A Comparison of Four Predator-Prey Differential Equation Models

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Overview

- Predator-prey models are relatively simple nonlinear two-component systems of ordinary differential equations.
- They can serve as good examples for nullcline analysis and stability analysis.
- They offer opportunities for critical examination of mathematical models.
- We consider 4 models:
  1. The Lotka-Volterra model.
  2. The "enhanced" Lotka-Volterra model.
  3. A plankton model that has a fixed total resource level.
  4. The Rosenzweig-MacArthur model.

- Special Addition: *We'll propose an update to the Turing test!*

What Should We Be Looking For?

- Useful models should at least produce the most important realistic outcomes.
  - Stable predator-prey coexistence.
  - Stable prey with predator extinction.
- Other outcomes are biologically possible, but less common.
  - Extinction of both predator and prey.
  - Unstable coexistence (oscillatory populations).

The Lotka-Volterra Model

- Model components:
  - prey biomass X
  - predator biomass Y
- Mechanisms of energy transfer:
  - prey biomass growth at rate RX
  - predator biomass loss at rate MY
  - predation at rate SXY with predator gain $CSXY$

$$\frac{dX}{dT} = RX - SXY = X(R - SY)$$
$$\frac{dY}{dT} = CSXY - MY = Y(CSX - M)$$

- (We use T for time to reserve t for the dimensionless model.)

Scaling the LV Model

$$\frac{dX}{dT} = X(R - SY)$$
$$\frac{dY}{dT} = Y(CSX - M)$$

- Scale X by M/CS, Y by R/S, $1/T$ by R.
  - $X \to \frac{M}{CS}x$, $Y \to \frac{R}{S}y$, $\frac{d}{dT} \to R\frac{d}{dt}$.

$$R\frac{d}{dt}\frac{R}{S}y = \frac{R}{S}y\left(CS\frac{M}{CS}x - M\right).$$

$$x' = x(1 - y) \qquad (1)$$
$$y' = \frac{M}{R}y(x - 1) = \hat{\delta}y(x - 1) \qquad (2)$$

Equilibria for the LV Model

$$x' = x(1 - y)$$

$$y' = \hat{\delta} y(x - 1)$$

- Equilibria are possible end states; these are the points where the derivatives are all 0.
- There are two cases to consider.
  1. We could have $y' = 0$ with $y = 0$. Then $x' = 0$ requires $x = 0$.
  2. We could have $y' = 0$ with $x = 1$. Then $x' = 0$ requires $y = 1$.
- There are two equilibria: an extinction equilibrium Φ: (0,0) and a mutual survival equilibrium XY: (1,1).
- **The Lotka-Volterra model does not allow for the realistic outcome in which only the prey survives!**

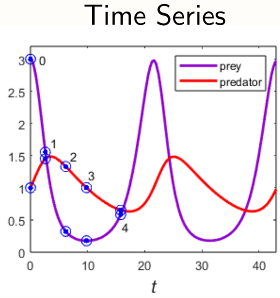
The Lotka-Volterra Model Fatal Flaw

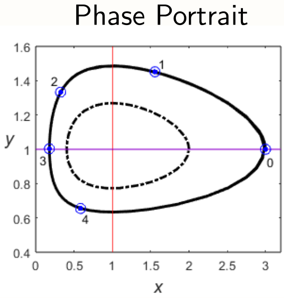
- **Why is the Lotka-Volterra model fatally flawed?**

$$\frac{dX}{dT} = RX - SXY$$
$$\frac{dY}{dT} = CSXY - MY$$

- **Predation is the only mechanism for reducing the prey.**
  - Predator extinction $\Rightarrow$ no limit to prey population.
  - Unlimited prey $\Rightarrow$ unlimited predation.
  - Unlimited predation $\Rightarrow$ predator growth can match any death rate.
- We need another mechanism for prey limitation: **environmental carrying capacity**.

