Lotka–Volterra predator–prey 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.

Can you put into words how these equations might indeed describe the interactions between predator and prey? (Here, $\alpha, \beta, \gamma, \delta$ are positive real constants.)

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 97. 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 $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$.

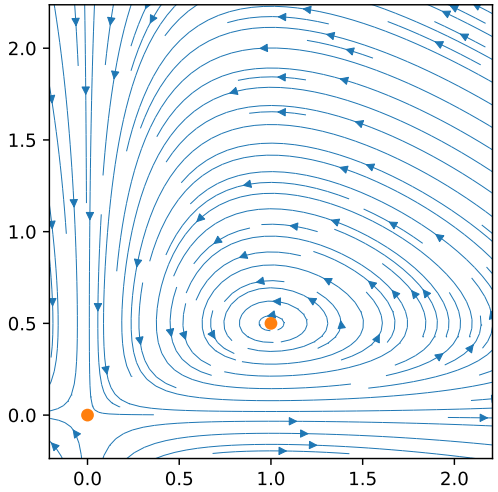
The Jacobian matrix of $\begin{bmatrix} f \\ g \end{bmatrix} = \begin{bmatrix} \alpha x - \beta x y \\ \delta x y - \gamma y \end{bmatrix}$ is $J = \begin{bmatrix} f_x & f_y \\ g_x & g_y \end{bmatrix} = \begin{bmatrix} \alpha - \beta y & -\beta x \\ \delta y & \delta x - \gamma \end{bmatrix}$.

- 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). For instance, increasing the birth rate α of the prey (for instance, by improving the environment for the prey) ends up benefitting the predator but not the prey! (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 this function has 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 98. (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

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

with γ modeling the recovery rate and β the infection rate. Note that this is a non-linear 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

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

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 99. (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.

Some special functions and the power series method

Review: power series

Definition 100. A function $y(x)$ is analytic around $x=x_0$ if it has a power series

$$y(x)=\sum_{n=0}^{\infty} a_n(x-x_0)^n.$$

Note. In the next theorem, we will see that this power series is the Taylor series of $y(x)$ around $x=x_0$.

Power series are very pleasant to work with because they behave just like polynomials. For instance, we can differentiate and integrate them:

- If $y(x)=\sum_{n=0}^{\infty} a_n(x-x_0)^n$, then $y'(x)=\sum_{n=1}^{\infty} n a_n(x-x_0)^{n-1}$ (another power series!).

  We can rewrite the series as $y'(x)=\sum_{n=1}^{\infty} n a_n(x-x_0)^{n-1}=\sum_{n=0}^{\infty}(n+1)a_{n+1}(x-x_0)^n$.

  The result is a power series just like the one we started with. Likewise, for higher derivatives.

- $\displaystyle\int y(x)\mathrm{d}x=\sum_{n=0}^{\infty}\frac{a_n}{n+1}(x-x_0)^{n+1}+C$

Theorem 101. If $y(x)$ is analytic around $x=x_0$, then $y(x)$ is infinitely differentiable and

$$y(x)=\sum_{n=0}^{\infty} a_n(x-x_0)^n \quad \text{with} \quad a_n=\frac{y^{(n)}(x_0)}{n!}.$$

Caution. Analyticity is needed in this theorem; being infinitely differentiable is not enough. For instance, $y(x)=e^{-1/x^2}$ is infinitely differentiable around $x=0$ (and everywhere else). However, $y^{(n)}(0)=0$ for all n.

In particular, if $y(x)$ is analytic at $x=0$, then

$$y(x)=\sum_{n=0}^{\infty}\frac{y^{(n)}(0)}{n!}x^n=y(0)+y'(0)x+\frac{1}{2}y''(0)x^2+\frac{1}{6}y'''(0)x^3+\ldots$$

We have already seen the following example.

Example 102. $e^x=\sum_{n=0}^{\infty}\frac{x^n}{n!}=1+x+\frac{1}{2}x^2+\frac{1}{3!}x^3+\ldots$

Once again, notice how the power series clearly has the property that $y'=y$ (as well as $y(0)=1$).

It follows from here that, for instance, $e^{2x}=\sum_{n=0}^{\infty}\frac{(2x)^n}{n!}=1+2x+2x^2+\frac{4}{3}x^3+\ldots$

Example 103. Determine the power series for $7e^{3x}$ (at $x=0$).

