

# MODELING SUPERINFECTION WITH LOTKA-VOLTERRA EQUATIONS

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## 1. ABSTRACT

In this paper, we discuss the Lotka-Volterra predator-prey model, as well as finding its steady-state solutions. Additionally, we will discuss the competitive Lotka-Volterra model, typically used to describe competitive population dynamics within a single environment, as well as the generalized Lotka-Volterra equation. Continuing, we will cover the basics of virology, including the SIR model which is typically used to describe infectious diseases, as well as the generalized superinfection model. We will find that this model is a Lotka-Volterra equation in of itself, and then cover applications with modeling COVID-19.

## 2. BACKGROUND ON THE LOTKA-VOLTERRA EQUATIONS

**2.1. The Predator-Prey Lotka-Volterra Model.** Lotka-Volterra equations are well known sets of differential equations that are typically used to describe predator-prey dynamics in ecological systems. The complexity and diversity of the situations that they model makes generalization difficult, but each Lotka-Volterra system typically makes several simplifying assumptions about the dynamics of the species that occasionally allow solutions to be found and conclusions to be drawn.

The most basic Lotka-Volterra model is a set of two nonlinear, first-order differential equations that demonstrate the theoretical dynamic between two species, one predator and one prey, (often referred to as 'foxes' and 'rabbits'). In this model, several assumptions are made that typically simplify situations that would occur in a realistic setting. These assumptions are the following:

- (1) That the prey will experience exponential growth in the absence of the predator population (i.e. the prey will always have sufficient food and shelter to survive and reproduce).
- (2) That the predator population will experience exponential decline in the absence of the prey population (i.e. the predator can only eat the prey to survive).
- (3) That there are no environmental specifics to be taken into account (i.e. genetic mutation is negligible and there is a random chance that any two animals will interact).
- (4) That the predator population has an unlimited appetite
- (5) That the predator population will react instantly to changes in the other population, and vice versa.

With these assumptions made, the system [GRD19] [MAM<sup>+</sup>21] is as follows:

$$\dot{x} = \alpha x - \beta xy \tag{2.1}$$

$$\dot{y} = \gamma xy - \delta y \tag{2.2}$$

where  $x$  represents the prey population,  $y$  represents the predator population,  $\alpha$  represents the constant rate of growth of the prey population,  $\delta$  represents the constant death rate of the predator population, and  $\beta$  and  $\gamma$  represent the constant rate of predation - that is, the rate of predatory interaction between predators and prey.

In the prey equation, we can observe the first term,  $\alpha x$ , satisfies the first assumption enumerated above - that is, that the prey will grow exponentially in the absence of a predator. More basically put, it also explains that the overall growth rate of the prey population at any moment in time will depend upon the number of prey in the population. Similarly, in the predator equation we see that the the death rate term,  $\delta y$ , where the overall death rate of the predator population will ultimately depend upon the number of predators. Similarly, we see that the predation rate terms in both equations,  $\beta xy$  and  $\gamma xy$  depend upon both the prey and predator population at any given moment in time.

It is also useful to consider the critical points of this equation, which represent the stable states of this two-species environment. By taking the left-hand side of both equations to be equal to zero, we find

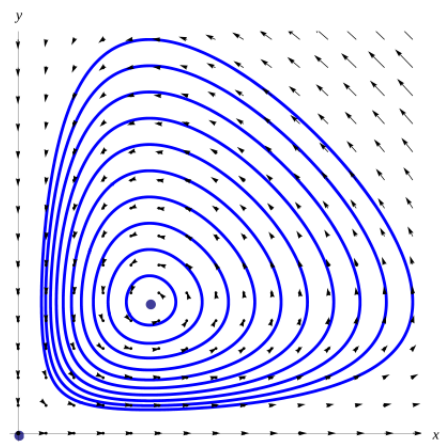
$$\begin{aligned}x(\alpha - \beta y) &= 0 \\y(\gamma x - \delta) &= 0.\end{aligned}$$

From this, we can immediately see the trivial critical point:  $\bar{x} = \bar{y} = 0$ . In this situation, both the predator and prey populations are zero, which, in the context of the situation, implies that no change will occur in either population as both populations are virtually extinct.

