

Lotka–Volterra

Predator–Prey Model

Equations · Assumptions · Equilibria · Stability · Phase plane · Conserved quantity · Volterra's principle · Extensions · Worked numericals · Exam questions · MCQs

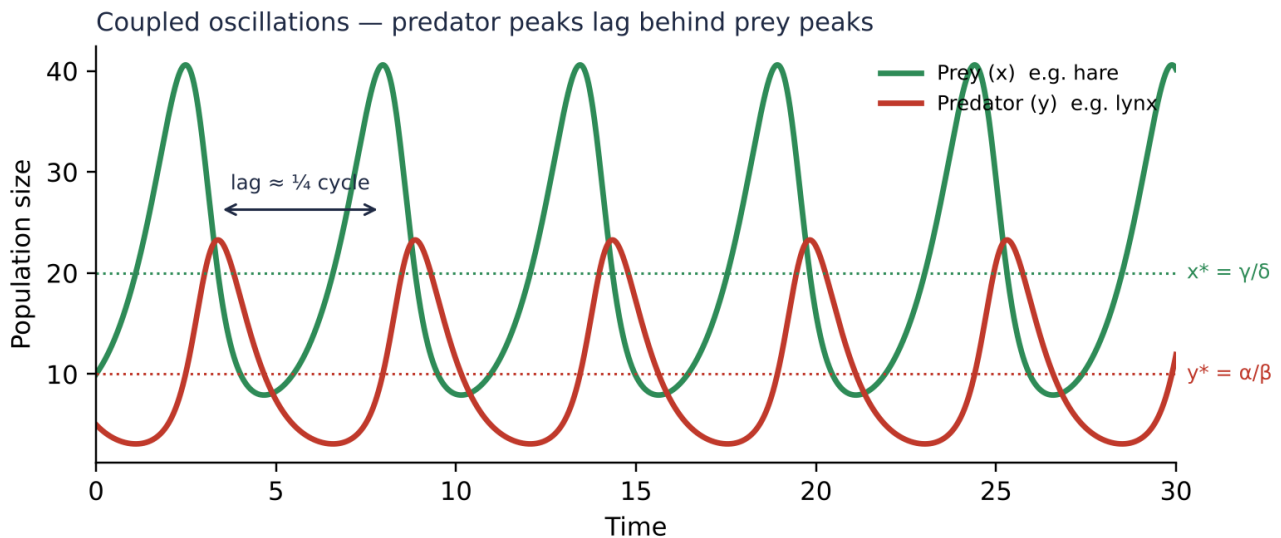


Fig. 1 — Numerical solution ($\alpha = 1$, $\beta = 0.1$, $\delta = 0.075$, $\gamma = 1.5$). Both populations cycle forever; predator peaks trail prey peaks.

At a glance

- Proposed independently by **Alfred J. Lotka** (1925, *Elements of Physical Biology*) and **Vito Volterra** (1926), who was explaining why predatory fish rose in the Adriatic catch during World War I when fishing slowed.
- Two coupled, non-linear first-order ODEs: one for prey, one for predator.
- Key prediction: **neutrally stable, periodic oscillations** with the predator lagging the prey by about a quarter cycle.
- Foundation of theoretical ecology; also used for competition, host–parasitoid, immune–pathogen and even economic models.

01 Assumptions of the model

#	Assumption	Biological meaning
1	Prey has unlimited food	Without predators, prey grows exponentially (no carrying capacity).
2	Predator depends only on this prey	Without prey, predators decline exponentially (starvation).
3	Encounters $\propto x \times y$ (mass action)	Random, well-mixed meeting, like molecules colliding in a solution.

#	Assumption	Biological meaning
4	Linear (Type I) functional response	Each predator eats βx prey per unit time — no satiation, no handling time.
5	Instant conversion of food to offspring	No time lags, no age/stage structure.
6	Constant environment and parameters	No seasonality, no migration, closed system.
7	Continuous, large populations	Deterministic — ignores randomness and individual differences.