"Cycles" in the Lotka-Volterra Model





- The plot on the right is a **phase portrait**.
  - The numbered points correspond to the numbered points in the time series plot.
  - The violet/red lines are points where x/y are not changing.
- This *appears* to capture the real possibility of oscillations.
  - *But here the amplitude depends on the initial conditions.* ☹

Lotka-Volterra Summary

- Things the Lotka-Volterra model gets wrong:
  1. Extinction of the predator is not possible.
     - Extinction of the prey is not possible either.
  2. There is no stable coexistence equilibrium.
  3. There is a cyclic pattern, but the randomness of the initial data persists for all time.
- Things the Lotka-Volterra model gets right:
  1. Nothing.

The Enhanced Lotka-Volterra Model

Let's add an environmental carrying capacity for the prey.

- Model components:
  - prey biomass X
  - predator biomass Y
- Mechanisms of energy transfer:
  - prey biomass growth at rate $RX\left(1-\frac{X}{K}\right)$
  - predator biomass loss at rate MY
  - predation at rate SXY with predator gain $CSXY$

$$\frac{dX}{dT} = RX\left(1-\frac{X}{K}\right) - SXY = RX\left[\left(1-\frac{X}{K}\right) - \frac{S}{R}Y\right]$$

$$\frac{dY}{dT} = CSXY - MY = Y(CSX - M)$$

Scaling the Enhanced LV Model

$$\frac{dX}{dT} = RX\left(1 - \frac{X}{K} - \frac{S}{R}Y\right)$$
$$\frac{dY}{dT} = Y(CSX - M)$$

- Scale X by K, Y by R/S, T by $1/R$.
  - $X \to Kx$, $Y \to \frac{R}{S}y$, $\frac{d}{dT} \to R\frac{d}{dt}$.

$$R\frac{d}{dt}Kx = RKx\left(1 - x - \frac{S}{R}\frac{R}{S}y\right)$$
$$R\frac{d}{dt}\frac{R}{S}y = \frac{R}{S}y\left(CSKx - M\right).$$

$$x' = x(1 - x - y) \tag{3}$$
$$y' = \frac{CSK}{R}y\left(x - \frac{M}{CSK}\right) = \delta y(x - \mu) \tag{4}$$

Equilibria for the Enhanced LV Model

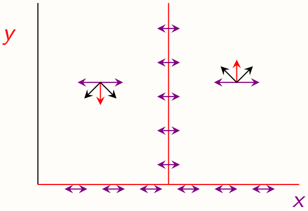
$$x' = x(1 - x - y)$$
$$y' = \delta y(x - \mu)$$

- **There are now 3 equilibria.**
  - With $y = 0$:
    - There is an extinction equilibrium Φ: (0,0).
    - There is also a prey-only equilibrium X: (1,0).
  - With $x - \mu = 0$:
    - There is a co-existence equilibrium XY: $(\mu, 1-\mu)$.
    - But only if $\mu < 1$.
- $\mu < 1$ is a necessary condition for predator survival.

The y-nullclines for the Enhanced LV Model

$$y' = \delta y(x - \mu)$$

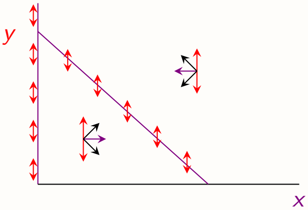
- y-nullclines are curves in the phase plane where y is constant.
  - The y-nullclines are $y = 0, \;\; x = \mu$
- They partition the plane into regions where y is increasing, not changing, and decreasing.
  - This information restricts the paths of solution curves.



The x-nullclines for the Enhanced LV Model

$$x' = x(1 - x - y)$$

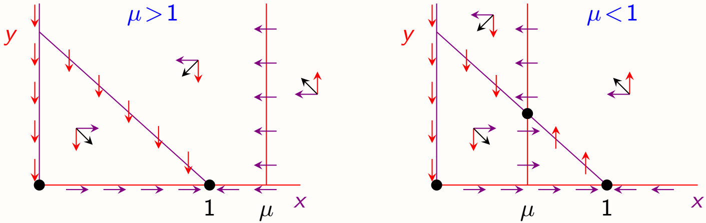
- x nullclines are $x = 0, \;\; x + y = 1$
- They partition the plane into regions where x is increasing, not changing, and decreasing.



