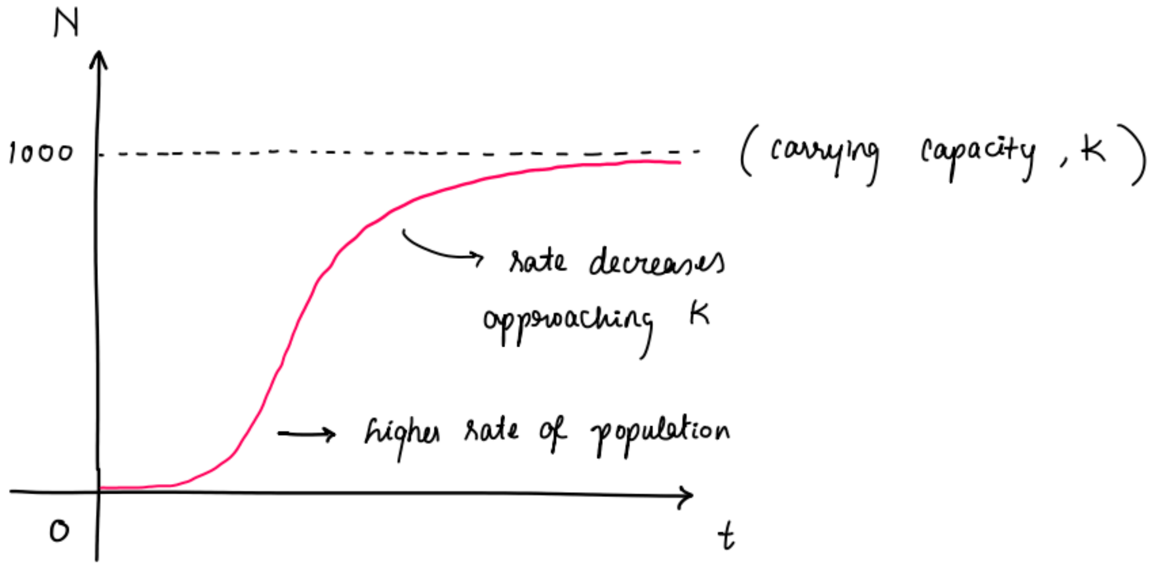
5. Qualitative analysis

It is possible to solve each of the D.E's mentioned above for the different values of a. Nevertheless, for the purpose of understanding the concept, we can graphically represent solutions and look at their long-term behaviour without actually solving the D.E. This is known as qualitative analysis. Solutions to D.E's are functions rather than a fixed value, and cannot graphically intersect each other.

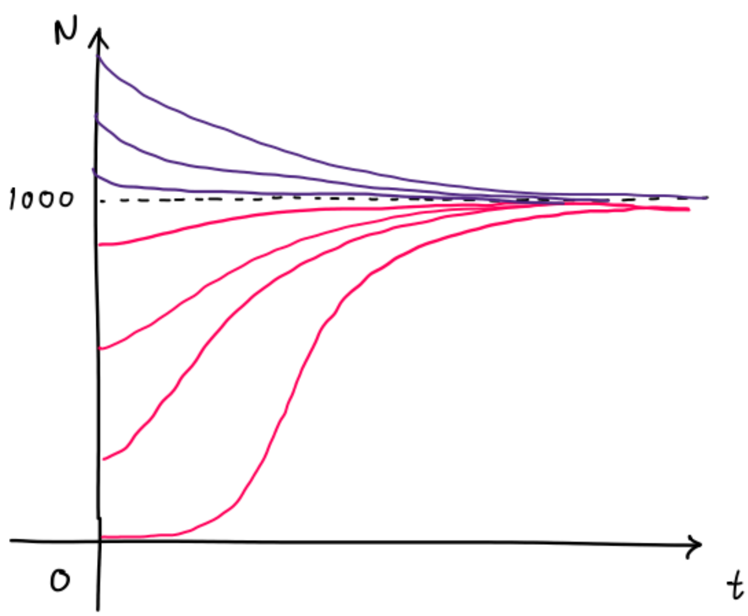
The example on the right shows how a solution can have a 'family' of different curves depending on the 'A' value.