02 The equations

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y$$

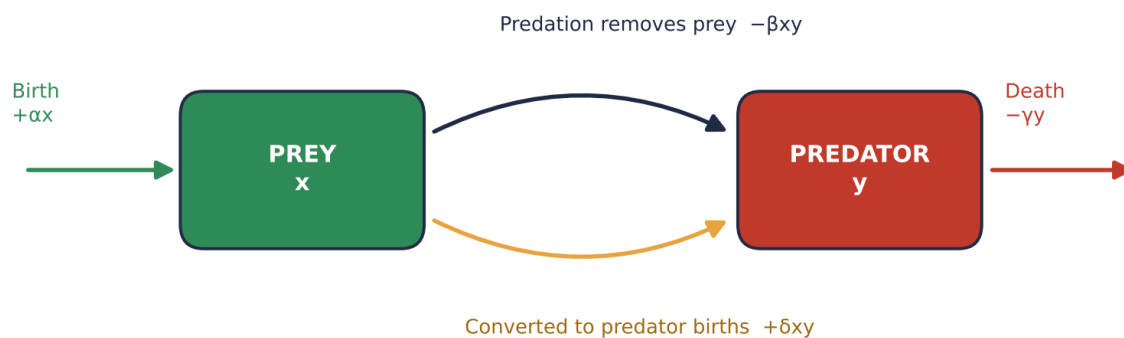


Fig. 2 — Flow diagram: where each term comes from.

Symbol	Name	Units / meaning
x (or N , H)	Prey density	individuals per area
y (or P)	Predator density	individuals per area
α (r)	Intrinsic growth rate of prey	per time; births — natural deaths of prey
β (a)	Predation (attack) rate coefficient	per predator per time; efficiency of capture
δ ($= e\beta$)	Predator conversion/growth coefficient	e = conversion efficiency of eaten prey into new predators
γ (m , q)	Predator mortality rate	per time; death rate when no prey

Reading the terms: αx = prey birth; $-\beta xy$ = prey killed (needs an encounter, so $\propto xy$); $+\delta xy$ = predator births fuelled by eaten prey; $-\gamma y$ = predator death. Note $\delta < \beta$ usually, because only a fraction of eaten biomass becomes new predators (ecological efficiency $\approx 10\%$).

03 Equilibrium points & zero-growth isoclines

Set both derivatives to zero: $x(\alpha - \beta y) = 0$ and $y(\delta x - \gamma) = 0$.

Equilibrium	Meaning	Stability
$E_0 = (0, 0)$	Both extinct	Saddle point (unstable): prey escapes along x-axis, predators die along y-axis
$E^* = (\gamma/\delta, \alpha/\beta)$	Coexistence	Neutral centre : closed orbits around it, neither attracting nor repelling

Remember the 'cross-over' — a favourite exam trap

The **prey** equilibrium $x^* = \gamma/\delta$ is set by **predator** parameters, and the **predator** equilibrium $y^* = \alpha/\beta$ is set by **prey** parameters. So making prey breed faster ($\uparrow \alpha$) raises the average number of *predators*, not prey!