The Nullcline Plot for the Enhanced LV Model

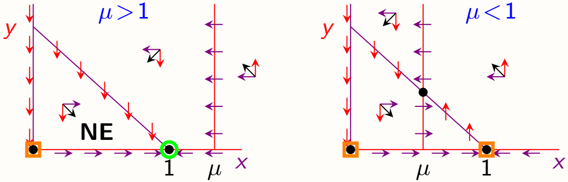
$$x' = x(1 - x - y), \qquad y' = \delta y(x - \mu)$$

- Combining the nullclines determines the arrows on the nullclines and quadrants for the regions.
- The equilibria are points where nullclines of different "color" intersect.



Drawing Conclusions from Nullcline Plots

- The region labeled **NE** is a **no-egress** region.
  - Curves here must all go to the (1,0) equilibrium.
  - All other curves eventually enter the no-egress region.*
- The (1,0) equilibrium is asymptotically stable if $\mu > 1$.



- Circles: [globally] stable (attractor in a no-egress region)
- Squares: unstable (repeller in some region)
- Coexistence equilibrium stability cannot be determined.

ELV Analytical Stability Calculation

$$x' = f(x, y) = x(1 - x - y)$$

$$y' = g(x, y) = \delta y(x - \mu)$$

- The Jacobian matrix is the matrix of partial derivatives of the differential equation functions.

$$J = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} = \begin{pmatrix} (1 - x - y) - x & -x \\ \delta y & \delta(x - \mu) \end{pmatrix}$$

$$J_{\Phi} = \begin{pmatrix} 1 & 0 \\ 0 & -\delta\mu \end{pmatrix}; \quad J_X = \begin{pmatrix} -1 & -1 \\ 0 & \delta(1 - \mu) \end{pmatrix};$$

$$J_{XY} = \begin{pmatrix} -x & -x \\ \delta y & 0 \end{pmatrix}, \quad y = 1 - \mu > 0.$$

ELV Analytical Stability Calculation

- An equilibrium is (locally) stable if $\mathrm{Re}\,\lambda_j < 0 \;\; \forall j$.
  - This happens when $\mathrm{tr}\,J < 0$ and $\det J > 0$.

$$J_\Phi = \begin{pmatrix} 1 & 0 \\ 0 & -\delta\mu \end{pmatrix} \;\Rightarrow\; \lambda_1 = 1.$$

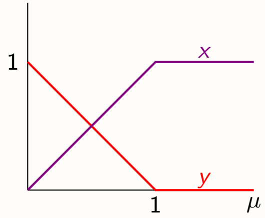
$$J_X = \begin{pmatrix} -1 & -1 \\ 0 & \delta(1-\mu) \end{pmatrix} \;\Rightarrow\; \lambda_1 = -1, \;\; \lambda_2 = \delta(1-\mu)$$

$$J_{XY} = \begin{pmatrix} -x & -x \\ \delta y & 0 \end{pmatrix} \;\Rightarrow\; \mathrm{tr}(J_{XY}) = -x, \;\; \det(J_{XY}) = \delta xy.$$

- Φ unstable; X stable when $\mu > 1$; XY stable when it exists.

Enhanced Lotka-Volterra Model Summary

- There is always a globally stable equilibrium solution with prey survival.
- The dimensionless equilibrium populations depend on the predator death rate parameter μ, but not the time scale parameter δ.



- The predictions cover most scenarios, but not full extinction or oscillation.