Let's recall our logistic D.E knowledge. A graph of N against t could possibly look like this, with the graphs resembling somewhat of an ‘S’ shape:



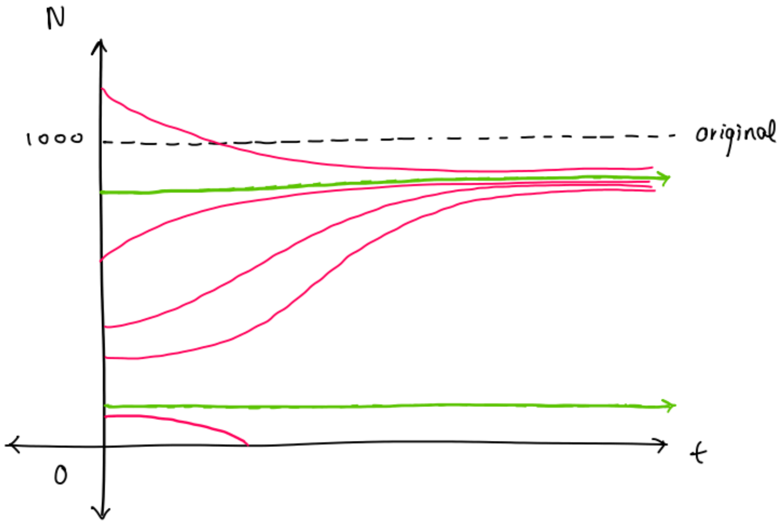
A family of solutions of our rabbit population equation without a could look like:



This graph shows us that all the solutions to the D.E tend towards 1000 (the stable equilibrium). The pink solutions are increasing functions, whereas the purple ones are decreasing. You can check this by looking at the arrows on the dN/dt against N graph or by plugging in a random value greater than 1000 into the D.E, which will result in a negative rate (therefore the purple functions tend back to 1000).

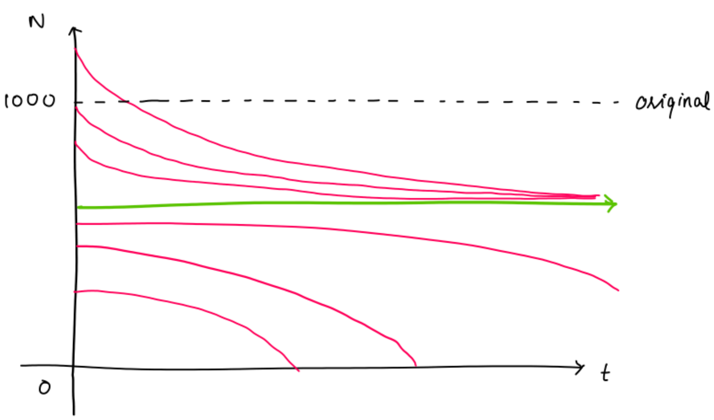
5.2 - Graphs for different a values

We can sketch more graphs for each of the 3 different scenarios.

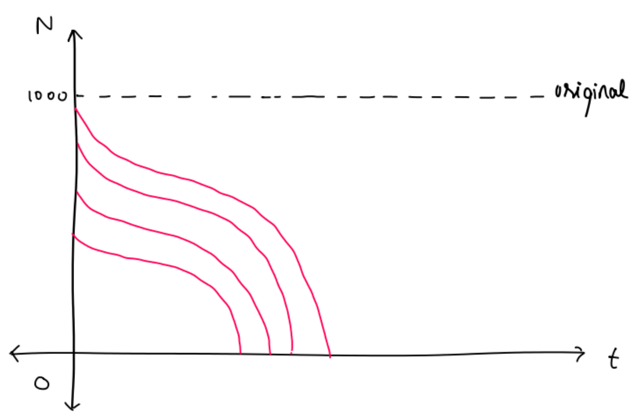


small value of α

For a small a value, the equilibrium points shift closer together. The solutions look fairly similar to the original graph, the only change being the decreasing function(s) seen when N < lower equilibrium. This shows that N values lower than this lead to extinction.



critical α



large value of α

You can apply the same logic to interpret these graphs. Critical a has only 1 equilibrium, so any solutions lower than that result in extinction in the long term, and the large a shows all solutions tend towards extinction. The best way to understand these graphs is to look at them in tandem with the dN/dt graphs from the previous section for each specific scenario.

6. Conclusion

As a next step, I would suggest looking at how to actually solve logistic D.E's. Maths has made its way to a number of different fields, the most common of them being physics, computer science, and economics. However, unlike F = ma, the ability to quite accurately model and simplify something as complex as life itself is what drew me to this topic in the first place! I hope that this is seen as an encouragement to look at maths as more than just a set of formulae, but rather as the language of the universe, both physical and biological. Bifurcation is just one of the several ways in which seemingly unrelated pure maths can be applied to your surroundings, and in your next maths lesson, will hopefully give you a reason to avoid saying: "But where will I *ever* use this in my life?"

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