MATH 448 — Lecture 9

Predator and prey: a nonlinear system

Romeo and Juliet were linear: the matrix's eigenvalues controlled the entire phase plane, not just the behavior near the origin. Today's system is not linear, so linearization is only a local statement — and, once, it will not even be enough to settle what happens locally.

Terms

- **Nullcline**: the curve where one variable's rate of change is zero. Equilibria are exactly where the nullclines for both variables cross.
- **Partial derivative** $\partial f/\partial x$: treat every other variable as a constant and differentiate as usual — the same habit used all semester when differentiating with r and K held fixed, now applied with one state variable held fixed instead.
- **Jacobian**: the matrix of partial derivatives that linearizes a nonlinear system near an equilibrium, playing the same role A played for Romeo and Juliet.

The Lotka–Volterra model

Let x be prey and y be predators:

$$\frac{dx}{dt} = x(\alpha - \beta y), \qquad \frac{dy}{dt} = y(\delta x - \gamma), \qquad \alpha, \beta, \gamma, \delta > 0.$$

Prey grow exponentially absent predators and are killed at a rate proportional to encounters (βxy); predators die absent prey and grow by consuming them (δxy).

Problem 9.1. Find the nullclines of the Lotka–Volterra system and use them to find both equilibria.

Solution. The x-nullcline ($dx/dt = 0$) is $x = 0$ or $y = \alpha/\beta$. The y-nullcline ($dy/dt = 0$) is $y = 0$ or $x = \gamma/\delta$. The nullclines cross at $(0, 0)$ and at $\big(\gamma/\delta,\ \alpha/\beta\big)$ — extinction, and coexistence.

Problem 9.2. Find the Jacobian of the system at the coexistence equilibrium, and classify it.

Solution. The Jacobian is

$$J(x, y) = \begin{pmatrix} \alpha - \beta y & -\beta x \\ \delta y & \delta x - \gamma \end{pmatrix}.$$

At $(x, y) = (\gamma/\delta,\ \alpha/\beta)$, the diagonal entries vanish:

$$J = \begin{pmatrix} 0 & -\beta\gamma/\delta \\ \alpha\delta/\beta & 0 \end{pmatrix}, \qquad T = 0, \qquad D = \alpha\gamma > 0.$$

Since $T = 0$ and $D > 0$, this is a **center** — for *every* choice of $\alpha, \beta, \gamma, \delta > 0$, not just special ones.

A gap in the argument

Every other classification (node, saddle, spiral) is robust: small nonlinear corrections cannot change the qualitative picture near the equilibrium. A **center is the one exception** — a nonlinear system linearizing to a center could actually be a very slowly spiraling equilibrium, in either direction, and the linear approximation alone cannot tell which. Problem 9.2 shows the linearization is a center; it does not yet show the real system has closed orbits.

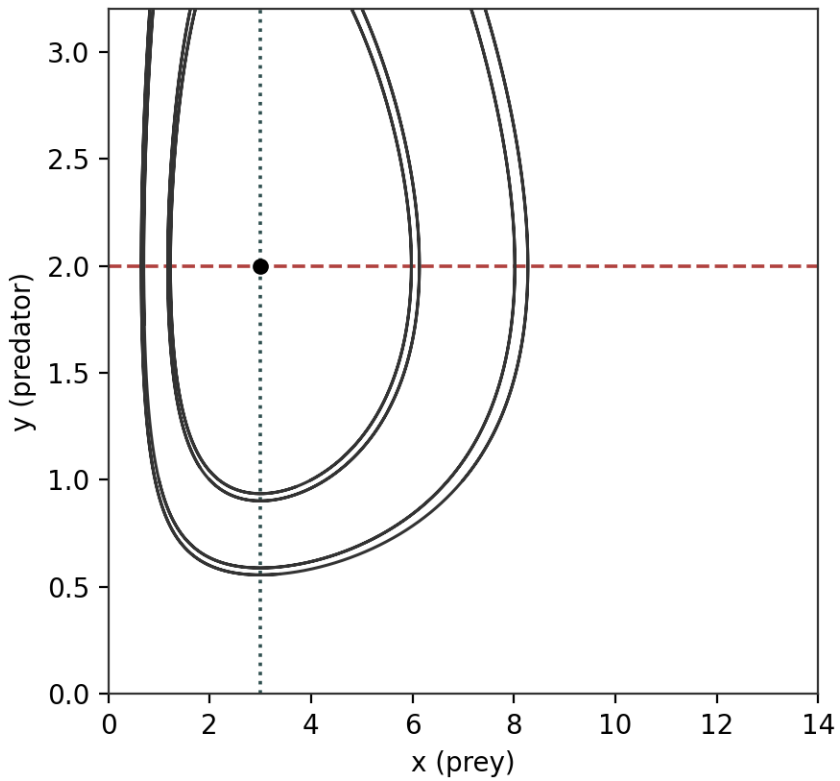
Problem 9.3. Show that $H(x, y) = \delta x - \gamma \ln x + \beta y - \alpha \ln y$ is constant along every trajectory of the Lotka–Volterra system, and explain why this settles the gap above.