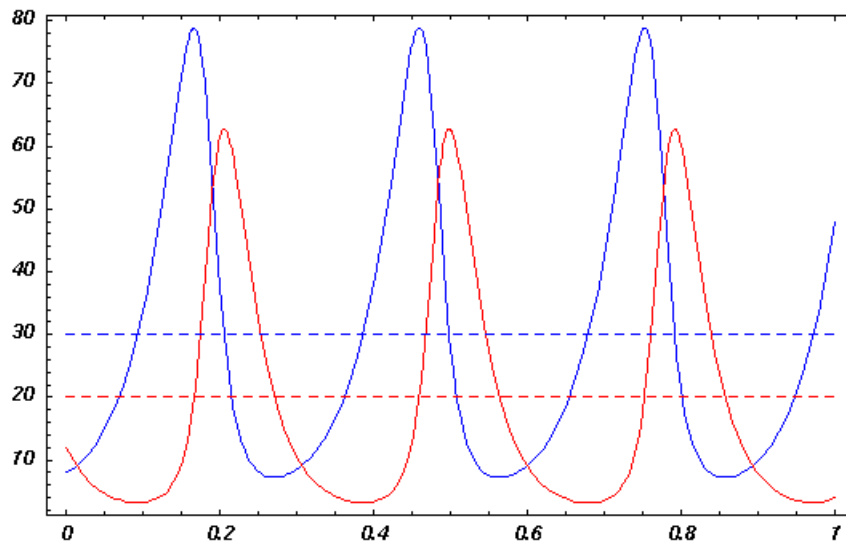
There is another equilibrium point, however, which can be found with

$$\begin{aligned}\bar{x} &= \frac{\delta}{\gamma} \\ \bar{y} &= \frac{\alpha}{\beta}.\end{aligned}$$

In this context,  $\bar{x}$  and  $\bar{y}$  also have a particular meaning. Here, if  $x > \bar{x}$ , we see that the sign of  $\frac{dx}{dt}$  is positive, and if  $x < \bar{x}$ ,  $\frac{dx}{dt}$  is negative. Similarly, if  $y > \bar{y}$ ,  $\frac{dy}{dt}$  is positive, and vice versa.



**Figure 1.** A phase portrait of the Predator-Prey Lotka-Volterra Equations. Note the periodic orbits surrounding a critical point.



**Figure 2.** Solutions to the Lotka-Volterra Equations with red representing predators, blue representing prey. The parameters used here are:  $x_0 = 8$ ,  $y_0 = 12$ ,  $\alpha = 20$ ,  $\delta = 30$ , and  $\gamma = \beta = 1$

While it isn't possible to linearize the basic Lotka-Volterra equations using their Jacobian matrix and eigenvalues, it is possible to solve the equations using other methods, such as with the separation of variables method. A summary of Sigmund and Hofbauer's particular method of solution is included here.

We begin by multiplying  $\frac{dx}{dt} = \alpha x - \beta xy$  by  $\frac{\delta - \gamma x}{x}$ , as well as multiplying  $\frac{dy}{dt}$  by  $\frac{\alpha - \beta y}{y}$ , and adding the results. This yields

$$\left(\frac{\delta}{x} - \gamma\right) \frac{dx}{dt} + \left(\frac{\alpha}{y} - \beta\right) \frac{dy}{dt} = 0.$$

This can be rewritten as

$$\frac{d}{dt}[\delta \log x - \gamma x + \alpha \log y - \beta y] = 0$$

Sigmund and Hofbauer [HS98] again rewrite this in terms of three functions,  $H(x)$ ,  $G(y)$ , and  $V(x, y)$ . They define  $H(x) = \left(\frac{\delta}{\gamma}\right) \log x - x$  and  $G(y) = \left(\frac{\alpha}{\beta}\right) \log y - y$ , and

