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M1M2: Unseen 5: Lotka-Volterra

2. (a). Divide $\frac{dy}{dt} = cxy - dy$ by $\frac{dx}{dt} = ax - bxy$

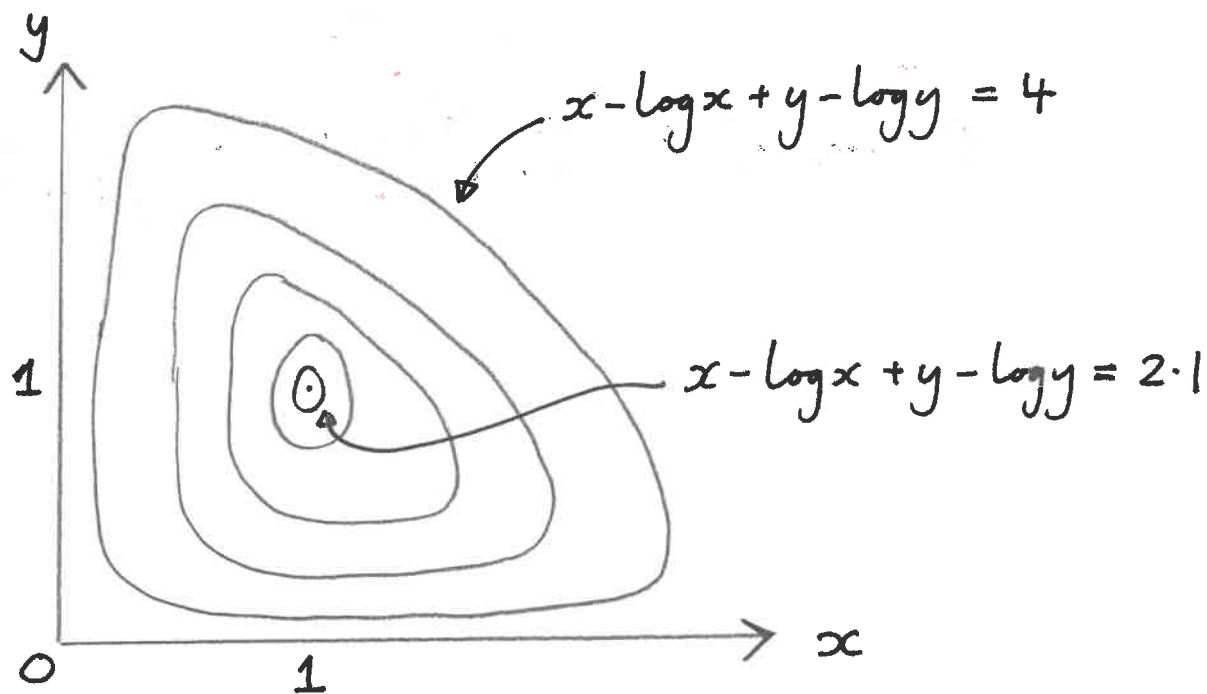
$$\Rightarrow \frac{dy}{dx} = \frac{y(cx-d)}{x(a-by)}$$

$$\Rightarrow \int \frac{(a-by)}{y} dy = \int \frac{(cx-d)}{x} dx \quad (\text{separation of variables})$$

$$\Rightarrow a \log y - by = cx - d \log x + K, \quad K \text{ constant of integration.}$$

$$\Rightarrow \boxed{cx - d \log x + by - a \log y = K}$$

(b).



The curves look something like the sketch above.

3. 2

(a). We solve simultaneously:

$$ax - bxy = 0 \quad (1)$$

$$cxy - dy = 0 \quad (2)$$

we can write: $x(a - by) = 0 \quad \wedge \quad (1)$

$$\Rightarrow \underline{x = 0} \text{ or } \underline{y = \frac{a}{b}}$$

If $x = 0$; then in (2): $-dy = 0 \Rightarrow \underline{y = 0}$

$\Rightarrow (x_0, y_0) = (0, 0)$ is an equilibrium point.

If $y = \frac{a}{b}$; then in (2): $\frac{ca}{b}x - \frac{da}{b} = 0$

$$\Rightarrow \underline{x = \frac{d}{c}}$$

$\Rightarrow (x_0, y_0) = \left(\frac{d}{c}, \frac{a}{b}\right)$ is the other equilibrium point.

