

Lotka-Volterra system of predator-prey

$$\frac{dR}{dt} = aR - cFR, \quad \frac{dF}{dt} = -bF + dFR$$

$R(t)$: the population of prey; $F(t)$: the population of predator

Original Lotka-Volterra problem: the proportion of predatory fish increases and the proportion of prey fish decreases during 1st world war, while the fishing is reduced.

equation with fishing: E is fishing effort, p, q : catchability coefficients for prey and predator

$$\frac{dR}{dt} = aR - cFR - pER, \quad \frac{dF}{dt} = -bF + dFR - qEF$$

Equilibrium solution $(R(E), F(E)) = \left(\frac{b+qE}{d}, \frac{a-pE}{c}\right)$

Proportion: $P = \frac{qEF(E)}{pER(E)}$, decreasing with respect to E

Summary of Lotka-Volterra predator-prey model:

1. Solutions are periodic solutions, and the orbit circles around the equilibrium.
2. The equilibrium represents the average population over different seasons.
3. Volterra's principle: if we kills or removes both prey and predators in proportion to their population sizes, then the average prey population increases while the average predator population decreases.
4. The model is flawed as no stable structure (equilibrium or periodic solution) in the model, thus it cannot be used to explain the stable oscillations in predator-prey interaction.



cottony cushion scale insect (prey, left), vedalia beetle (predator, right)

An application of Volterra Principle on pest control: In 1868 the cottony cushion scale insect was introduced accidentally from Australia to America, and it became a serious pest of citrus in the 1880's. In one of the classical success stories for biological control, cottony cushion scales were completely controlled by the introduction of a ladybeetle called the vedalia beetle. When the insecticide DDT was discovered, it was applied in the hope of further control. But instead the result was an increase in the scale insect population.

Designing better models of predator-prey:

More general predation equation: (prey P , predator Q)

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - h(P)Q$$

$h(P)$ is the “functional response” of predators to prey population

Assumptions:

1. $h(0) = 0$: when the population is zero, there is nothing to harvest
2. $h'(P) \geq 0$: when there is more can be harvested, then the harvest rate is higher

In Lotka-Volterra model: $h(P) = kP$ (linear predation)

Holling's type II functional response $h(P) = \frac{AP}{1 + BP}$

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N}\right) - \frac{AP}{1 + BP}Q$$

Assumptions: The number of predator is assumed to be constant, and they cannot consume more preys when P is large. It takes the predator a certain amount of time to kill and eat each prey. So suppose that in one hour, the predator (a wolf) can catch AP number of prey (rabbits) (it is proportional to P since when P is larger, the wolf has better chance to meet rabbits,) but it needs T hour to handle and eat each rabbit caught. So for all AP rabbits, it takes ATP hours, and in fact the wolf spends $1 + ATP$ hours on these AP rabbits. So in 1 hour, the wolf actually only eats $\frac{AP}{1 + ATP}$ rabbits. We use $B = AT$ as a new parameter in the equation.

Holling's type I model

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - h(P)$$

where $h(P) = aP$ when $0 \leq P \leq P_0$ and $h(P) = aP_0$ when $P > P_0$.

Assumptions: The number of predator is assumed to be constant, and they cannot consume more preys when P is large. Type I is unusual, except for the case of filter-feeding crustacea feeding on algal cells.

Holling's type III model

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - \frac{AP^n}{1 + BP^n}$$

spruce budworm model (lecture 8)

Predator-prey model with Holling type II predation
 (saturating interaction) (non-dimensionalized)

$$\frac{du}{ds} = u(1 - mu) - \frac{uv}{u + 1}, \quad \frac{dv}{ds} = -cv + \frac{puv}{u + 1}.$$

u -nullcline: $u = 0, v = (1 - mu)(u + 1)$ v -nullcline: $v = 0,$
 $u = \frac{c}{p - c}$

Equilibrium points: $(0, 0), (m^{-1}, 0), (\frac{c}{p - c}, \frac{p(p - c - mc)}{(p - c)^2})$.

Case 1: $(p < (m + 1)c)$ Two equilibrium points at $(0, 0)$ and $(m^{-1}, 0)$, and $(m^{-1}, 0)$ is a sink which attracts any initial values.

Case 2: $(p > (m + 1)c)$ Three equilibrium points at $(0, 0), (m^{-1}, 0), (u_0, v_0) = (\frac{c}{p - c}, \frac{p(p - c - mc)}{(p - c)^2})$.

Stability of (u_0, v_0) ?

A brief theory of periodic orbits

Theorem 1 Inside a periodic orbit, there is at least one equilibrium point.

Corollary 2 Let (x_0, y_0) be an equilibrium point. If there is a stable or unstable orbit of this equilibrium going to infinity as $t \rightarrow \pm\infty$, then there is no periodic orbit around this equilibrium point.

Corollary 3 Let (x_0, y_0) be an equilibrium point. If the direction of vector field on the nullclines near (x_0, y_0) is not clockwise or counterclockwise, then there is no periodic orbit around this equilibrium point.

Theorem 4 (Poincaré-Bendixon) If there is a “donut” region (a region without equilibrium point) that the vector field is pointing inside at any point on the boundary, then there is a periodic orbit in the “donut” region.

