ES.1803 Topic 30 Notes

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30 Applications to population biology

30.1 Modeling examples

30.1.1 Volterra predator-prey model

The Volterra predator-prey system models the populations of two species with a predator-prey relationship. The equations are

$$\begin{aligned} x' &= \quad ax - pxy = \quad x(a - py) \qquad &(x = \text{prey population}) \\ y' &= -by + qxy = y(-b + qx) \qquad &(y = \text{predator population}), \end{aligned}$$

where a, b, p, q are all positive constants.

Notice, if $y = 0$, then there is no predator and the prey population grows exponentially. If $x = 0$, then there is no prey and the predator population decays exponentially.

It is easy to find that there are two critical points

Critical points: $(0, 0)$, $\left(\dfrac{b}{q}, \dfrac{a}{p}\right)$.

Volterra's Principle: Looking at the critical point $(b/q, a/p)$ we see:

If you increase a (the growth rate of prey) this leaves the equilibrium for x (the prey population) unchanged but increases the equilibrium for y (the predator population).

Likewise, increasing b (the decay rate of the predator) leaves the equilibrium for y unchanged, but increases the equilibrium for x (the prey population).

Volterra was studying fish and sharks. His principle says that if you want to increase the fish population, you need to catch more sharks. It's not enough to catch fewer fish, since, even though this will increase the growth rate of fish, it will just increase the shark population, which will eat up all the extra fish.

Let's draw a phase portrait for this system by linearizing near the critical points.

$J(0, 0) = \begin{bmatrix} a & 0 \\ 0 & -b \end{bmatrix}$. This has eigenvalues $= a, -b$, with eigenvectors $= \begin{bmatrix} 1 \\ 0 \end{bmatrix}, \begin{bmatrix} 0 \\ 1 \end{bmatrix}$.

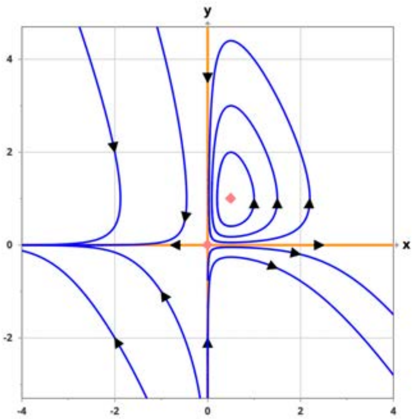
The linearized system is a saddle. It is structurally stable, so the nonlinear system also has a saddle at $(0, 0)$, (See plot below).

$J\left(\dfrac{b}{q}, \dfrac{a}{p}\right) = \begin{bmatrix} 0 & -\frac{pb}{q} \\ \frac{qa}{p} & 0 \end{bmatrix}$. This has eigenvalues $\pm i\sqrt{ab}$.

The linearized system is a center. This not structurally stable, so the nonlinear system has either a center, spiral sink or spiral source at $(b/q, a/p)$.

Since $J\left(\dfrac{b}{q}, \dfrac{a}{p}\right)\begin{bmatrix} 1 \\ 0 \end{bmatrix} = \begin{bmatrix} 0 \\ \frac{qa}{p} \end{bmatrix}$, we know that the center or spiral turns counterclockwise.

It turns out the nonlinear system has a center. (The proof of this is given below.) Here is a diagram:



Volterra predator-prey: $x' = ax - pxy, \quad y' = -bx + qxy$
$a = 1,\ b = 1,\ p = 1,\ q = 2$

30.1.2 Fancier predator-prey

Example 30.1. Consider the following predator-prey population model

$$x' = 3x - x^2 - xy$$
$$y' = y - y^2 + xy.$$

(a) Which one of the variables represents the predator population and which the prey?

(b) Describe the population growth of each species in the absence of the other.

(c) Analyze the critical points and use that to sketch a phase portrait.

(d) Describe what happens to the populations over time.

Solution: **(a)** We see that the presence of y, i.e., $y > 0$ decreases the growth rate of x and the presence of x increases the growth rate of y. Therefore, x represents the prey population and y the predator.

(b) If $y = 0$ then $x' = 3x - x^2$. This is a logistic population model with carrying capacity 3. Likewise, if $x = 0$ then $y' = y - y^2$ is a logistic population model. So, in the absence of the other, each population stabilizes at the carrying capacity of its logistic model.

(c) Finding the critical points is relatively easy. The two equations are

$$x' = 3x - x^2 - xy = x(3 - x - y) = 0$$
$$y' = y - y^2 + xy = y(1 - y + x) = 0$$

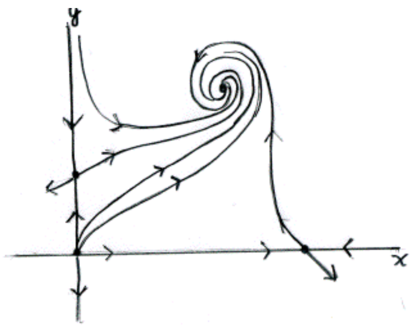
In each equation one of the factors must be 0. This gives four critical points

$$(0,0),\ (0,1),\ (3,0),\ (1,2).$$

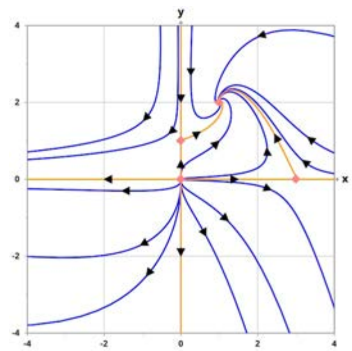
We compute the Jacobian $= \begin{bmatrix} 3 - 2x - y & -x \\ y & 1 - 2y + x \end{bmatrix}$. Next we linearize at each critical point. You should do this yourself. The results are compiled in the following table.