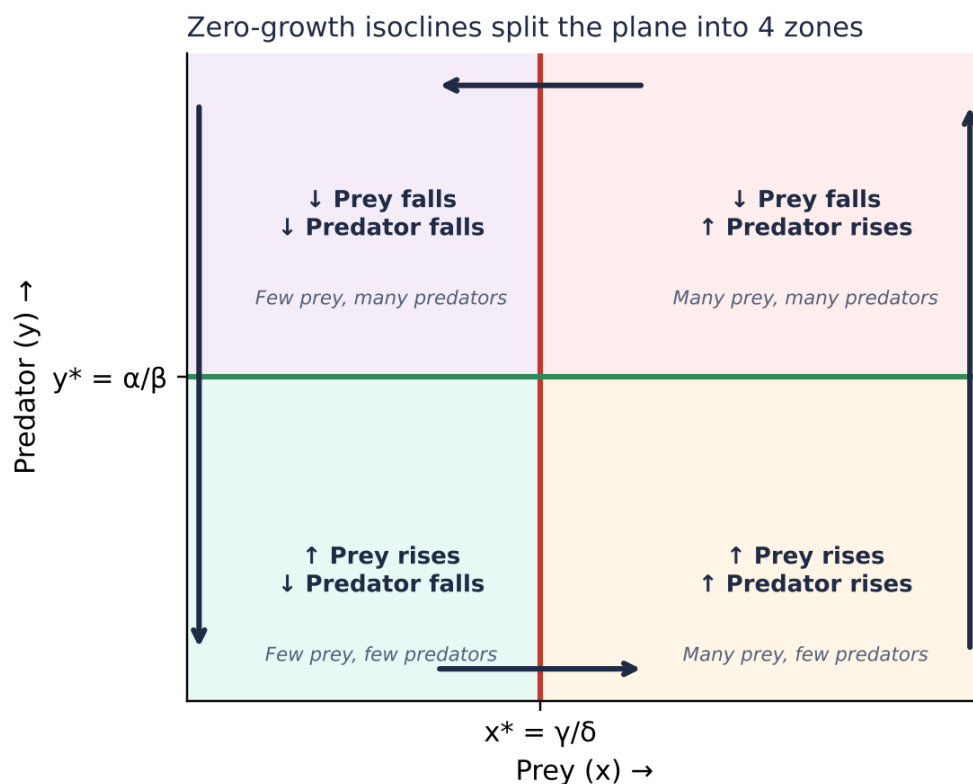


Fig. 3 — Isocline analysis. The vertical line is the predator isocline ($dy/dt = 0$), the horizontal line is the prey isocline ($dx/dt = 0$). Arrows trace the anticlockwise cycle.

The four phases of a cycle: (1) Many prey, few predators → predators multiply. (2) Many predators eat prey down → prey crash. (3) Few prey → predators starve and decline. (4) Few predators → prey recover. Repeat.

04 Linear stability analysis (Jacobian)

J	$\partial/\partial x$	$\partial/\partial y$
$f = dx/dt$	$\alpha - \beta y$	$-\beta x$
$g = dy/dt$	δy	$\delta x - \gamma$

At $(0, 0)$: $J = \text{diag}(\alpha, -\gamma)$. Eigenvalues $\lambda_1 = \alpha > 0$, $\lambda_2 = -\gamma < 0$ → opposite signs → **saddle**. Extinction of both is never approached (except along the y-axis when prey is absent).

At $(\gamma/\delta, \alpha/\beta)$: J^* has zeros on the diagonal, top-right $-\beta\gamma/\delta$, bottom-left $\delta\alpha/\beta$.

$$\text{tr}J^* = 0, \quad \det J^* = \alpha\gamma > 0 \quad \Rightarrow \quad \lambda^2 + \alpha\gamma = 0, \quad \lambda = \pm i\sqrt{\alpha\gamma}$$

Purely imaginary eigenvalues $\Rightarrow$ **centre**. Small oscillations have angular frequency $\omega = \sqrt{\alpha\gamma}$, so the **period** $T \approx 2\pi/\sqrt{\alpha\gamma}$ (exact only for small orbits; large orbits are slower).

Why 'neutral' is a weakness

Imaginary eigenvalues mean linearisation alone can't prove stability — here the conserved quantity V (next section) confirms closed orbits. But a centre is **structurally unstable**: any tiny change to the model (logistic prey, satiation, noise) turns the cycles into spirals or limit cycles. That is why real populations don't follow the classic model exactly.