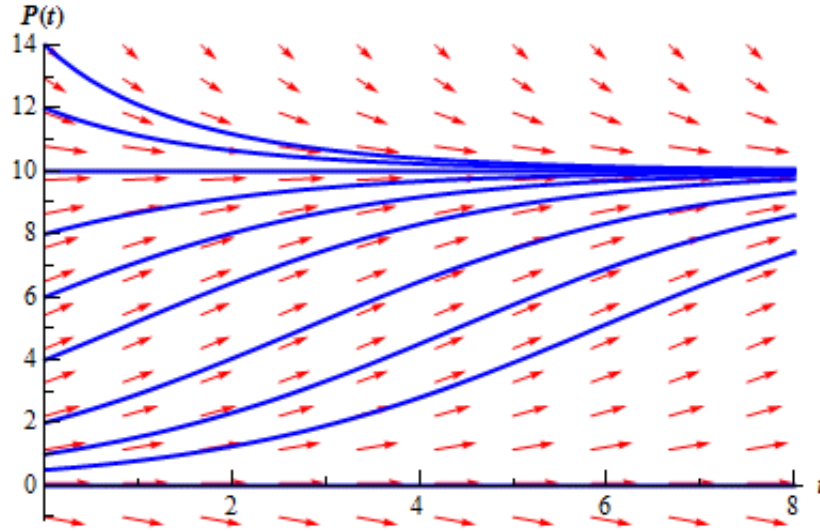
$$V(x, y) = \gamma H(x) + \beta G(y).$$

With these definitions, it is then possible to rewrite  $\frac{d}{dt}[\delta \log x - \gamma x + \alpha \log y - \beta y] = 0$  as

$$\frac{d}{dt}V(x(t), y(t)) = 0$$

And therefore,  $V(x(t), y(t))$  is a constant. These  $V(x(t), y(t))$  can be interpreted as a function of constant level sets, in which each of the solutions to the system exist. A three-dimensional visualization of the solutions to the Lotka-Volterra system allows one to consider  $V(x(t), y(t))$  as the "height" of each solution, where the apex exists at the point  $(\bar{x}, \bar{y}) = \left(\frac{\delta}{\gamma}, \frac{\alpha}{\beta}\right)$ .

Overall, this analysis reveals that solutions to the Lotka-Volterra system can be viewed as infinitely many periodic orbits surrounding  $(\bar{x}, \bar{y})$ . From this, we understand that in this



**Figure 3.** A phase portrait of the Logistic Population Model. The parameters are  $r = \frac{1}{2}$  and  $K = 10$ . Note the change in concavity at  $\frac{K}{2} = 5$ .

system, the predator and prey population undergo infinite oscillations which are typically modeled by variations of trigonometric functions. Nowak adds that the period of these solutions is given by  $\frac{2\pi}{\sqrt{\alpha\delta}}$ , and solutions have an amplitude that varies depending on the initial conditions given.

**2.2. The Logistic Equation.** Before introducing the Competitive Lotka-Volterra equation that will later also be applied to superinfection and virology, it is helpful to first review the basic logistic population model. This is largely due to the fact that many characteristics are shared between the two sets of equations, including numerous fundamental similarities in their structures. This section will provide an overview to the logistic equation as a population model, reviewing its solutions as well as its significance in the more general field of theoretical ecology.

To provide a brief background, the logistic equation was first applied to population dynamics in the mid nineteenth century by Belgian mathematician Pierre-Francois Verhulst after Thomas Malthus had first introduced the concept of exponential population growth in his work, *An Essay on the Principle of Population*. Following Verhulst's initial breakthrough, the logistic model of population growth would later be rediscovered by several other notable mathematicians in the early twentieth centuries, including Alfred Lotka.

The logistic population model is often considered to be the simplest equation modeling population dynamics besides the exponential model. As such, it makes several assumptions that typically simplify situations that would occur in a more realistic setting. Among these assumptions are the following:

- (1) That all individuals are genetically (and therefore reproductively-speaking) equivalent
- (2) That the single population exists within a closed environment (i.e. no immigration or emigration)
- (3) That factors within the population such as age, size, etc. are negligible

- (4) That all limiting factors in the environment such as food supply and shelter can be extracted into a single constant carrying capacity

The most commonly used and widespread logistic model is a first-order ordinary differential equation of the form:

$$\dot{y}(t) = ry(t) \left( 1 - \frac{y(t)}{K} \right) \quad (2.3)$$

This equation can be rewritten as

$$\dot{y}(t) = ry(t) - r \frac{y(t)^2}{K}$$

which more closely matches the most general logistic equation (not used for population modeling):  $\dot{y} = ay - by^2$  where  $a$  and  $b$  are constants.