The Plankton Food Web Model

- Model components:
  - free nitrogen F
  - phytoplankton biomass X
  - zooplankton biomass Y
- Mechanisms of energy transfer:
  - phytoplankton loss ($X \to F$) at rate KX.
  - zooplankton loss ($Y \to F$) at rate MY.
  - free nitrogen consumption ($F \to X$) at rate QFX.
  - predation ($X \to Y$), at rate SXY.

$$
\begin{aligned}
\frac{dF}{dT} &= KX + MY - QFX \\
\frac{dX}{dT} &= -KX + QFX - SXY \\
\frac{dY}{dT} &= -MY + SXY
\end{aligned}
$$

Scaled Plankton Food Web Model

- Note: $N = F + X + Y$ is constant.

$$\frac{dX}{dT} = -KX + QFX - SXY.$$

$$\frac{dX}{dT} = -KX + Q(N - X - Y)X - SXY$$

$$\frac{dX}{dT} = X\left[(QN - K) - QX - (Q + S)Y\right].$$

- Scaling: $\frac{d}{dT} \to QN\frac{d}{dt}, \quad X \to Nx, \quad (Q+S)Y \to QNy.$

$$x' = x\left(1 - \frac{K}{QN} - x - y\right) = x(1 - \kappa - x - y)$$

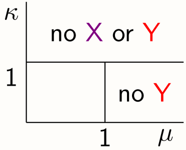
$$y' = \frac{S}{Q}y\left(x - \frac{M}{SN}\right) = \delta y(x - \mu)$$

Plankton Model: Significance of κ (prey death rate)

$$\frac{dX}{dT} = -KX + QFX - SXY, \qquad \kappa = \frac{K}{QN}$$

- Suppose $\kappa > 1$ (and recall $N = F + X + Y$).

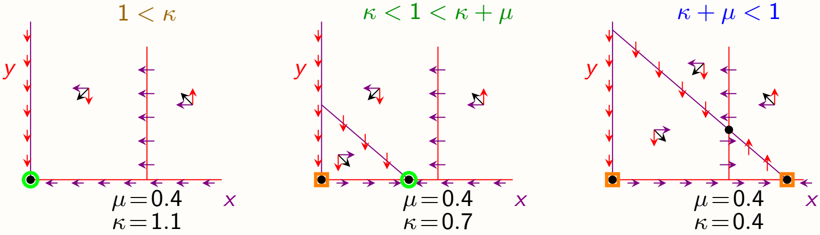
1. $F \leq N \quad \Rightarrow \quad \kappa = \frac{K}{QN} \leq \frac{KX}{QFX}$
2. $1 < \kappa \quad \Rightarrow \quad 1 < \frac{KX}{QFX} \quad \Rightarrow \quad QFX < KX \quad \Rightarrow \quad X' < 0$
3. $X' < 0 \quad \Rightarrow \quad X \to 0 \quad \Rightarrow \quad Y \to 0 \quad \Rightarrow$ Neither persists.



Plankton Model: Nullclines

$$x' = x(1 - \kappa - x - y)$$
$$y' = \delta y(x - \mu)$$

- Three cases: $1 < \kappa$, $\kappa < 1 < \kappa + \mu$, $\kappa + \mu < 1$



Φ is globally stable | X is globally stable | XY unclear

Plankton Model: Stability Analysis

$$x' = x(1 - \kappa - x - y)$$
$$y' = \delta y(x - \mu)$$

- An equilibrium point is asymptotically stable iff

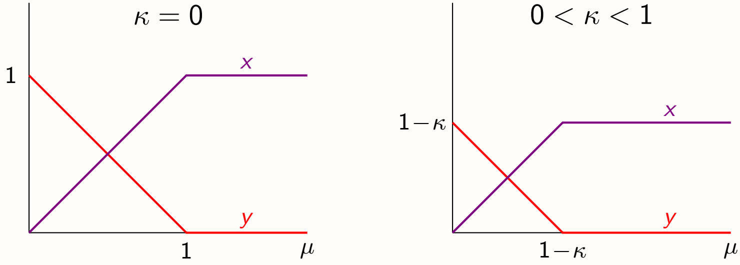
$$\text{tr}(J) < 0, \qquad \det(J) > 0$$

$$J_{XY} = \begin{pmatrix} -x & -x \\ \delta y & 0 \end{pmatrix}, \quad \text{tr}(J_{XY}) = -x, \quad \det(J_{XY}) = \delta xy.$$

- XY is stable whenever it exists.
- Note: We did not need the formulas for x and y.

