

Lotka-Volterra equations in Superinfection

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Basic Lotka-Volterra Model

The most simple Lotka-Volterra model is a set of first order ordinary differential equations used to describe predator-prey dynamics:

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

$$\dot{y} = -\delta y + \gamma xy$$

Equilibria of Basic Lotka-Volterra Model

The system has the following equilibria:

$$\bar{x} = 0, \quad \bar{y} = 0 \quad (1)$$

$$\bar{x} = \frac{\delta}{\gamma}, \quad \bar{y} = \frac{\alpha}{\beta} \quad (2)$$

Solutions to Basic Lotka-Volterra Model

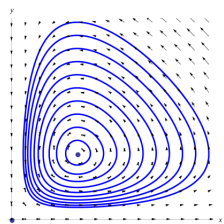


Figure: A phase portrait of the Predator-Prey Lotka-Volterra Equations. Note the periodic orbits surrounding a critical point.

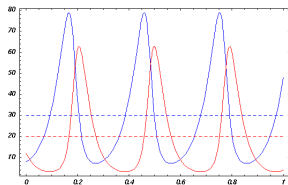


Figure: Solutions to the Lotka-Volterra Equations with red representing predators, blue representing prey. The parameters used here are: $x_0 = 8$, $y_0 = 12$, $\alpha = 20$.

Logistic Equation

Basic Logistic Equation modelling population growth

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

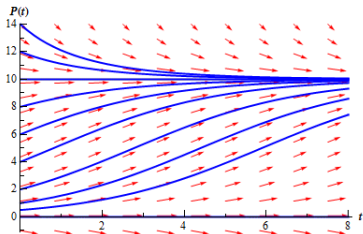


Figure: A phase portrait of the Logistic Population Model. The parameters are $r = \frac{1}{2}$ and $K = 10$. Note the change in concavity at $\frac{K}{2} = 5$.

Competitive Lotka-Volterra Equation

This is the competitive Lotka-Volterra Model describing population dynamics between two species in an environment with a carrying capacity, K .

$$\dot{y}_1(t) = r_1 y_1 \left(\frac{K_1 - y_1 - a_{12} y_2}{K_1} \right) \quad (3)$$

$$\dot{y}_2(t) = r_2 y_2 \left(\frac{K_2 - y_2 - a_{21} y_1}{K_2} \right) \quad (4)$$

Generalized Lotka-Volterra Equation

The generalized Lotka-Volterra Equation has since been used to describe more complex evolutionary systems and dynamics across a theoretically infinite amount of species.

$$\frac{dy_i}{dt} = y_i \left(r_i + \sum_{j=1}^n y_j b_{ij} \right), \quad i = 1, \dots, n. \quad (5)$$

Basic Model of Infection

This is the basic model of infection with a single virus within a population split into infected and susceptible

$$\frac{dx}{dt} = k - ux - \beta xy \quad (6)$$

$$\frac{dy}{dt} = y(\beta x - u - v) \quad (7)$$

Competitive Model of Infection

This is the competitive model of infection with multiple viruses within a population split into infected and susceptible

$$\frac{dx}{dt} = k - ux - x(\beta_1 y_1 + \beta_2 y_2) \quad (8)$$

$$\frac{dy_1}{dt} = y_1(\beta_1 x - u - v_1) \quad (9)$$

$$\frac{dy_2}{dt} = y_2(\beta_2 x - u - v_2) \quad (10)$$

The Basic Model of Superinfection

Superinfection is the scenario in which an already-infected host is infected with a second virus strain. It can be represented with the following ODE system:

$$\begin{aligned}\dot{x} &= k - ux + x \sum_{i=1}^n \beta_i y_i \\ \dot{y} &= y_i \left(\beta_i x - u - v_i + s \beta_i \sum_{j=1}^{i-1} -s \sum_{j=i+1}^n \beta_j y_j \right)\end{aligned}$$

Reproductive Ratio in Superinfection

The reproductive ratio is the number of new cases generated if a single infected individual should enter a susceptible population.

$$R_0 = \frac{akv_i}{u(c + v_i)(u + v_i)}$$

This gives us that optimal virulence is:

$$v_{opt} = \sqrt{cu}$$

An Analytical Model of Superinfection

If we assume $k = ux + uy + \sum_{i=1}^n v_i y_i$ and $x + y = 1$, we have

$$\dot{y} = y_i \left(\beta_i (1 - y) - u - v_i + s \left(\beta_i \sum_{j=1}^{i-1} y_j - \sum_{j=i+1}^n \beta_j y_j \right) \right), \quad i = 1, 2, \dots, n \quad (11)$$

An Analytical Model of Superinfection Cont.

This can be rewritten as a Generalized Lotka-Volterra Equation of the form

$$\dot{y} = y_i \left(R_i + \sum_{j=1}^n A_{ij} y_j \right), \quad i = 1, 2, \dots, n$$

Where $R_i = \beta_i - v_i - u_i$ and

$$A = - \begin{bmatrix} \beta_i & \beta_1 + s\beta_2 & \beta_1 + s\beta_3 & \dots & \beta_1 + s\beta_n \\ \beta_2(1-s) & \beta_2 & \beta_2 + s\beta_3 & \dots & \beta_2 + s\beta_n \\ \beta_3(1-s) & \beta_3(1-s) & \beta_3 & \dots & \beta_3 + s\beta_n \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ n(1-s) & \beta_n(1-s) & \beta_n(1-s) & \dots & \beta_n \end{bmatrix}$$

Competitive Lotka-Volterra Equation in Virology

If we set all infection rates to be equivalent, so $\beta_i = \beta$, we see that

$$\dot{y}_i = y_i \beta \left(1 - y - \frac{v_i + u}{\beta} + s \left(\sum_{j=1}^{i-1} y_{ij} - \sum_{j=i+1}^n y_j \right) \right)$$

(This is a competitive Lotka-Volterra equation). Additionally, the matrix A

becomes $A = - \begin{bmatrix} 1 & 1+s & 1+s & \dots & 1+s \\ 1-s & 1 & 1+s & \dots & 1+s \\ 1-s & 1-s & 1 & \dots & 1+s \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 1-s & 1-s & 1-s & \dots & 1 \end{bmatrix}$

Equilibrium of the Model

If we set $f_i = 1 - \frac{v_i+u}{\beta} - (1-s)y - 2s \sum_{j=i+1}^n y_j$ then the model can be rewritten as

$$\dot{y} = y_i \beta (f_i - s y_i)$$

So, the equilibria can be seen to require that either $y_n = 0$ or $y_n = \frac{f_n}{s}$. Through this, we can define y_n recursively as:

$$y_n = \max\{0, f_n/s\}$$

Hofbauer and Sigmund show that this is the only equilibrium.