05 Phase plane & the conserved quantity

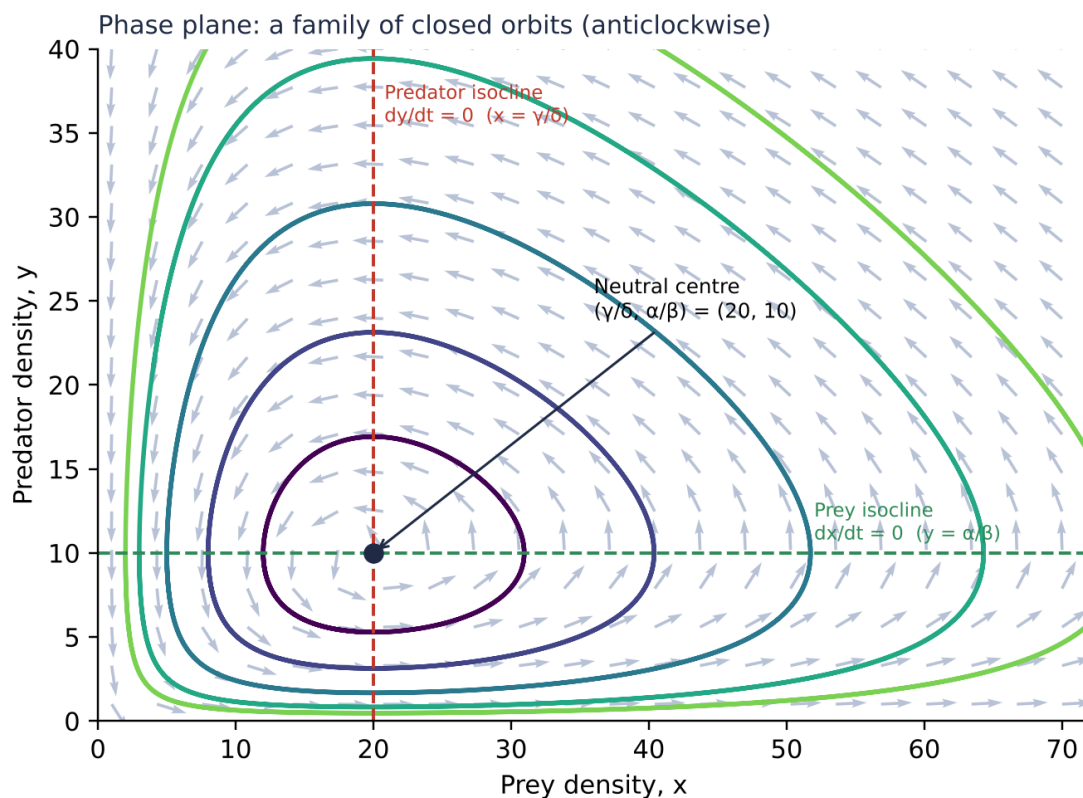


Fig. 4 — Each initial condition gives its own closed orbit. Larger orbits = bigger, sharper booms and crashes.

Divide the two equations to remove time, separate variables and integrate:

$$\frac{dy}{dx} = \frac{y(\delta x - \gamma)}{x(\alpha - \beta y)} \Rightarrow \int \frac{\alpha - \beta y}{y} dy = \int \frac{\delta x - \gamma}{x} dx$$

$$V(x, y) = \delta x - \gamma \ln x + \beta y - \alpha \ln y = \text{constant}$$

V is a **first integral** (constant along every trajectory, like energy in a frictionless pendulum). V has its minimum at the equilibrium, so its level curves are nested closed loops $\Rightarrow$ **every solution is**

periodic. The amplitude depends entirely on the starting populations — the system has no 'preferred' cycle and 'remembers' its initial conditions.

Average over one cycle. Integrate $d(\ln x)/dt = \alpha - \beta y$ over one period T ; since x returns to its start, the left side is zero:

$$\bar{x} = \frac{1}{T} \int_0^T x dt = \frac{\gamma}{\delta} \quad \bar{y} = \frac{1}{T} \int_0^T y dt = \frac{\alpha}{\beta}$$

So the long-term **averages equal the equilibrium values**, whatever the amplitude.

