Modelling populations with the Lotka-Volterra Equations

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The History of the Lotka-Volterra Equations

The Lotka-Volterra Equations, or predator-prey equations, are a pair of first-order differential equations designed to model the changing populations of a biological system between two species[1]. Developed initially by Alfred J. Lotka in 1910 to predict the rate of autocatalytic chemical reactions, he further adapted the mathematical model in 1920 to include 'organic systems', an example of which is the biological dynamic interaction between a plant species and a herbivorous species. This was essential in his analysis of different predator-prey relationships, which he included in his book on biomathematics in 1925 titled "Elements of Physical Biology" in which he ultimately determined that populations of both host and parasite show damped oscillations[2].

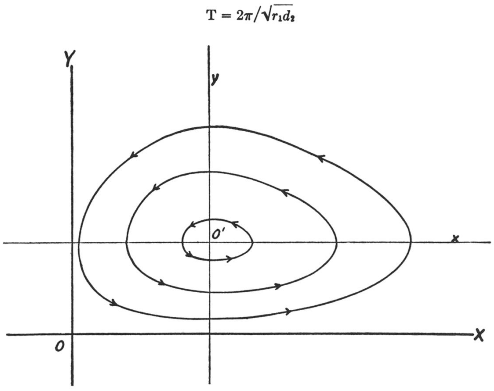
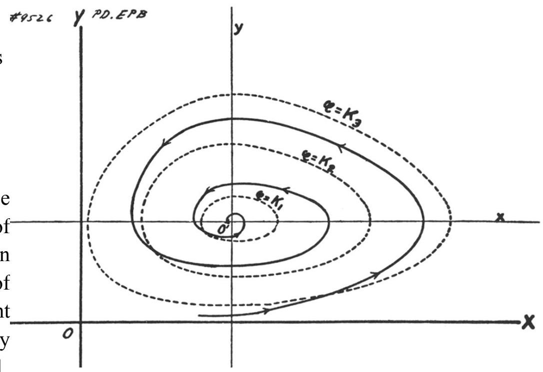


Fig 1.1 (left) - Phase space showing undamped oscillations in both populations, relating to the classic hypothetical Lotka-Volterra equations.

Fig 1.2 (right) - Phase space showing damped oscillations of both populations, as an expanded-upon system of equations that took into account advancements in entomology not present in Fig 1.1.



Meanwhile, Vito Volterra, a prominent mathematician from Italy, had decided to separately pursue the goal of finding a system of equations to model predator-prey relationships, eventually leading to the publication of a short discussion in 1926. He was inspired by the work of Umberto D'Ancona, a marine biologist who eventually became his son-in-law, who had previously found that more predatory fish were being caught during the first world war, despite the decrease in fishing levels over that time period. Consequently, he helped refine the Lotka-Volterra model through fitting it to results garnered from experiments. However, interestingly Volterra's interests differed greatly from Lotka's; while Lotka largely ignored competition between predator and prey, Volterra allowed it to greatly influence his equations. Therefore, Volterra ended up producing new equations to model competition, also known as the "Volterra-Gause equations", which were firmly based in the original Lotka-Volterra equations.

Importance of the Lotka-Volterra equations

Through natural selection, species force others to evolve[3]. The relationship between predator and prey is a perfect microcosm of modelling this, because the aims of the predator and prey are incompatible with one another. The predator requires a reliable food source to reproduce and pass on their genes, as they require more energy to perform their eight life processes, hence they want to consume as many prey as possible. On the contrary, considering the prey have an abundance of food and require less energy to function, they only need to survive in order to reproduce, which involves not being eaten by predators. This conflict of goals acts as a

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1 Wikipedia Contributors (2021). *Lotka–Volterra equations*. [online] Wikipedia. Available at: https://en.wikipedia.org/wiki/Lotka%E2%80%93Volterra_equations#History [Accessed 25 Mar. 2021]

2 Kingsland, S. (2015). Alfred J. Lotka and the origins of theoretical population ecology. *Proceedings of the National Academy of Sciences*, 112(31), pp.9493–9495

3 Utk.edu. (2019). *PREDATOR-PREY DYNAMICS.* [online] Available at: http://www.tiem.utk.edu/~gross/bioed/bealsmodules/predator-prey.html

"biological pressure", whereby mutations that assist an organism in achieving their primitive goals of survival and reproduction get passed on to their offspring, whereas organisms that do not die out.