Critical points	$(0,0)$	$(0,1)$	$(3,0)$	$(1,2)$
J	$\begin{bmatrix} 3 & 0 \\ 0 & 1 \end{bmatrix}$	$\begin{bmatrix} 2 & 0 \\ 1 & -1 \end{bmatrix}$	$\begin{bmatrix} -3 & -3 \\ 0 & 4 \end{bmatrix}$	$\begin{bmatrix} -1 & -1 \\ 2 & -2 \end{bmatrix}$
λ	$3, 1$	$2, -1$	$-3, 4$	$(-3 \pm \sqrt{7}\, i)/2$
linear type	source	saddle	saddle	spiral sink
$\mathbf{v}$	Not needed	$\begin{bmatrix} 3 \\ 1 \end{bmatrix}, \begin{bmatrix} 0 \\ 1 \end{bmatrix}$	$\begin{bmatrix} 1 \\ 0 \end{bmatrix}, \begin{bmatrix} 3 \\ -7 \end{bmatrix}$	Not needed
Structural stability	stable	stable	stable	stable

By considering the tangent vector at $(u, v) = (1, 0)$, we see the spiral sink at $(1, 2)$ turns in the counterclockwise direction.



Hand sketch of phase portrait



Computer plot of phase portrait

(d) As long as both populations are initially positive, the model predicts they will go asymptotically to the dynamically stable equilibrium at (1,2).

30.1.3 Proof the Volterra predator-model has closed trajectories

You are not responsible for the following proof.

Claim: In the Volterra predator-prey model the critical point at $(\frac{b}{q}, \frac{a}{p})$ is a center.

More precisely, every trajectory with initial condition (x_0, y_0) in the first quadrant is a closed loop in the first quadrant that circles the critical point.

Proof: Because the positive x and y axis are trajectories, existence and uniqueness implies a trajectory that starts in the first quadrant must stay there –i.e., it can't cross out of the quadrant.

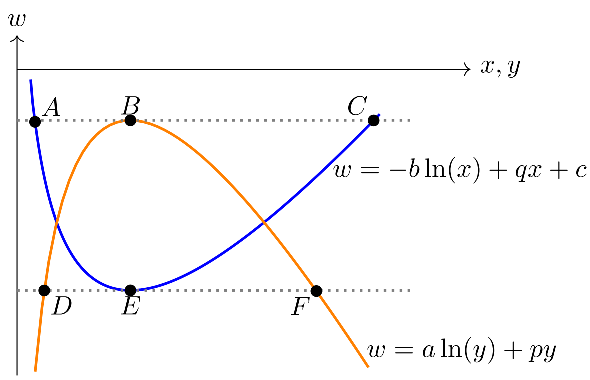
To understand the trajectory in more detail we use the following trick.

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt} = \frac{y(-b+qx)}{x(a-py)}.$$

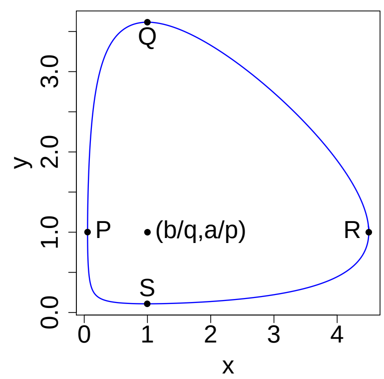
This is a separable equation:

$$dy\, \frac{(a-py)}{y} = dx\, \frac{(-b+qx)}{x} \;\Rightarrow\; a \ln y - py = -b \ln x + qx + c. \qquad (*)$$

This is an implicit equation: each value of c corresponds to a different trajectory.



w vs. x and w vs. y



Phase plane trajectory

Now we have to show that the graph of the implicit function defined in (∗) is a closed loop.

Using 18.01 techniques, we can show that the graphs of

$$w = -b \ln x + qx + c \quad \text{and} \quad w = a \ln y - py$$

are as shown above. Equation (∗) tells us that a point (x, y) is on the trajectory if the $w = a\ln(y) - py$ curve and $w = -b\ln(x) + qx + c$ curve are at the same height.

We can translate this to the phase plane trajectory as follows:

Draw any horizontal line in the first graph. Its points of intersection with the two curves give x and y coordinates of points on the trajectory.

Let A_1, B_1, etc. be the first coordinate of A, B, etc. Then the points A, B and C in the first plot correspond to the points $P = (A_1, B_1)$ and $R = (C_1, B_1)$ in the second plot. The points D, E and F in the first plot correspond to the points $S = (E_1, D_1)$ and $Q = (E_1, F_1)$ in the second plot.

Now pay attention, the closed loop corresponds to the following path along the two curves in the first graph. As the horizontal line goes down from its peak, its intersection points travel from A to E along the x curve and from B to F along the y curve. This means that both x and y are increasing since they are the first coordinates of their respective curves. So this corresponds to the trajectory from P to Q on the second graph.

Continuing, here's a table describing the closed trajectory (proving it's closed).

horizontal line	x, y curves	x, y	trajectory
top to bottom	A, B to E, F	increase, increase	P to Q
bottom to top	E, F to C, B	increase, decrease	Q to R
top to bottom	C, B to E, D	decrease, decrease	R to S
bottom to top	E, D to A, B	decrease, increase	S to P

Easier, indirect argument

There is an easier indirect argument that the trajectory must be closed.

Since, in the left-hand graph above, each horizontal line intersects each curve in at most 2 points there are at most 2 points on a trajectory with the same y-value. This means the trajectory cannot be a spiral. Hence it must be a center.