Effect of κ on Populations

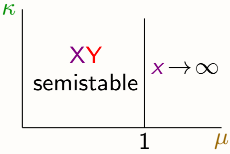
- We have the enhanced Lotka Volterra model if $\kappa = 0$.
- Total population is $1 - \kappa$ until extinction at $\kappa = 1$.



Comparison of Outcomes

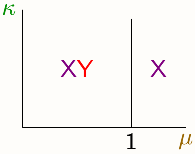
Lotka-Volterra

$$x' = x(1 - x - y)$$
$$y' = \delta y(x - \mu)$$



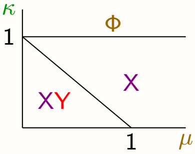
Enhanced LV

$$x' = x(1 - x - y)$$
$$y' = \delta y(x - \mu)$$



Plankton

$$x' = x(1 - \kappa - x - y)$$
$$y' = \delta y(x - \mu)$$



- Larger κ and/or μ decreases viability of zooplankton.
- Larger κ can cause extinction for the whole system.
- The Lotka-Volterra results are ridiculous!!

The Turing Test $\Rightarrow$ The Ledder Test

- The Turing Test is intended to determine whether a machine has achieved intelligence.
- The test is whether the machine can carry on a conversation without being identifiable as a machine.
- Neural networks ("AI" is a misnomer) are close to passing this test, but they have clearly not achieved intelligence.
- My improved test:
  1. Train the neural network with biology and mathematical biology writings that omit the Lotka-Volterra model.
  2. Then ask it to assess the Lotka-Volterra model.
     - If it can make a correct assessment, I'll consider it to have achieved intelligence.

The Holling Type 2 Predation Rate

- We've been using a linear predation rate per unit predator: $P = SX$.
  - This assumes prey can be eaten and digested as quickly as it is found.
- Instead, we could assume that each unit of prey consumed requires time H for eating/digesting.

$$\frac{\text{food}}{\text{total t}} = \frac{\text{search t}}{\text{total t}} \cdot \frac{\text{area}}{\text{search t}} \cdot \frac{\text{food}}{\text{area}}, \qquad \frac{\text{search t}}{\text{total t}} + \frac{\text{handling t}}{\text{total t}} = 1.$$

$$P = F \quad S \quad X, \qquad F + HP = 1.$$

$$P = \frac{SX}{1 + HSX}$$

The Rosenzweig-MacArthur Model

- Model components:
  - prey biomass X
  - predator biomass Y
- Mechanisms of energy transfer:
  - prey biomass growth at rate $RX\left(1-\frac{X}{K}\right)$
  - predator biomass loss at rate MY
  - predation at rate $PY = \frac{SXY}{1+HX}$ with predator gain CPY

$$\frac{dX}{dT} = RX\left(1-\frac{X}{K}\right) - \frac{SXY}{1+HX}, \quad \frac{dY}{dT} = C\frac{SXY}{1+HX} - MY$$

$$x' = x\left(1 - x - \frac{y}{1+hx}\right), \quad y' = \delta y\left(\frac{x}{1+hx} - \mu\right) \tag{5}$$

Equilibria for the RM Model

$$x' = x\left(1 - x - \frac{y}{1+hx}\right)$$

$$y' = \delta y\left(\frac{x}{1+hx} - \mu\right)$$

- There are again 3 equilibria.
  - With $y = 0$:
    - There is an extinction equilibrium Φ: (0,0).
    - There is a prey-only equilibrium X: (1,0).
  - With $\frac{x}{1+hx} - \mu = 0$:
    - There is a coexistence equilibrium XY, but only if $\mu(1+h) < 1$.