Solution. By the chain rule, along a trajectory,

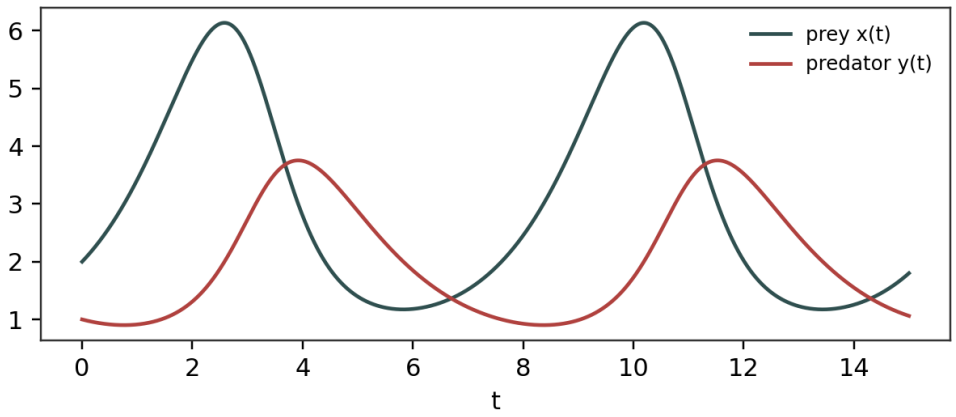
$$\frac{dH}{dt} = \Big(\delta - \frac{\gamma}{x}\Big)\frac{dx}{dt} + \Big(\beta - \frac{\alpha}{y}\Big)\frac{dy}{dt} = (\delta x - \gamma)(\alpha - \beta y) + (\beta y - \alpha)(\delta x - \gamma) = 0.$$

So H never changes along a trajectory: every trajectory stays on a single level curve of H forever. Near the coexistence equilibrium these level curves are closed loops, so trajectories there are genuinely periodic — not just

centers in the linear approximation, but closed orbits in the real, nonlinear system. This required no integration, only differentiation.



Nullclines (dashed/dotted) and several closed trajectories ($\alpha = 1, \beta = 0.5, \gamma = 0.75, \delta = 0.25$), each conserving its own value of H.



Prey and predator over time: predator peaks visibly lag prey peaks, and both cycle with the same period forever.

The dimension count, cashed in. Lecture 4 claimed that two coupled continuous variables can oscillate but never become chaotic. Predator–prey is the concrete instance: real, sustained cycling, and Problem 9.3 shows it is not an artifact of approximation.

Do real populations actually do this? The classic evidence is the Hudson's Bay Company's fur-trading records for Canadian lynx and snowshoe hare, spanning roughly a century.[1] Pelt counts show a lynx-follows-hare

[1] D. A. MacLulich, *Fluctuations in the Numbers of the Varying Hare (Lepus americanus)*, University of Toronto Press, 1937; commonly re-tabulated following E. P. Odum, *Fundamentals of Ecology*, 1953.

cycle strikingly close to the model's prediction — though the data collection method changed partway through the record, and later reanalyses have questioned some of it, so treat the fit as suggestive evidence, not proof.

MATLAB: phase portrait and time series

```
al=1; be=0.5; ga=0.75; de=0.25; % change these to explore
f = @(t,z) [z(1)*(al-be*z(2)); z(2)*(de*z(1)-ga)];

figure
subplot(1,2,1)
[X,Y] = meshgrid(0:0.7:14, 0:0.2:3.2);
dX = X.*(al-be*Y); dY = Y.*(de*X-ga);
quiver(X,Y,dX,dY)
hold on
for x0 = [1 2 4 7]
    [t,Z] = ode45(f, [0 15], [x0;1]);
    plot(Z(:,1), Z(:,2))
end
xlabel('x (prey)'); ylabel('y (predator)')
title('Phase plane')

subplot(1,2,2)
[t,Z] = ode45(f, [0 15], [2;1]);
plot(t, Z(:,1), t, Z(:,2))
xlabel('t'); legend('prey x(t)', 'predator y(t)')
title('Time series')
```

Now do Exercise 9.1 from Homework 6.