In the logistic population model, we have  $y(t)$  representing the population size at time  $t$ . The constant  $K > 0$  is typically referred to as the carrying capacity of the population - that is, it is the maximum size of the population that can be supported by the environment. There is also the constant  $r > 0$ , which can be understood to represent the growth rate of the species.

Notice that without the factor  $(1 - \frac{y(t)}{K})$ , the logistic population model would be equivalent to the exponential population model with species size  $y(t)$  and growth rate  $r > 0$ . In fact, when  $y(t)$  is far enough below  $K$ , it is possible to approximate the logistic model with the exponential model:

$$\dot{y}(t) = ry(t)$$

However, it is not difficult to see that as  $y(t)$  approaches  $K$ , the exponential population model will lose its accuracy as the term  $(1 - \frac{y(t)}{K})$  becomes more significant in 2.3

Additionally, it is also useful to consider the stationary solutions to the logistic equation. By setting  $\dot{y}(t) = 0$ , we can immediately see that the logistic population model will have a stable solution at the following places:

$$y(t) = 0 \quad (2.4)$$

$$y(t) = K$$

We can interpret the trivial equilibrium solution  $y(t) = 0$  as the following: the population is virtually extinct, leading to no growth or variation from anything except extinction. This solution can be categorized as unstable. We can interpret the non-trivial equilibrium solution  $y(t) = K$  as the following: the population size is perfectly calibrated to the environment of the species, preventing any meaningful deviation from  $K$ . In the logistic population model, the equilibrium solution  $y(t) = K$  can be categorized as being asymptotically stable. It should be noted that in a realistic setting, if a population of a species were to approach this type of equilibrium, the population size would obviously not remain constant at  $K$ , but oscillate slightly around this value.

Since the logistic population model is fairly basic, it is possible to solve it using the separation of variables method. Doing this yields the solution

$$y(t) = \frac{Ky_0e^{rt}}{K + y_0(e^{rt} - 1)} \quad (2.5)$$

where the constants  $K, r > 0$  and  $y(0) = y_0$  such that  $y_0 \geq 0$  and  $t \geq 0$ . Examples of various solution curves are depicted in 3.

Alternatively, the solutions to the Logistic Population Model can take the form

$$y(t) = \frac{K}{1 + \left(\frac{K-y_0}{y_0}\right)e^{rt}}$$

**2.3. The Competitive Lotka-Volterra Model.** Having covered the logistic population model in detail, we can now advance on to discussing the Competitive Lotka-Volterra Model. This model is well known in the study of population dynamics, and can be categorized as a subset of the equations that are included in the generalized Lotka-Volterra model of theoretical ecology.

To begin, we will consider the competitive Lotka-Volterra model in the case of having only two competing species, with equations given by

$$\dot{y}_1(t) = r_1y_1 \left( \frac{K_1 - y_1 - a_{12}y_2}{K_1} \right) \quad (2.6)$$

$$\dot{y}_2(t) = r_2y_2 \left( \frac{K_2 - y_2 - a_{21}y_1}{K_2} \right) \quad (2.7)$$

Like stated previously, there is some carry-over between the Logistic population model and the competitive Lotka-Volterra equations. In the competitive Lotka-Volterra model, we can first observe the two species' populations,  $y_2(t)$  and  $y_1(t)$ . (It should also be noted that the equations for both populations are symmetric). Like before, we see  $r_1$  and  $r_2$  representing the growth rates for each population, and similarly, we have  $K_1$  and  $K_2$  as constants representing the carrying capacities for each population. However, in the competitive Lotka-Volterra model, we notice that there is an addition of the term  $\frac{-a_{12}y_2}{K_1}$  in 2.6 and  $\frac{-a_{21}y_1}{K_2}$  in 2.7. The constants  $a_{12}$  and  $a_{21}$  represent the

**2.4. The Generalized Lotka-Volterra Equation.** Having covered the most simple Lotka-Volterra models, we can now move on to discussing the generalized Lotka-Volterra equation. This model was independently discovered by Alfred Lotka for research in the field of chemical kinetics approximately a year after Volterra first published his version.