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4.1

(a). We put: $(x, y) = \overbrace{(x_0, y_0)}^{\text{constants}} + \varepsilon \overbrace{(x_1, y_1)}^{\text{variables}}$ into LV eqs:

$$\varepsilon \frac{dx_1}{dt} = a(x_0 + \varepsilon x_1) - b(x_0 + \varepsilon x_1)(y_0 + \varepsilon y_1)$$

$$\Rightarrow \varepsilon \frac{dx_1}{dt} = \cancel{ax_0} + \varepsilon ax_1 - \cancel{bx_0y_0} - \varepsilon bx_0y_1 - \varepsilon bx_1y_0 - \cancel{\varepsilon^2 bx_1y_1}$$

$$\Rightarrow O(\varepsilon): \underline{\frac{dx_1}{dt} = (a - by_0)x_1 - bx_0y_1} \quad (3)$$

And its second LV equation:

$$\varepsilon \frac{dy_1}{dt} = c(x_0 + \varepsilon x_1)(y_0 + \varepsilon y_1) - d(y_0 + \varepsilon y_1)$$

$$\Rightarrow \varepsilon \frac{dy_1}{dt} = \cancel{cx_0y_0} + \varepsilon cx_0y_1 + \varepsilon cx_1y_0 + \cancel{\varepsilon^2 cx_1y_1} - \cancel{dy_0} - \varepsilon dy_1$$

$$\Rightarrow O(\varepsilon): \underline{\frac{dy_1}{dt} = cy_0x_1 + (cx_0 - d)y_1} \quad (4)$$

So; Case 1: $(x_0, y_0) = (0, 0)$, we have: (from (3), (4))

$$\frac{dx_1}{dt} = ax_1, \quad \frac{dy_1}{dt} = -dy_1$$

$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix} \quad (\text{linear system})$$

$$\text{e. values: } \underline{\lambda_1 = a}, \underline{\lambda_2 = -d}$$

e. vectors:

$$\begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix} \begin{pmatrix} v_{1x} \\ v_{1y} \end{pmatrix} = a \begin{pmatrix} v_{1x} \\ v_{1y} \end{pmatrix} \Rightarrow \left. \begin{matrix} av_{1x} = av_{1x} \\ -dv_{1y} = av_{1y} \end{matrix} \right\} \Rightarrow \underline{v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}}$$

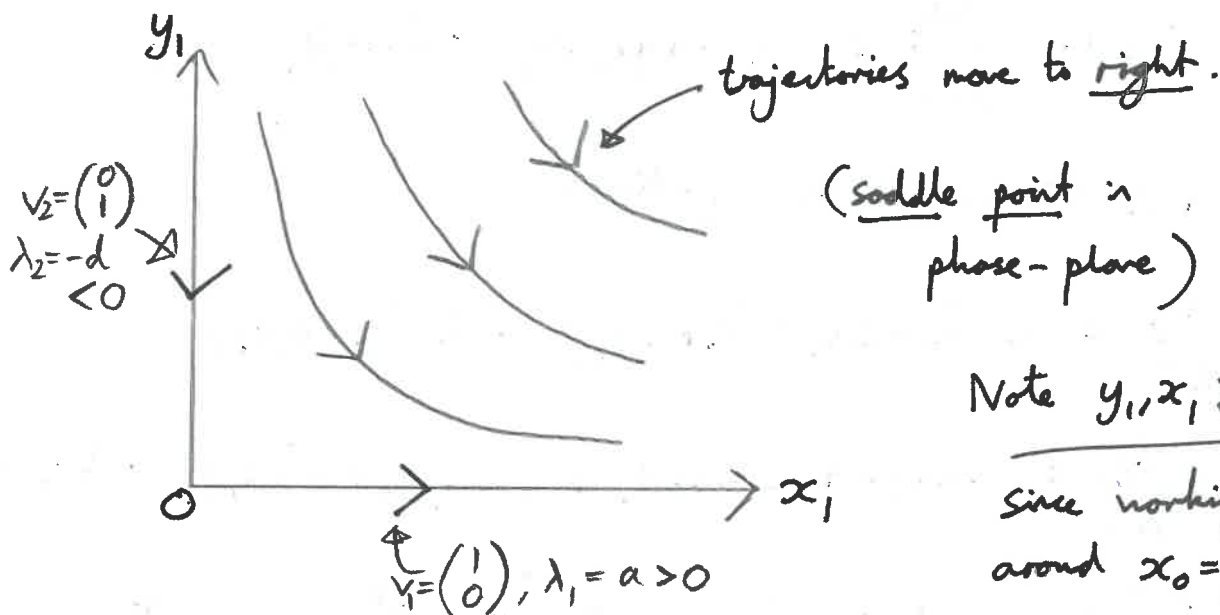
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and:

$$\begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix} \begin{pmatrix} v_{2x} \\ v_{2y} \end{pmatrix} = -d \begin{pmatrix} v_{2x} \\ v_{2y} \end{pmatrix} \Rightarrow \left. \begin{aligned} av_{2x} &= -dv_{2x} \\ -dv_{2y} &= -dv_{2y} \end{aligned} \right\} \Rightarrow \underline{v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}}$$

$$\Rightarrow \underline{\begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = A \begin{pmatrix} 1 \\ 0 \end{pmatrix} e^{at} + B \begin{pmatrix} 0 \\ 1 \end{pmatrix} e^{-dt}} \quad (\text{general solution})$$

Phase-plane



Case 2: $(x_0, y_0) = (\frac{d}{c}, \frac{a}{b})$, we have (from ③, ④):

$$\frac{dx_1}{dt} = -\frac{bd}{c} y_1, \quad \frac{dy_1}{dt} = \frac{ca}{b} x_1$$

$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \underbrace{\begin{bmatrix} 0 & -\frac{bd}{c} \\ \frac{ca}{b} & 0 \end{bmatrix}}_{\text{e. values:}} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix} \quad (\text{linear system})$$

$$\text{e. values: } \begin{vmatrix} -\lambda & -\frac{bd}{c} \\ \frac{ca}{b} & -\lambda \end{vmatrix} = 0$$

$$\Rightarrow \lambda^2 - \left(\frac{ac}{b}\right)\left(-\frac{bd}{c}\right) = 0$$

$$\Rightarrow \lambda^2 + ad = 0$$

$$\Rightarrow \underline{\lambda_1 = \sqrt{ad} i}, \quad \underline{\lambda_2 = -\sqrt{ad} i}$$

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e. vectors:

$$\begin{bmatrix} 0 & -\frac{bd}{c} \\ \frac{ac}{b} & 0 \end{bmatrix} \begin{pmatrix} v_{1x} \\ v_{1y} \end{pmatrix} = \sqrt{ad} i \begin{pmatrix} v_{1x} \\ v_{1y} \end{pmatrix} \Rightarrow \left. \begin{aligned} -\frac{bd}{c} v_{1y} &= \sqrt{ad} i v_{1x} \\ \frac{ac}{b} v_{1x} &= \sqrt{ad} i v_{1y} \end{aligned} \right\}$$

$$\Rightarrow \underline{v_1 = \begin{pmatrix} 1 \\ -\omega i \end{pmatrix}}, \text{ where } \underline{\omega = \frac{c\sqrt{a}}{b\sqrt{d}}}$$