06 Volterra's principle (the fishing paradox)

Add a uniform harvesting/insecticide rate ϵ that kills both species: $\alpha \rightarrow \alpha - \epsilon$ and $\gamma \rightarrow \gamma + \epsilon$. New averages:

$$\bar{x} = (\gamma + \epsilon)/\delta \uparrow \text{ (prey increases)} \quad \bar{y} = (\alpha - \epsilon)/\beta \downarrow \text{ (predator decreases)}$$

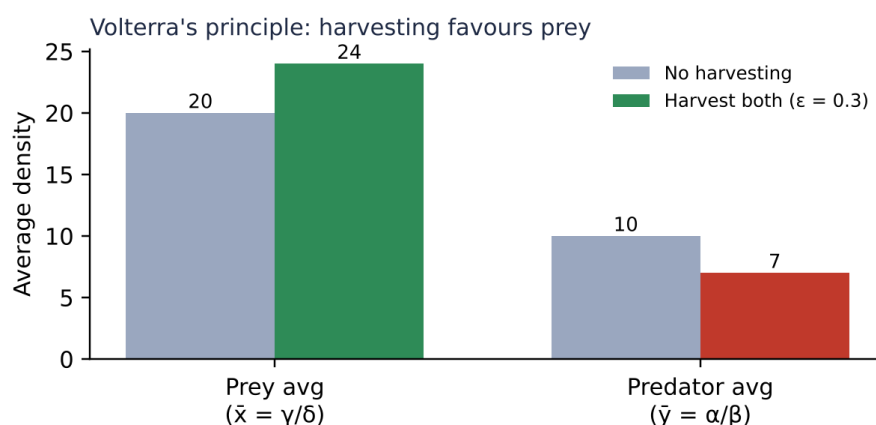


Fig. 5 — Same parameters as Fig. 1 with $\epsilon = 0.3$.

- **Adriatic fisheries (D'Ancona's data):** WWI reduced fishing ($\downarrow \epsilon$) $\rightarrow$ proportion of predatory fish (sharks, rays) in catches rose. Volterra built the model to explain this.
- **Pest control:** a broad-spectrum insecticide that kills both pest and its natural enemy can *increase* the pest — e.g. DDT on citrus allowed cottony-cushion scale to resurge as its predator, the vedalia beetle, was killed.

07 Real-world & experimental evidence

System	Observation	Lesson
Canada lynx & snowshoe hare (Hudson's Bay Co. fur records, ~1845–1935)	~10-year cycles, lynx peaks lag hare peaks	Classic textbook example — but hares also cycle where lynx are absent; food quality and other predators matter too
Gause (1934): <i>Didinium</i> eats <i>Paramecium</i>	In a simple tube, predator ate all prey, then starved $\rightarrow$ both extinct	Coexistence needed refuges (sediment) or periodic immigration

System	Observation	Lesson
Huffaker (1958): predatory mite <i>Typhlodromus</i> & six-spotted mite on oranges	Sustained oscillations only in a complex, patchy arena with barriers	Spatial heterogeneity and dispersal stabilise predator-prey dynamics
Utida (bean weevil & parasitoid wasp)	Several cycles of host-parasitoid oscillation in the lab	Supports coupled oscillations in host-parasitoid systems

08 Limitations & improved models

Limitation	Fix / extension
Prey grows without limit	Logistic prey: $\alpha x(1 - x/K) \rightarrow$ oscillations damp to a stable point (Fig. 6)
Predators never get full	Holling Type II functional response $axy/(1 + ahx)$ (h = handling time)
Neutral cycles (structurally unstable)	Rosenzweig-MacArthur model $\rightarrow$ stable limit cycles (fixed amplitude, independent of start)
Prey-only dependence on prey	Ratio-dependent / Beddington-DeAngelis models include predator interference
No time delays	Delay-differential equations; Nicholson-Bailey (discrete host-parasitoid)
Deterministic, well-mixed	Stochastic & spatial (metapopulation) models; refuges