$$x = \frac{\mu}{1-\mu h}, \quad y = \frac{1-\mu(1+h)}{(1-\mu h)^2}$$

RM Analytical Stability Calculation

- The Jacobian is a little simpler with an imposed structure.

$$x' = xf(x,y), \qquad f(x,y) = 1 - x - \frac{y}{1+hx}$$
$$y' = \delta y g(x), \qquad g(x) = \frac{x}{1+hx} - \mu$$

$$J = \begin{pmatrix} f + xf_x & xf_y \\ \delta y g' & \delta g \end{pmatrix}$$

$$J_\Phi = \begin{pmatrix} 1 & 0 \\ 0 & -\delta\mu \end{pmatrix} \quad J_X = \begin{pmatrix} -1 & f_y \\ 0 & \delta g(1) \end{pmatrix}$$

$$J_{XY} = \begin{pmatrix} xf_x & -\mu \\ \delta a^2 y & 0 \end{pmatrix}, \quad a = 1-\mu h, \quad f_x = ha^2y-1.$$

RM Analytical Stability Results

$$J_{\Phi} = \begin{pmatrix} 1 & 0 \\ 0 & -\delta\mu \end{pmatrix} \Rightarrow \lambda_1 = 1, \text{ unstable}$$

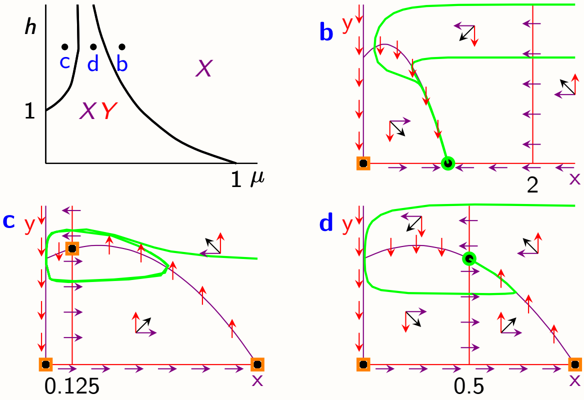
$$J_X = \begin{pmatrix} -1 & f_y \\ 0 & \delta g(1) \end{pmatrix} \Rightarrow \text{stable if } g(1) < 0$$

- X is stable $\iff$ XY does not exist.

$$J_{XY} = \begin{pmatrix} x f_x & -\mu \\ \delta a^2 y & 0 \end{pmatrix} \Rightarrow \text{stable if } f_x < 0$$

- The stability condition for XY is not always satisfied.
  - There are no stable equilibria for some (μ, h).

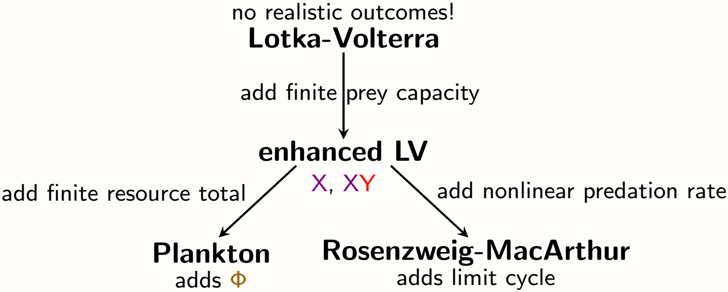
Rosenzweig-MacArthur Results Summary



- Lower μ and/or h benefits the predator.
- Very low μ with high h (high prey capacity) is destabilizing.

Comparison of Models

- How are the models related?
- What realistic outcomes does each model predict?



- More features could be added to make a model that can predict a greater variety of outcomes.

Shameless Self Promotion

- My new book, *Mathematical Modeling for Epidemiology and Ecology*, published by Springer, should be out by May.
- All problems in the book are accessible to students taking a first course in ODEs.
- Contact me at gledder@unl.edu with questions, comments, or a copy of my presentation.