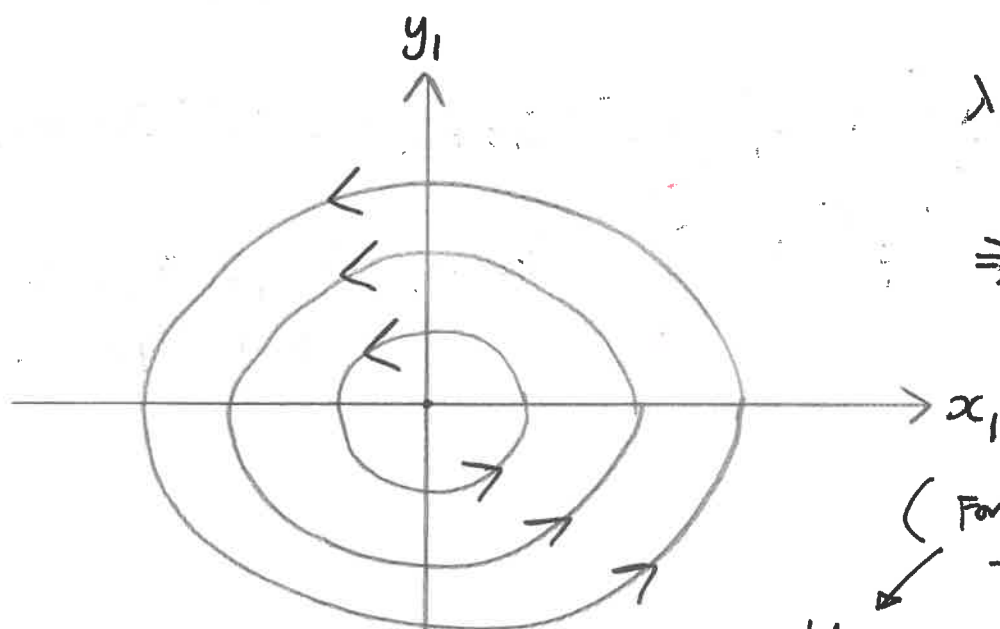
and:

$$\begin{bmatrix} 0 & -\frac{bd}{c} \\ \frac{ac}{b} & 0 \end{bmatrix} \begin{pmatrix} v_{2x} \\ v_{2y} \end{pmatrix} = -\sqrt{ad} i \begin{pmatrix} v_{2x} \\ v_{2y} \end{pmatrix} \Rightarrow \left. \begin{aligned} -\frac{bd}{c} v_{2y} &= -\sqrt{ad} i v_{2x} \\ \frac{ac}{b} v_{2x} &= -\sqrt{ad} i v_{2y} \end{aligned} \right\}$$

$$\Rightarrow \underline{v_2 = \begin{pmatrix} -\frac{1}{\omega} i \\ 1 \end{pmatrix}}, \text{ where } \underline{\omega = \frac{c\sqrt{a}}{b\sqrt{d}}}$$

$$\Rightarrow \begin{bmatrix} x_1 \\ y_1 \end{bmatrix} = A \begin{pmatrix} 1 \\ -\omega i \end{pmatrix} e^{\sqrt{ad} i t} + B \begin{pmatrix} -\frac{1}{\omega} i \\ 1 \end{pmatrix} e^{-\sqrt{ad} i t}, \quad \omega = \frac{c\sqrt{a}}{b\sqrt{d}}$$

Phase-plane



λ_1, λ_2 Complex conjugate pair
 \Rightarrow centre

v. field at $\begin{pmatrix} 0 \\ y_1 \end{pmatrix}$: $\begin{pmatrix} \dot{x}_1 \\ \dot{y}_1 \end{pmatrix} = A \begin{pmatrix} 0 \\ y_1 \end{pmatrix} = \begin{pmatrix} -\frac{bd}{c} y_1 \\ 0 \end{pmatrix} \Rightarrow$ Anti-clockwise direction.

(For $y_1 > 0$, $-\frac{bd}{c} y_1 < 0$.)

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(b). (i). The local solutions are:

$$\begin{bmatrix} x_1 \\ y_1 \end{bmatrix} = A \begin{pmatrix} 1 \\ -\omega i \end{pmatrix} e^{\sqrt{ad} it} + B \begin{pmatrix} -\frac{1}{\omega} i \\ 1 \end{pmatrix} e^{-\sqrt{ad} it}, \quad \omega = \frac{c\sqrt{a}}{b\sqrt{d}}$$

This can be equivalently written as:

$$\begin{aligned} x_1(t) &= C_1 \cos(\sqrt{ad}t + C_2) \\ y_1(t) &= C_1 \omega \sin(\sqrt{ad}t + C_2) \end{aligned} \quad (5), \quad C_1, C_2 \text{ arbitrary constants.}$$

To see this you could start from these expressions and use the formulae for $\sin(\theta + \phi)$ and $\cos(\theta + \phi)$ to expand to retrieve the previous expressions.