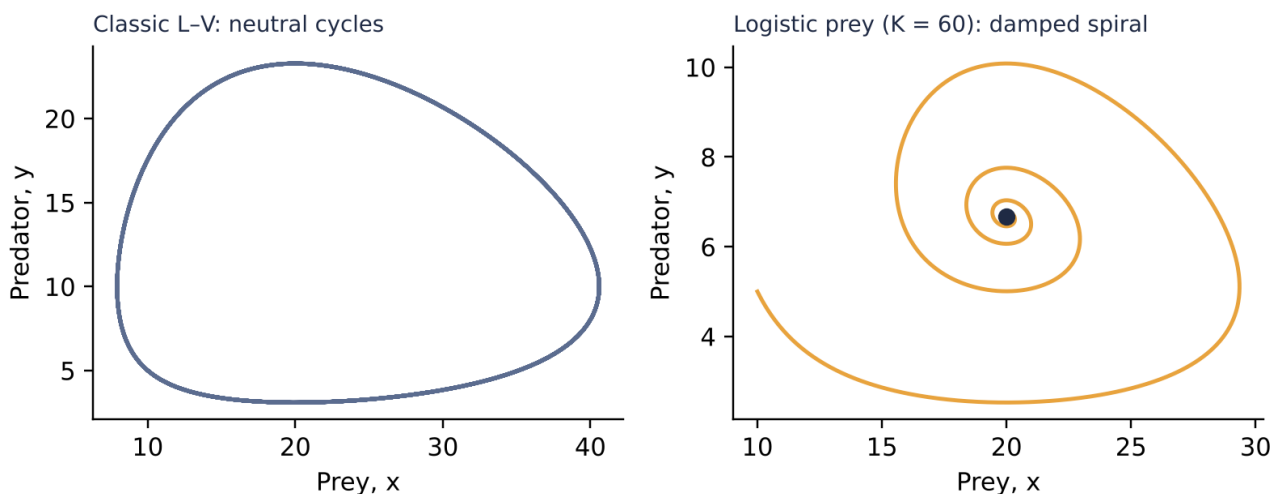


Fig. 6 — Adding a carrying capacity (K) converts neutral cycles into a damped spiral toward a stable equilibrium.

Rosenzweig-MacArthur model (logistic prey + Type II predator):

$$\frac{dx}{dt} = \alpha x \left(1 - \frac{x}{K}\right) - \frac{axy}{1 + ahx} \quad \frac{dy}{dt} = \frac{eaxy}{1 + ahx} - \gamma y$$

Paradox of enrichment (Rosenzweig, 1971): raising K (enriching the prey's resources) destabilises the equilibrium, producing larger cycles that can drive populations to near-extinction.

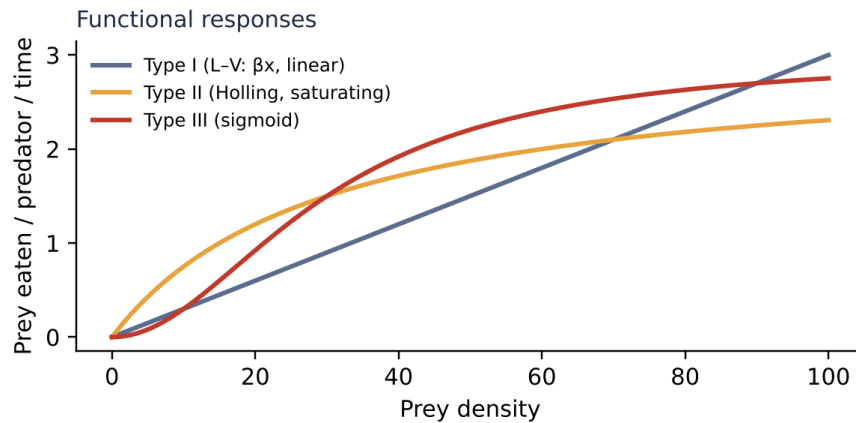


Fig. 7 — Classic L-V assumes the straight-line Type I response.