Solution. Instead of starting from scratch, we can use that $e^x=\sum_{n=0}^{\infty}\frac{x^n}{n!}$ to conclude that

$$7e^{3x}=7\sum_{n=0}^{\infty}\frac{(3x)^n}{n!}=\sum_{n=0}^{\infty}\frac{7\cdot 3^n}{n!}x^n=7+21x+\frac{63}{2}x^2+\frac{63}{2}x^3+\frac{189}{8}x^4+\ldots$$

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Example 104. Determine the first several terms in the power series of $\sin(2x^3)$ at $x=0$.

Solution. (direct—unpleasant) If $f(x)=\sin(2x^3)$, then $f'(x)=6x^2\cos(2x^3)$ as well as $f''(x)=12x\cos(2x^3)-36x^4\sin(2x^3)$ and $f'''(x)=12\cos(2x^3)-216x^3\sin(2x^3)+216x^6\cos(2x^3)$.
In particular, $f(0)=0$, $f'(0)=0$, $f''(0)=0$ and $f'''(0)=12$.
It follows that $f(x)=f(0)+f'(0)x+\frac{1}{2}f''(0)x^2+\ldots=0+0x+0x^2+\frac{12}{3!}x^3+\ldots=2x^3+\ldots$

Solution. (via series for sine)

Example 105. Determine the power series for $\cos(x)$ at $x=0$.

Solution. (via DE) $\cos(x)$ is the unique solution to the IVP $y''=-y$, $y(0)=1$, $y'(0)=0$.
It follows that $\cos(x)=\sum_{n=0}^{\infty}a_nx^n$ with $a_n=\frac{y^{(n)}(0)}{n!}$. The DE implies that $y^{(2n)}(x)=(-1)^ny(x)$ and $y^{(2n+1)}=(-1)^ny'(x)$ so that $y^{(2n)}(0)=(-1)^n$ and $y^{(2n+1)}(0)=0$. Consequently, $\cos(x)=\sum_{n=0}^{\infty}\frac{(-1)^n}{(2n)!}x^{2n}$.

Solution. (via Euler's formula) Recall that $e^{ix}=\cos(x)+i\sin(x)$. Since
$$e^{ix}=\sum_{n=0}^{\infty}\frac{(ix)^n}{n!}=\sum_{m=0}^{\infty}\frac{(ix)^{2m}}{(2m)!}+\sum_{m=0}^{\infty}\frac{(ix)^{2m+1}}{(2m+1)!}=\sum_{m=0}^{\infty}\frac{(-1)^mx^{2m}}{(2m)!}+i\sum_{m=0}^{\infty}\frac{(-1)^mx^{2m+1}}{(2m+1)!},$$
we conclude that $\cos(x)=\sum_{n=0}^{\infty}\frac{(-1)^n}{(2n)!}x^{2n}$ and $\sin(x)=\sum_{n=0}^{\infty}\frac{(-1)^n}{(2n+1)!}x^{2n+1}$.

Example 106. Determine the first several terms in the power series of $\sin(2x^3)$ at $x=0$.

Solution. (direct—unpleasant) If $f(x)=\sin(2x^3)$, then $f'(x)=6x^2\cos(2x^3)$ as well as $f''(x)=12x\cos(2x^3)-36x^4\sin(2x^3)$ and $f'''(x)=12\cos(2x^3)-216x^3\sin(2x^3)+216x^6\cos(2x^3)$.
In particular, $f(0)=0$, $f'(0)=0$, $f''(0)=0$ and $f'''(0)=12$.
It follows that $f(x)=f(0)+f'(0)x+\frac{1}{2}f''(0)x^2+\ldots=0+0x+0x^2+\frac{12}{3!}x^3+\ldots=2x^3+\ldots$

Solution. (via series for sine) As derived in the previous example, we have
$$\sin(x)=\sum_{n=0}^{\infty}\frac{(-1)^n}{(2n+1)!}x^{2n+1}=x-\frac{1}{6}x^3+\frac{1}{120}x^5-\ldots$$
It follows that
$$\begin{aligned}\sin(2x^3) &= \sum_{n=0}^{\infty}\frac{(-1)^n}{(2n+1)!}(2x^3)^{2n+1}=\sum_{n=0}^{\infty}\frac{(-1)^n2^{2n+1}}{(2n+1)!}x^{6n+3}\\ &= \frac{2^1}{1!}x^3-\frac{2^3}{3!}x^9+\frac{2^5}{5!}x^{15}-\ldots=2x^3-\frac{4}{3}x^9+\frac{4}{15}x^{15}-\ldots\end{aligned}$$