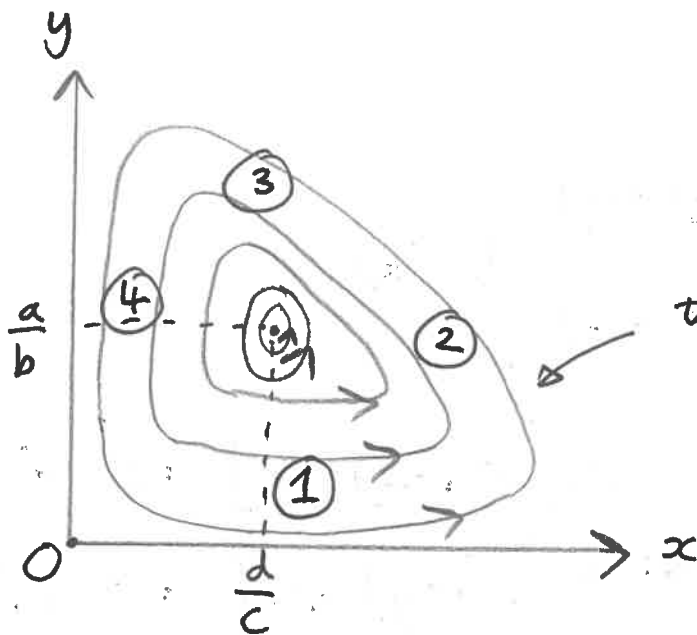
Now it is clear to see the predator population $y_1(t)$ lags behind the prey population $x_1(t)$ by $\frac{\pi}{2}$ since sine lags behind cosine by $\frac{\pi}{2}$ (and they are sin/cosine of the same argument: $\sqrt{ad}t + C_2$).

(ii). With the local solutions as written in (5), we see

$$\begin{aligned} x_1^2 + \left(\frac{y_1}{\omega}\right)^2 &= C_1^2 \left(\cos^2(\sqrt{ad}t + C_2) + \sin^2(\sqrt{ad}t + C_2) \right) \\ \Rightarrow \quad \boxed{x_1^2 + \left(\frac{y_1}{\omega}\right)^2} &= C_1^2 \quad (\text{i.e. } x_1 \text{ and } y_1 \text{ satisfy the equation of an ellipse}). \end{aligned}$$

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(c).



the trajectories ~~point to~~ are anticlockwise as this follows the direction found in the previous analysis.

There are 4 key regions:

- ①: The predator population, y , is low here, so the prey population grows as there are less predators to eat them.
- ②: The prey population, x , is high, hence there is more food for the predators, so the predator population grows.
- ③: The predator population, y , is high and eats the prey, so the prey population decreases.
- ④: The prey population is low, so there is less food for the predators, so the predator population starves and decreases.

The cycle then repeats itself.

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5. Extension:

$$(a). \left. \begin{aligned} \frac{dx}{dt} &= \alpha x(1-x) - xy \\ \frac{dy}{dt} &= \beta y(1-y) - xy \end{aligned} \right\} (*)$$

Equilibrium points when: $x[\alpha(1-x) - y] = 0$ ⑥

and: $y[\beta(1-y) - x] = 0$ ⑦

⑥ gives: $x=0$ or $y=\alpha(1-x)$

when $x=0$; ⑦ gives: $\beta y(1-y) = 0 \Rightarrow$ $y=0$ or $y=1$

\Rightarrow Two equilibria are: $(x_0, y_0) = (0, 0)$
 $(x_0, y_0) = (0, 1)$

when $y=\alpha(1-x)$; ⑦ gives: $\alpha(1-x)[\beta(1-\alpha(1-x)) - x] = 0$

$$\Rightarrow \alpha(1-x)[(\alpha\beta-1)x + \beta(1-\alpha)] = 0$$

$$\Rightarrow \underline{x=1} \text{ or } x = \underline{\frac{\beta(\alpha-1)}{\alpha\beta-1}}$$

\Rightarrow The remaining equilibria are: $(x_0, y_0) = (1, 0)$

$$\underline{(x_0, y_0) = \left(\frac{\beta(\alpha-1)}{\alpha\beta-1}, \frac{\alpha(\beta-1)}{\alpha\beta-1} \right)}$$

$y=\alpha(1-x)$

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Substitute: $x = x_0 + \varepsilon x_1$, $y = y_0 + \varepsilon y_1$, $\varepsilon \ll 1$ into (*) equations.