09 Worked numericals

Q1. Equilibrium & period

$\alpha = 0.5$, $\beta = 0.02$, $\delta = 0.01$, $\gamma = 0.4$ (per month). Find the coexistence equilibrium and approximate period.

Solution: $x^* = \gamma/\delta = 0.4/0.01 = \mathbf{40 \text{ prey}}$; $y^* = \alpha/\beta = 0.5/0.02 = \mathbf{25 \text{ predators}}$. $\sqrt{\alpha\gamma} = \sqrt{0.2} = 0.447$; $T \approx 2\pi/0.447 \approx \mathbf{14.05 \text{ months}}$.

Q2. Direction of change at a point

Same parameters, populations $x = 60$, $y = 30$. Are they rising or falling?

Solution: $dx/dt = 0.5(60) - 0.02(60)(30) = 30 - 36 = \mathbf{-6}$ (prey falling). $dy/dt = 0.01(60)(30) - 0.4(30) = 18 - 12 = \mathbf{+6}$ (predator rising). Point lies in the 'many prey, many predators' zone $\rightarrow$ moving left and up, i.e. anticlockwise. ✓

Q3. Eigenvalues

Find the eigenvalues at both equilibria for Q1.

Solution: $(0, 0)$: $\lambda = 0.5, -0.4 \rightarrow$ saddle. $(40, 25)$: $\lambda = \pm i\sqrt{\alpha\gamma} = \pm \mathbf{0.447 \text{ i}} \rightarrow$ centre.

Q4. Harvesting

In Q1, both species are harvested at $\epsilon = 0.1$. Find the new average populations.

Solution: $\bar{x} = (0.4 + 0.1)/0.01 = \mathbf{50}$ (up from 40); $\bar{y} = (0.5 - 0.1)/0.02 = \mathbf{20}$ (down from 25). Volterra's principle confirmed. If $\epsilon \geq \alpha = 0.5$, predators go extinct.

Q5. Conversion efficiency

Each predator kills prey at $\beta = 0.02$. If 25% of eaten prey is converted into predator offspring, what is δ ?

Solution: $\delta = e\beta = 0.25 \times 0.02 = \mathbf{0.005}$. With $\gamma = 0.4$, prey equilibrium becomes $0.4/0.005 = 80$ — less efficient predators allow more prey.

Q6. Logistic prey equilibrium

Add carrying capacity $K = 100$ to Q1's prey. Find the coexistence point.

Solution: x^* still = $\gamma/\delta = 40$. Prey isocline: $\alpha(1 - x/K) = \beta y \rightarrow y^* = 0.5(1 - 0.4)/0.02 = 15$. (Exists only if $K > \gamma/\delta$.) Fewer predators than the classic 25, and the point is now a stable spiral.

10 End-semester exam questions

Short answer (2-3 marks)

- Write the Lotka-Volterra equations and state the meaning of each parameter.
- Why is the interaction term proportional to the product xy ?
- Define a zero-growth isocline. Give both isoclines of the L-V model.
- What is meant by 'neutral stability'? Why is it biologically unrealistic?
- State Volterra's principle with one practical example.
- Why does the predator population peak after the prey population?
- Distinguish between a neutral cycle and a limit cycle.
- What is the paradox of enrichment?

Long answer (8-15 marks)

1. Derive the equilibrium points of the Lotka-Volterra predator-prey model and analyse their stability using the Jacobian matrix.
2. Show that $V = \delta x - \gamma \ln x + \beta y - \alpha \ln y$ is conserved along trajectories. What does this imply about the solutions?
3. Describe the phase-plane analysis of the L-V model with a neat labelled diagram of isoclines and trajectories.
4. Prove that the time-averaged populations over one cycle equal the equilibrium values. Use this to explain Volterra's principle.
5. Critically evaluate the assumptions of the Lotka-Volterra model. How do the logistic-prey and Rosenzweig-MacArthur models overcome them?
6. Discuss experimental and field evidence (Gause, Huffaker, lynx-hare) for predator-prey oscillations.

