4-26-1994

The Lotka-Volterra model.

The Lotka-Volterra model describes an ecosystem with two species: **predators** and **prey**. As the names imply, the predators eat the prey, while the prey thrive on vegetation (or something else in the ecosystem which does not come in here). Let x stand for the number of prey and y for the number of predators.

In the absence of predators, the prey population is assumed to increase exponentially:

$$\frac{dx}{dt} = ax, \qquad a > 0.$$

In the absence of prey, the predator population is assumed to decrease exponentially:

$$\frac{dy}{dt} = -cy, \qquad c > 0.$$

With both species present, the predators eat the prey. Assume that the prey population decreases at a rate proportional to the number of encounters between predators and prey. It's reasonable to measure the number of encounters by the product of the predator and prey populations. This gives a factor of bxy. Thus,

$$\frac{dx}{dt} = ax - bxy, \qquad a, b > 0.$$

The predator population increases at a rate proportional to the number of encounters between predators and prey. Again, it's reasonable to measure the number of encounters by the product of the predator and prey populations. This gives a factor of dxy. Thus,

$$\frac{dy}{dt} = -cy + dxy, \qquad c, d > 0.$$

The predator-prey equations are

$$\frac{dx}{dt} = ax - bxy,$$
$$\frac{dy}{dt} = -cy + dxy.$$

The constants a, b, c, and d are assumed to be positive.

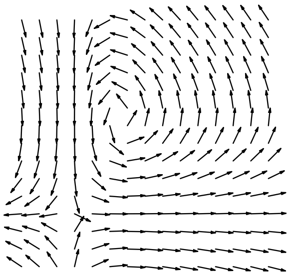
Example. Consider the predator-prey equations

$$\frac{dx}{dt} = x(2 - y),$$
$$\frac{dy}{dt} = y(x - 1).$$

First, I'll find the critical points:

$$\begin{array}{ccc} & x(2-y) = 0 & \\ \swarrow & & \searrow \\ x = 0 & & y = 2 \\ y(x-1) = 0 & & y(x-1) = 0 \\ -y = 0 & & 2(x-1) = 0 \\ y = 0 & & x = 1 \\ (0, 0) & & (1, 2) \end{array}$$

The critical points are $(0, 0)$ and $(1, 2)$.



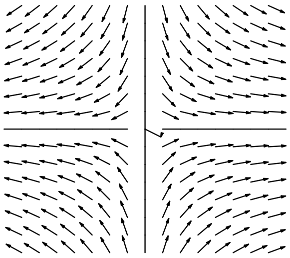
The matrix of partial derivatives is

$$A = \begin{bmatrix} 2 - y & -x \\ y & x - 1 \end{bmatrix}.$$

At $(0, 0)$,

$$A = \begin{bmatrix} 2 & 0 \\ 0 & -1 \end{bmatrix}.$$

$\det = -2$, so the point is a saddle, and it's unstable.



The eigenvalues are 2 and -1; the corresponding eigenvectors are $\langle 1, 0\rangle$ and $\langle 0, 1\rangle$.
At $(1, 2)$,

$$A = \begin{bmatrix} 0 & -1 \\ 2 & 0 \end{bmatrix}.$$

$\det = 2$ and $\operatorname{tr} = 0$. This is an indeterminate case: The point could be either a center or a spiral.

Why is this? Recall that to get the linear system above, I neglected higher order terms from the original system. The problem is that in the case where $\operatorname{tr} = 0$, a small perturbation of the system can change the system from a center to a spiral.

$$\vec{x}\,' = \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \vec{x}$$

is a center. But if $\epsilon > 0$ is a small number,

$$\vec{x}\,' = \begin{bmatrix} \epsilon & 1 \\ -1 & \epsilon \end{bmatrix} \vec{x}$$

is a spiral.

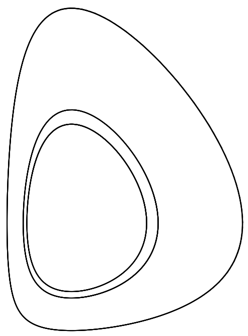
Thus, the higher order terms might be enough to change the type of the critical point.

However, it's possible (but not trivial) to show that for the predator-prey equations, the solutions which appear to go around the critical point in the first quadrant really are **cycles** — periodic solutions. Thus, the point is a stable center.

Here's some empirical evidence for this claim. I used *Mathematica*'s `Runge-Kutta[]` function to plot the solution curves which pass through $(1, 1)$, $(2, 2)$, and $(3, 3)$:

```
cycle1 = RungeKutta[{2x - x y, x y - y}, {x, y}, {2.0, 2.0},
    {20, 0.05}];
cycle2 = RungeKutta[{2x - x y, x y - y}, {x, y}, {1.0,1.0},
    {20, 0.05}];
cycle3 = RungeKutta[{2x - x y, x y - y}, {x, y}, {3.0, 3.0},
    {20, 0.05}];

Show[Graphics[{Line[cycle1], Line[cycle2],
    Line[cycle3]}], AspectRatio->Automatic]
```



I get 3 apparently closed curves.

Here's another approach.

$$\frac{dy}{dx} = \frac{\dfrac{dy}{dt}}{\dfrac{dx}{dt}} = \frac{y(x-1)}{x(2-y)}.$$

Separate variables and integrate:

$$\int \frac{2-y}{y}\,dy = \int \frac{x-1}{x}\,dx,$$

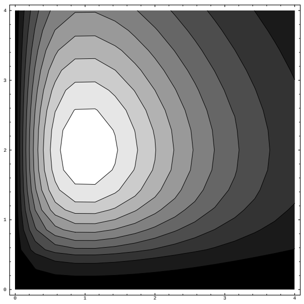
$$2\ln y - y = x - \ln x + c,$$

$$y^2 e^{-y} = \frac{c_0 e^x}{x},$$

$$xy^2 e^{-y} e^{-x} = c_0.$$

I get different solutions by changing the value of the constant c_0. This is the same as asking for the *level curves* of the function $f(x, y) = xy^2 e^{-y} e^{-x}$:

```
ContourPlot[x y^2 E^(-y) E^(-x), {x, 0, 4}, {y, 0, 4}]
```



Again, it appears that the solution curves are closed curves. From the field plot, they circulate counterclockwise around the critical point.

What does this mean? It means that the predator and prey populations *oscillate*. This makes sense: As the number of prey increases, the predators have more food. The number of predators increases. As they snarf more prey, the number of prey decreases. With less food, the number of predators decreases. With fewer enemies, the number of prey increases. And so on.

There is some evidence for this kind of cyclic behavior in real ecosystems; the case of the Canadian lynx and the snowshoe hare is documented in [1]. However, because real ecosystems are not closed systems, there is some question as to whether the cyclic phenomena actually results from a predator-prey relationship. □

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[1] C. Elton and M. Nicholson, The ten-year cycle in numbers of lynx in Canada, *J. Anim. Ecol.*, 11(1942), 215-244.