$$\varepsilon \frac{dx_1}{dt} = \alpha(x_0 + \varepsilon x_1)(1 - (x_0 + \varepsilon x_1)) - (x_0 + \varepsilon x_1)(y_0 + \varepsilon y_1)$$

$$\Rightarrow \varepsilon \frac{dx_1}{dt} = \cancel{\alpha x_0} + \varepsilon \alpha x_1 - \cancel{\alpha x_0^2} - \varepsilon \alpha x_0 x_1 - \varepsilon \alpha x_0 x_1 - \cancel{\varepsilon^2 \alpha x_1^2} - \cancel{x_0 y_0} - \varepsilon x_0 y_1 - \varepsilon x_1 y_0 - \cancel{\varepsilon^2 x_1 y_1}$$

$$\Rightarrow O(\varepsilon): \frac{dx_1}{dt} = (\alpha - 2\alpha x_0 - y_0)x_1 - x_0 y_1$$

Similarly from the other equation, one finds:

$$\frac{dy_1}{dt} = (\beta - 2\beta y_0 - x_0)y_1 - y_0 x_1$$

$$(1) (x_0, y_0) = (0, 0)$$

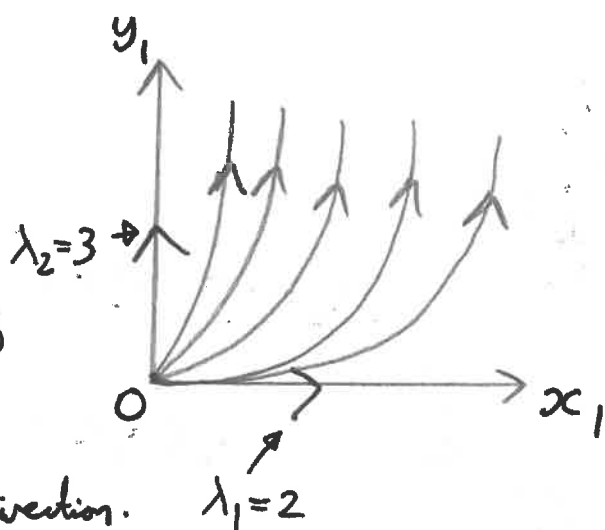
$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} \alpha & 0 \\ 0 & \beta \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix}$$

e. values: $\lambda_1 = \alpha$, $\lambda_2 = \beta$. e. vers: $v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$, $v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$

(i).

$$\alpha = 2$$

$$\beta = 3$$

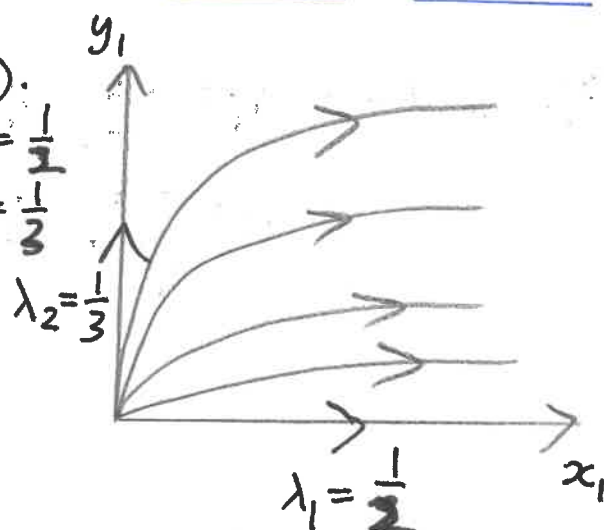


(ii).

$$\alpha = \frac{1}{2}$$

$$\beta = \frac{1}{3}$$

$$\lambda_2 = \frac{1}{3}$$



$$(2)^{10} (x_0, y_0) = (1, 0)$$

$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} -\alpha & -1 \\ 0 & \beta-1 \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix}$$