Now do Exercise 9.2 from Homework 6.

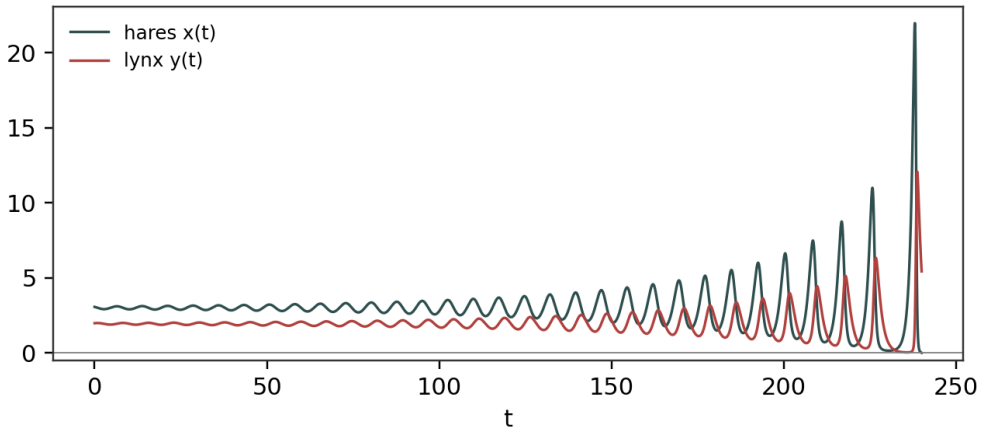
Discussion: breaking the center. A center is fragile: Problem 9.3 shows real Lotka–Volterra orbits are exactly neutrally stable, neither approaching nor leaving the equilibrium. What could be added to the model to make the equilibrium genuinely attracting — or to relocate the equilibrium, or produce more than one?

A natural first guess, echoing Lecture 6, is a harvesting term. Try replacing α by $\alpha - H$ in the code above (harvesting prey at a rate proportional to their population) and recompute the Jacobian at the new equilibrium. Perhaps surprisingly, this alone does *not* break the center — it only moves the equilibrium: the term $-Hx$ is just a change to a coefficient that was already linear in x, so it cannot change the qualitative type of the system, only its parameters. A genuinely different kind of term is needed: one that does work is giving the prey logistic growth in the absence of predators, $\dot{x} = x\big(\alpha(1 - x/K) - \beta y\big)$, instead of unlimited exponential growth — modify the code above and see what appears in place of the closed loops.

Constant-yield harvesting is a genuinely different kind of term, and it does break the center, for either species alone:

- Harvesting hares at a constant rate, $\dot{x} = x(\alpha - \beta y) - H$, gives a coexistence equilibrium with $T = H\delta/\gamma$ — strictly positive for any $H > 0$. It also creates a second equilibrium, $(H/\alpha, 0)$, that did not exist before: hares alone, held at the harvested level, no lynx. As H increases the two equilibria approach each other and collide at $H^* = \alpha\gamma/\delta$.
- Culling lynx at a constant rate, $\dot{y} = y(\delta x - \gamma) - C$, gives $T = C\beta/\alpha$ — strictly positive for any $C > 0$. There is no second equilibrium here: setting $x = 0$ forces $y < 0$, which is not biologically meaningful, so lynx alone (no hares) is never an equilibrium of this model.

Both destabilize the coexistence point into a growing spiral rather than shrinking it into a stable one. Simulating either case — not just linearizing, but actually running the trajectory — shows the oscillation growing cycle over cycle until *whichever species is being harvested* hits zero, robustly across many choices of H (or C) and starting point.



Harvesting hares at a constant rate $H = 0.1$: the oscillation visibly grows cycle over cycle until the hares — the harvested species — collapse to zero, here around $t \approx 240$.

It is tempting to guess that lynx are always the ones at risk, since there is no equilibrium where lynx survive without hares, while hares have no such structural dependence on lynx. That is a real asymmetry in the model, but it is not what decides the outcome here: in simulation it is consistently the *targeted* species that collapses, hares included. The mechanism is closer to Lecture 6 than to that asymmetry: a constant removal term is a fixed drag that does not shrink as the population does, and once the growing oscillation's troughs get low enough, the removal term pushes that trough the rest of the way to zero — the same extinction-threshold mechanism as the 1D constant-harvest model, now compounding with an amplitude that is already growing on its own.

Harvesting both species at once is messier, and does not reduce to comparing H and C: harvesting hares harder than lynx does not reliably mean hares are the ones that collapse. Left as a genuinely open question — try it in the code above.