The Lotka-Volterra equations only model the rate of change of populations, or populations against time. However, this in itself is extremely useful, because the variables in this equation are dependent on each other, so the peaks of one population coincide with the troughs of another. These peaks and troughs are often representative of "biological pressure", as it forces adaptation to overcome competition, whether through increased hunting capabilities or heightened chance of survival in the face of predation. Consequently, these predictive models can be compared to graphs and deviation from the expected value found, using features such as these, in order to date when a mutation in a species may have happened. For example, this may determine the exact point at which a species of bacteria mutated to become far more contagious/dangerous than before.

Assumptions made in the Lotka-Volterra equations

- Prey populations will grow exponentially in the absence of a predator

This stems from the assumption that resources are effectively infinite for the prey, thus they never compete for resources and are free to reproduce as they like. Additionally, as their reproduction is exponential, it is taken for granted that no given prey dies of any cause other than predation.

- Predators will starve to death in the absence of prey

This assumption is based upon the predator having only one food source, the prey. Multiple food sources lower the competition between predators, and the populations of predators and prey become less dependent on each other, meaning we would need more than two variables for our two sets of differential equations, making them unsolvable.

- Populations' rates of change are proportional to their size

Here, one must believe that each organism gives birth at a constant rate, which entails ignoring maturity (no reproduction as a child) and external pressures (e.g. disease). Moreover, this implies the general solution to the differential equations is continuous, and has no randomness within it, implying that the generations of consumer and prey are continually and consistently overlapping.

- The environment is "simple" and genetic variation is inconsequential

A "simple" environment is one where the habitat of the predator and prey does not change to suit the outlined aims of either species. Therefore, an environment with no complexity and no advantageous adaptation essentially creates a homogenous environment, where the only changes are the numbers in the population of species. This would mean the entropy in the environment was zero, thus this is theoretically impossible, and so can be considered a simplification.

- Predators have unlimited appetite

The implication here is that at times of relatively low predator populations compared to their prey counterparts, the predators are not limited by appetite and can eat all organisms of the prey species they come across, otherwise a damping term would be required to facilitate the maximum possible food eaten by a population of predators at any given moment in time.

Building up the Lotka-Volterra equations

Consider the situation of foxes (predators and rabbits). Let R and F signify the numbers of rabbits and foxes respectively, t represent the passage of time and the terms α, β, γ, Δ be constants pertaining to the biological situation of rabbits as prey and foxes as predators (i.e. α signifies the fox mortality rate, β represents the hunting efficiency of foxes, γ is the growth rate of rabbits and Δ be the efficiency of turning food into offspring for the foxes).

For foxes, the rate of change of population depends on two variables: the population size of rabbits and the population size of the foxes. The hunting efficiency and conversion of food into offspring are two major components in the increase in fox population and are dependent on both the populations of foxes and rabbits, although the fox mortality rate due to factors like competition results in an overall decrease in the numbers of foxes, and are specific to foxes, thus we can consider these as positive or negative terms in our equation to get:

$$\frac{\partial F}{\partial t} = -\alpha F + \Delta\beta FR$$

For rabbits, the rate of change of population depends on the same two variables. However, in this case there is no competition between rabbits, hence rabbit mortality rate is entirely dependent on being eaten by foxes. Consequently, the birth of rabbits only serves to increase the population with infinite resources, even if the fox attack efficiency lowers the overall population of rabbits. Once again, the latter factor is dependent on both variables, but the positive term in this equation is dependent on the population of rabbits, not foxes. Hence:

$$\frac{\partial R}{\partial t} = \gamma R - \beta FR$$

Depicting the Lotka-Volterra equations graphically

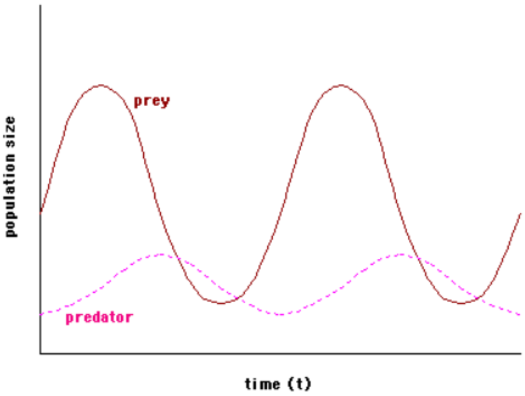
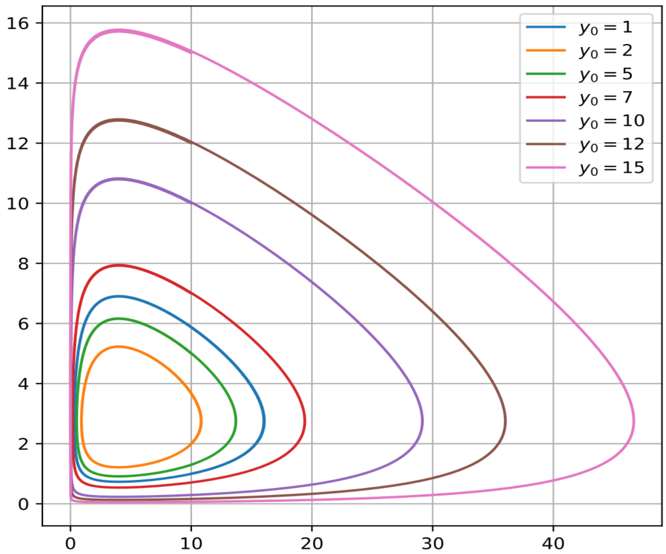


Fig 2.1 - On the left is a representation of one of the general solutions to the set of Lotka-Volterra differential equations. It very clearly shows the cyclical nature of the populations, as when the population of foxes gets small, the rate of the population change for rabbits is high in magnitude and positive, whereas when there are less rabbits, the rate of population change for foxes is high in magnitude but negative, creating a cycle. Interestingly, this also demonstrates the slight lag between the peaks of prey populations and fox populations, which makes sense as predators cannot instantaneously eat all the extra food and reproduce.

Fig 2.2[4] **-** This phase-space plot on the right shows specific solutions of populations of predators and prey relative to each other, with each line representing one set of initial conditions. Here, the constant overlap of the two species' populations and dependence on one another is very clear, as whenever one gets too large or small relative to the other, they tend back towards/away from the axes respectively, leading to these strange looking orbits. It must be noted that all of these phase-space plots travel clockwise, as when predator numbers (y-axis) are low, prey numbers (x-axis) begin to increase.



4 By Krishnavedala - Own work, CC BY-SA 4.0 Available at:, https://commons.wikimedia.org/w/index.php?curid=75213940

Problems with the Lotka-Volterra Equations

Finally, there are notable problems with this model. A particularly prominent one with regards to biological systems in particular is the Lotka-Volterra equations predict population sizes reaching ridiculously low sizes, such as having (1×10^{-18}) foxes at a particular point on the phase-space plot, which is impossible. This is caused by the model being continuous in nature, despite reaching cases where determining the rate of population change of foxes becomes a discrete problem; each individual fox's success or failure to reproduce has a far larger impact on the numbers of foxes, since the percentage of the total fox population each fox makes up is much higher. In these cases, the Lotka-Volterra equations break down and are shown to be flawed.

Furthermore, the axiomatic statements that the Lotka-Volterra model is founded upon almost never hold up in the real world, because there is entropy everywhere in the universe. This inherent randomness completely throws off the predictions made by the equations because they presume the biological system to be completely uniform, therefore having no randomness within it whatsoever. Additionally, this model completely ignores competition, which is integral to any biological dynamic system because all of them have finite resources within them. Having said that, this model is surprisingly accurate considering it was conceived in the 1920s, before computers had developed. Even still, there are more accurate population models to use, such as the logistic population model, derived from the logistic map.