Corollary 5 If in a region, there is only one equilibrium point which is a source or spiral source, and the vector field is pointing inside at any point on the boundary, then there is a periodic orbit around this equilibrium point.

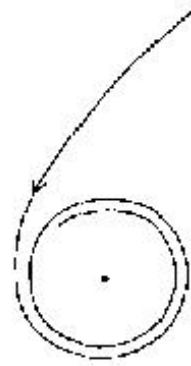
A typical case: the solutions from outside are spiraling in, and the equilibrium point is a spiral source.

Theorem 6 (Hopf bifurcation) If there is a bifurcation occurring that an equilibrium point changes from a spiral sink to spiral source, and the solutions from outside are always spiraling in, then there is a periodic orbit around the spiral source.

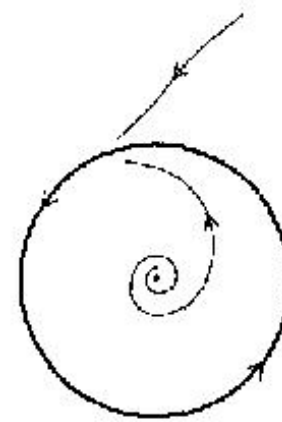
Hopf bifurcation is similar to flip bifurcation for difference equation.



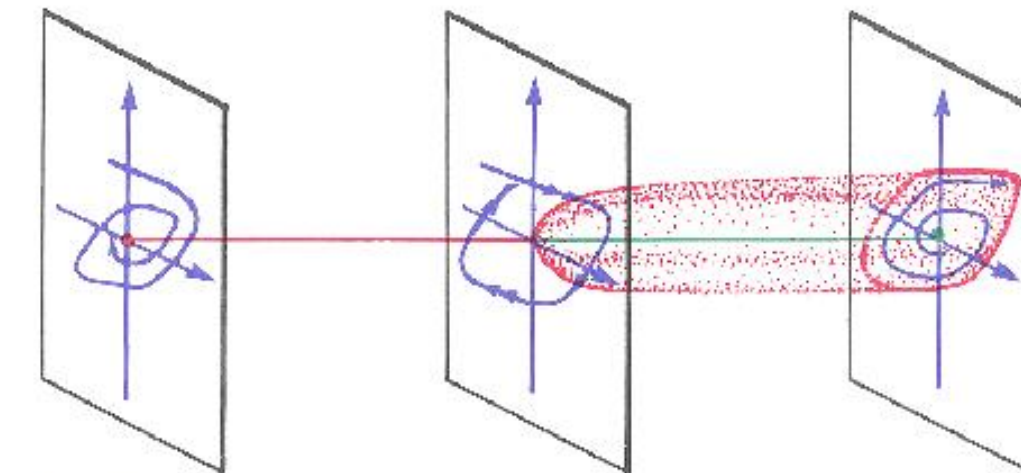
$\beta < 0$



$\beta = 0$



$\beta > 0$



Hopf Bifurcation

$$\frac{du}{ds} = u(1 - mu) - \frac{uv}{u+1}, \quad \frac{dv}{ds} = -cv + \frac{puv}{u+1}.$$

Stability of (u_0, v_0) :

$$J = \begin{pmatrix} \frac{c(p-c-mp-mc)}{p(p-c)} & -\frac{c}{p} \\ p-(m+1)c & 0 \end{pmatrix}$$

Eigenvalue equation: $\lambda^2 - \frac{c(p-c-mp-mc)}{p(p-c)}\lambda + \frac{c}{p}(p-c-mc) = 0$

Spiral sink or sink: $p-c-mp-mc < 0$ (or $m > \frac{p-c}{p+c}$)

Spiral source or source: $p-c-mp-mc > 0$ (or $0 < m < \frac{p-c}{p+c}$)

Conclusion: $m = \frac{p - c}{p + c}$ is where Hopf bifurcation occurs. When $m > \frac{p - c}{p + c}$ but near $\frac{p - c}{p + c}$, (u_0, v_0) is a spiral sink, and all solutions tend to (u_0, v_0) in an oscillating fashion; when m passes $\frac{p - c}{p + c}$ but near $\frac{p - c}{p + c}$, (u_0, v_0) becomes a spiral source, but all solutions away from (u_0, v_0) still tends toward (u_0, v_0) (spiral inward), thus a periodic solution (with small oscillation) emerges around (u_0, v_0) , and it is a limit cycle.

Examples:

$p = 1$, $c = 0.5$, the Hopf bifurcation point is $m = 1/3 \approx 0.33333$

Hopf bifurcation destabilizes the equilibrium (from stable spiral sink to unstable spiral source)

$$\frac{du}{ds} = u(1 - mu) - \frac{uv}{u + 1}, \quad \frac{dv}{ds} = -cv + \frac{puv}{u + 1}.$$

What can cause Hopf bifurcation:

m is small ! m^{-1} is carrying capacity, so that m is smaller implies carrying capacity is larger. Larger carrying capacity for the prey is called enrichment, which seems lead to stabilizing. But instead it leads to Hopf bifurcation and destabilizing of the equilibrium. This is called **paradox of enrichment**