This model has since been used to describe more complex evolutionary systems and dynamics across a theoretically infinite amount of species. More practically speaking, many have used this model to capture various topic (food-web) dynamics, and, as we will later cover, special cases in virology such as superinfection.

The generalized Lotka-Volterra equation is given by Nowak [Now06] as:

$$\frac{dy_i}{dt} = y_i \left( r_i + \sum_{j=1}^n y_j b_{ij} \right), \quad i = 1, \dots, n. \quad (2.8)$$

In the generalized Lotka-Volterra equation,  $y_i$  denotes the population of the  $i$ th species. Similar to the previous set of equations, we also see that  $r_i$  represents the growth rates (or

death rates, when negative) of every population, analogous to  $\alpha$  and  $\delta$  in the basic model and again allowing for exponential growth (or decay) in the absence of populations of other species. Furthermore, we see that  $b_{ij}$  is representative of the rate of predatory interaction, analogous to  $\beta$  and  $\gamma$  in the basic equation.

While this format most easily allows the connections between the basic Lotka-Volterra model and the generalized model to be comprehended, the system is better represented through matrices. The short-hand for this is as follows:

$$\dot{\mathbf{y}} = \mathbf{D}(\mathbf{y})(\mathbf{r} + \mathbf{A}\mathbf{y}) \quad (2.9)$$

Here,  $\mathbf{y}$  represents the column vector of  $y_i(t)$  - that is, populations of species  $1, \dots, n$  at time  $t$ . Likewise,  $\dot{\mathbf{y}}(\mathbf{t})$  represents the column vector containing all  $\frac{dy_i}{dt}$ . Additionally,  $\mathbf{D}(\mathbf{y})$  represents the diagonal matrix with entries of the vector  $\mathbf{y}$  on the diagonal, analogous to the factor of  $(y_i)$  in (2.8). We also have  $\mathbf{r}$  as the column vector of inherent growth rates, again analogous to  $r_i$  in non-matrix form of the generalized Lotka-Volterra equation. Finally, we have  $\mathbf{A}$  which is an  $n \times n$  matrix the rates of predatory interaction.

### 3. BASICS OF VIROLOGY AND SUPERINFECTION

**3.1. The Basic Model of Infection.** Having introduced the basic and generalized Lotka-Volterra model, we can now continue to cover the basic differential equations describing virology, as well as the application of Lotka-Volterra equations in the context of superinfection.

To begin, it is helpful to consider an extremely basic model as presented by Nowak. Like many others, this model also makes several assumptions that would be false in a realistic setting, among these that there is a single, closed population, an individual can become instantaneously infected, and the environmental setting has no bearing on infection rates - that is, individuals are mixed and interact randomly and constantly. Its limitations often cause it to be useless for most real-world applications, but it provides a base on top of which more complicated models can be built.

The equations [NM00] are as follows:

$$\frac{dx}{dt} = k - ux - \beta xy \quad (3.1)$$

$$\frac{dy}{dt} = y(\beta x - u - v) \quad (3.2)$$

The equations above consider a model in which there is a single species split into two separate populations: an infected population and a susceptible population. The susceptible population is represented by  $x$  (meaning that it is correlated with the top equation). Perhaps redundantly,  $y$  represents the infected population, which must therefore be correlated with the bottom equation.

In the top equation,  $k$  represents the growth rate of the susceptible population, typically through immigration. In both equations,  $u$  is used to represent the natural death rate, occurring in both equations because both represent the same species. Again, in both equations, there is a  $\beta xy$  term that is used to describe the growth rate of the infected population. We can explain the presence of both  $x$  and  $y$  in this term, as the infection rate depends on the

interaction, and therefore size, of both the infected population and the susceptible population. Finally, the term  $vy$  in the bottom equation represents the added death factor that is caused by the virus in the infected population, also known as the virulence of the virus.

