Modeling & Applications

Application: Lotka–Volterra predator–prey model

Review. Exponential model, logistic model, ...

The Lotka–Volterra equations

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta x y, \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \delta x y - \gamma y,$$

are used, for instance, in biology to describe the dynamics of two species that interact, one as a predator and the other as prey. (Here, $\alpha, \beta, \gamma, \delta$ are positive real constants.)

Can you put into words how these equations might indeed describe the interactions between predator and prey? To begin with, which of x and y is the predator and which is the prey? What are the equations saying about a population of only predator or only prey?

For more information: https://en.wikipedia.org/wiki/Lotka-Volterra_equations

Example 88. Determine the equilibrium points of the Lotka–Volterra equations and classify their stability. What does this mean for this problem?

Solution. Solving $\alpha x - \beta x y = x(\alpha - \beta y) = 0$ and $\delta x y - \gamma y = (\delta x - \gamma) y = 0$, we find that there are two equilibrium points: $(0, 0)$ and $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$.

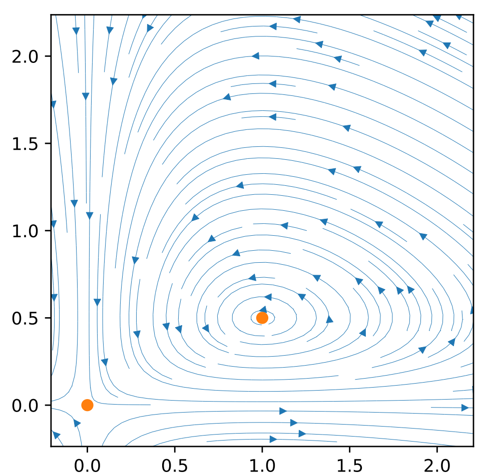
The Jacobian matrix of $\begin{bmatrix} f \\ g \end{bmatrix} = \begin{bmatrix} \alpha x - \beta x y \\ \delta x y - \gamma y \end{bmatrix}$ is $J = \begin{bmatrix} f_x & f_y \\ g_x & g_y \end{bmatrix} = \begin{bmatrix} \alpha - \beta y & -\beta x \\ \delta y & \delta x - \gamma \end{bmatrix}$.

- At $(0, 0)$, the Jacobian matrix is $J = \begin{bmatrix} \alpha & 0 \\ 0 & -\gamma \end{bmatrix}$. The eigenvalues are α and $-\gamma$.

  Since these are real with opposite signs, $(0, 0)$ ("extinction") is a saddle and, in particular, unstable.

- At $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$, the Jacobian matrix is $J = \begin{bmatrix} 0 & -\beta\gamma/\delta \\ \alpha\delta/\beta & 0 \end{bmatrix}$. The characteristic polynomial is $\lambda^2 + \alpha\gamma$ so that the eigenvalues are $\pm i\sqrt{\alpha\gamma}$.

  Since the eigenvalues are pure imaginary, we cannot immediately predict stability (the equilibrium point of the linearization is a center but our equilibrium point could be either a center or a spiral source/sink). A closer inspection shows that the equilibrium point here is a center (see the comment below). This is confirmed by the following phase portrait for $\alpha = \frac{2}{3}$, $\beta = \frac{4}{3}$, $\gamma = \delta = 1$.



Comment. The equilibrium point $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$ has the interesting feature that the stable population for y (the predator) depends on the growth parameters for x (the prey). This is somewhat paradoxical: for instance, if we increase the birth rate α of the prey (for instance, by improving the environment for the prey), we would expect the long-term population levels of the prey to increase. But our calculations say that this is not the case: instead only the long-term levels of the predator increase. (See the wikipedia article for links with the "paradox of enrichment" and how such effects can indeed be observed in actual populations.)

Comment. Here is one way to conclude that $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$ is a center and, therefore, stable.

We can eliminate t from the DEs to arrive at $\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{(\delta x - \gamma)y}{x(\alpha - \beta y)}$.

In general, solutions to this DE describe the trajectories in our phase plots.

Here, the DE for $\frac{\mathrm{d}y}{\mathrm{d}x}$ is separable: $\frac{\alpha - \beta y}{y}\mathrm{d}y = \frac{\delta x - \gamma}{x}\mathrm{d}x$. Integrating (and using that $x, y > 0$), we find that

$$\alpha \ln(y) - \beta y = \delta \ln(x) - \gamma x + C.$$

This means that the trajectories in our phase portrait are level curves of the function $\alpha \ln(y) - \beta y - \delta \ln(x) + \gamma x$. Since there are no anomalies for $x, y > 0$, these level curves cannot be spiralling towards the equilibrium point (for instance, we can fix values for $x > 0$ and C, and then observe that $\alpha \ln(y) - \beta y = D$ with $D = \delta \ln(x) - \gamma x + C$ has at most two solutions for y and certainly not infinitely many). Thus, the equilibrium point is a center.

Bonus: Two more applications of systems of DEs

Example 89. (epidemiology) Let us indicate the popular SIR model for short outbreaks of diseases among a population of constant size N.

In a SIR model, the population is compartmentalized into $S(t)$ susceptible, $I(t)$ infected and $R(t)$ recovered (or resistant) individuals ($N = S(t) + I(t) + R(t)$). In the Kermack-McKendrick model, the outbreak of a disease is modeled by

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \gamma I, \quad \frac{\mathrm{d}S}{\mathrm{d}t} = -\beta S I, \quad \frac{\mathrm{d}I}{\mathrm{d}t} = \beta S I - \gamma I,$$

with γ modeling the recovery rate and β the infection rate. Note that this is a nonlinear system of differential equations. For more details and many variations used in epidemiology, see:

`https://en.wikipedia.org/wiki/Compartmental_models_in_epidemiology`

Comment. The following variation

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \gamma I R, \quad \frac{\mathrm{d}S}{\mathrm{d}t} = -\beta S I, \quad \frac{\mathrm{d}I}{\mathrm{d}t} = \beta S I - \gamma I R,$$

which assumes "infectious recovery", was used in 2014 to predict that facebook might lose 80% of its users by 2017. It's that claim, not mathematics (or even the modeling), which attracted a lot of media attention.

`http://blogs.wsj.com/digits/2014/01/22/controversial-paper-predicts-facebook-decline/`

Example 90. (military strategy) Lanchester's equations model two opposing forces during "aimed fire" battle.

Let $x(t)$ and $y(t)$ describe the number of troops on each side. Then Lanchester (during World War I) assumed that the rates $-x'(t)$ and $-y'(t)$, at which soldiers are put out of action, are proportional to the number of opposing forces. That is:

$$\begin{bmatrix} x'(t) \\ y'(t) \end{bmatrix} = \begin{bmatrix} -\alpha y(t) \\ -\beta x(t) \end{bmatrix}, \quad \text{or, in matrix form: } \begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} 0 & -\alpha \\ -\beta & 0 \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix}.$$

The proportionality constants $\alpha, \beta > 0$ indicate the strength of the forces ("fighting effectiveness coefficients").

These are simple linear DEs with constant coefficients, which we have learned how to solve.

For more details, see: `https://en.wikipedia.org/wiki/Lanchester%27s_laws`

Comment. The "aimed fire" means that all combatants are engaged, as is common in modern combat with long-range weapons. This is rather different than ancient combat where soldiers were engaging one opponent at a time.