11 Case-based MCQs

1. A lake has stable average numbers of pike (predator) and perch (prey) following L-V dynamics. A fertiliser run-off doubles perch birth rate α . Long-term average:
(A) Perch doubles (B) Pike doubles (C) Both double (D) Neither changes
2. Farmers spray a non-selective insecticide killing aphids and ladybirds equally. According to L-V, the average aphid population will:
(A) Fall (B) Rise (C) Stay the same (D) Go extinct
3. The eigenvalues at the coexistence equilibrium of the classic model are:
(A) Both real negative (B) Real, opposite signs (C) Purely imaginary (D) Complex with negative real part
4. A researcher records $x = 50$, $y = 5$ when $x^* = 20$, $y^* = 10$. The next phase will see:
(A) Prey $\uparrow$, predator $\downarrow$ (B) Prey $\uparrow$, predator $\uparrow$ (C) Prey $\downarrow$, predator $\downarrow$ (D) Prey $\downarrow$, predator $\uparrow$

5. Two L-V lab systems with identical parameters start from different densities. Their cycles will have:

- (A) Same amplitude, same period (B) Different amplitude, same mean (C) Same amplitude, different mean (D) Both collapse to equilibrium

6. Gause's Didinium-Paramecium tubes collapsed to extinction. Which change allowed coexistence?

- (A) Adding more Didinium (B) Adding sediment refuges (C) Raising temperature (D) Removing food for Paramecium

7. If $\alpha = 0.8$ and $\gamma = 0.2$, the period of small oscillations is about:

- (A) 3.1 (B) 7.9 (C) 15.7 (D) 31.4

8. Adding prey carrying capacity K converts the coexistence point into a:

- (A) Saddle (B) Unstable node (C) Stable spiral/node (D) Centre

9. Enriching a predator-prey system ($\uparrow K$) with a Type II response tends to:

- (A) Stabilise it (B) Destabilise it into larger cycles (C) Eliminate the predator immediately (D) Have no effect

10. The term δxy in the predator equation primarily represents:

- (A) Predator death (B) Prey captured per predator (C) Predator births from consumed prey (D) Competition among predators

Answer key

1 B ($y^* = \alpha/\beta$) · 2 B ($\bar{x} = (\gamma+\epsilon)/\delta$) · 3 C · 4 B (bottom-right zone) · 5 B (amplitude set by start; mean always = equilibrium) · 6 B · 7 C ($2\pi/\sqrt{0.16} = 15.7$) · 8 C · 9 B (paradox of enrichment) · 10 C

One-page revision summary

Concept	Key result
Equations	$dx/dt = \alpha x - \beta xy$; $dy/dt = \delta xy - \gamma y$
Equilibria	(0,0) saddle; $(\gamma/\delta, \alpha/\beta)$ centre
Eigenvalues at E^*	$\pm i\sqrt{\alpha\gamma}$
Period (small orbits)	$T \approx 2\pi/\sqrt{\alpha\gamma}$
Conserved quantity	$V = \delta x - \gamma \ln x + \beta y - \alpha \ln y$
Averages	$\bar{x} = \gamma/\delta$, $\bar{y} = \alpha/\beta$
Harvesting ϵ	Prey $\uparrow$ to $(\gamma+\epsilon)/\delta$; predator $\downarrow$ to $(\alpha-\epsilon)/\beta$
Phase shift	Predator lags prey by $\sim 1/4$ cycle; orbits anticlockwise (x horizontal)
Main weakness	Neutral cycles are structurally unstable
Fixes	Logistic prey, Holling II, Rosenzweig-MacArthur, refuges, space