As with the basic Lotka-Volterra equation, it is possible to analyze the equilibrium points of this simple system. Beginning with 3.2, we set  $\frac{dy}{dt} = 0$  and obtain

$$0 = y(\beta x - u - v) \quad (3.3)$$

Similarly, we set  $\frac{dx}{dt} = 0$  in 3.1, we have

$$0 = k - x(u + \beta y) \quad (3.4)$$

From 3.3 we have that the the equilibrium point for  $x$  will be

$$\bar{x} = \frac{u + v}{\beta}$$

Substituting this value into the 3.4, we have

$$0 = k - \left(\frac{u + v}{\beta}\right)(u + \beta y)$$

Solving for  $y$  yields

$$\left(\frac{1}{\beta}\right)\left(\frac{\beta k}{u + v} - u\right) = y$$

And simplifying, we then have

$$y = \frac{\beta k - u(u + v)}{\beta(u + v)}$$

Therefore, the point of equilibrium for this system is given by the following:

$$\bar{x} = \frac{u + v}{\beta}, \quad \bar{y} = \frac{\beta k - u(u + v)}{\beta(u + v)} \quad (3.5)$$

Also important to consider is the reproductive ratio,  $R_0$  of this model. The reproductive ratio is a commonly used metric in epidemiological studies that describes the transmissibility of a virus. In more complex settings, the reproductive ratio can accommodate underlying factors in disease spread including those of behavior, environment, etc. Accounting for these often make calculating the reproductive ratio particularly difficult, and as such, it is rarely measured directly. Additionally, the reproductive ratio should not be used alone as a full measure of the danger of a particular virus. In this case, the simplicity of this model aids with this calculation.

The reproductive ratio is defined to be the number of new infections caused if a single infected host were to be introduced to the entire susceptible population.

As given by Nowak, the reproductive ratio of this system is

$$R_0 = \frac{\beta k}{u(u + v)}$$

It is important to note that if  $R_0$  is less than one, then the virus cannot spread. However, if the reproductive ratio is greater than one, then the virus will spread exponentially, eventually reaching the equilibrium point (3.5).



**3.2. Competitive Model of Infection.** The Competitive model of infection that is discussed here is based heavily on the previous basic model of infection. However, the models differ in the situations that they represent: now being introduced is a second type of virus, creating competition within the susceptible population. Despite this addition, many of the previous limitations on the model remain the same - that is, we are assuming that infection is instantaneous (i.e. immediately after contraction, an individual becomes contagious), that there is no genetic mutation of the viruses or development of immunity, and that the environment of the population has negligible effect on the spread of the virus (i.e. the population mixes randomly and constantly).

The simple competitive model [NM00] can be written as such:

$$\frac{dx}{dt} = k - ux - x(\beta_1 y_1 + \beta_2 y_2) \quad (3.6)$$

$$\frac{dy_1}{dt} = y_1(\beta_1 x - u - v_1) \quad (3.7)$$

$$\frac{dy_2}{dt} = y_2(\beta_2 x - u - v_2) \quad (3.8)$$

Many of the notation carries over from the previous model. Again, we have that  $x$  is the susceptible population, with infected populations of  $y_1$  and  $y_2$ . We again have a constant immigration rate  $k$  into the uninfected population, as well as a constant death rate,  $u$ , affecting all subpopulations in this model. Continuing, we have  $\beta_1$  and  $\beta_2$ , representing the infection rate of both viruses. Finally, the terms  $v_1$  and  $v_2$  are used to denote the virulence of both populations.

As discussed previously, we can also write the reproductive ratios of both strains of viruses in the competitive model:

The equilibrium points in the competitive model of infection are as follows:

To begin, the trivial case in which

$$\bar{x} = 0 \quad \bar{y} = 0$$

#### 4. LOKTA-VOLTERRA EQUATIONS IN SUPERINFECTION

#### 5. APPLICATIONS WITH COVID

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