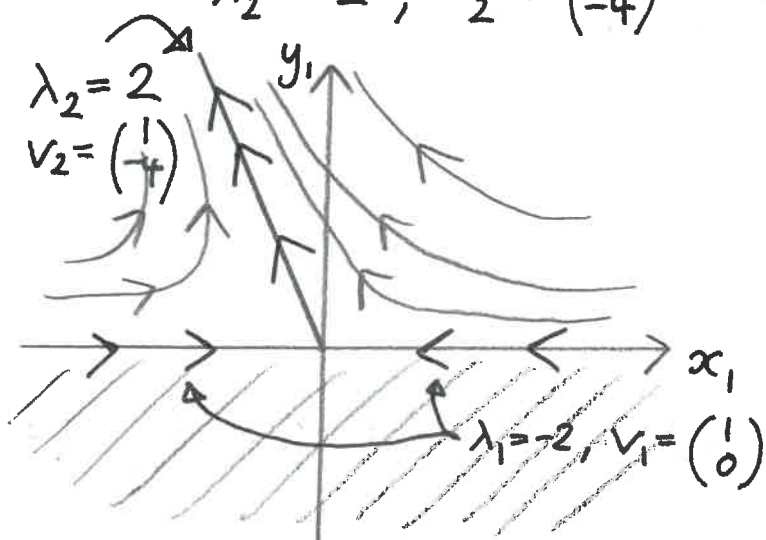
$$\text{e. values: } (-\alpha-\lambda)(\beta-1-\lambda) = 0$$

$$\Rightarrow \underline{\lambda_1 = -\alpha}, \underline{\lambda_2 = \beta-1}$$

$$\text{e. vectors: } \underline{v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}}, \underline{v_2 = \begin{pmatrix} 1 \\ 1-\alpha-\beta \end{pmatrix}}$$

$$(i). \text{ e. values: } \lambda_1 = -2, v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

$$\lambda_2 = 2, v_2 = \begin{pmatrix} 1 \\ -4 \end{pmatrix}$$

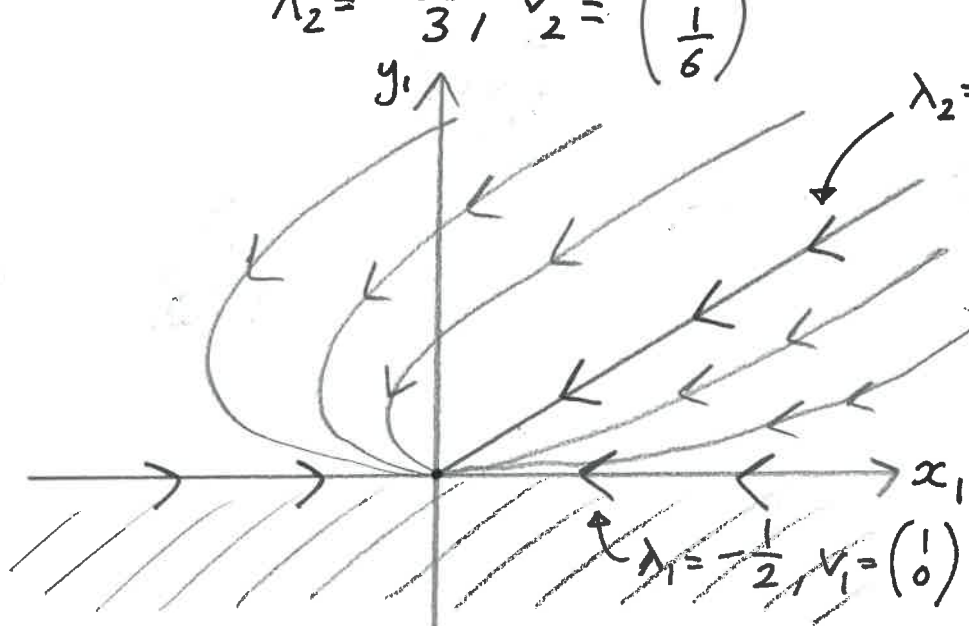


$y_1 > 0$ as $y_0 = 0$ here.
so lower half plane not needed

Saddle point

$$(ii). \text{ e. values: } \lambda_1 = -\frac{1}{2}, v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

$$\lambda_2 = -\frac{2}{3}, v_2 = \begin{pmatrix} 1 \\ \frac{1}{6} \end{pmatrix}$$



$$\lambda_2 = -\frac{2}{3}, v_2 = \begin{pmatrix} 1 \\ \frac{1}{6} \end{pmatrix}$$

$$\lambda_2 < \lambda_1 < 0$$

Stable or
attracting node

III

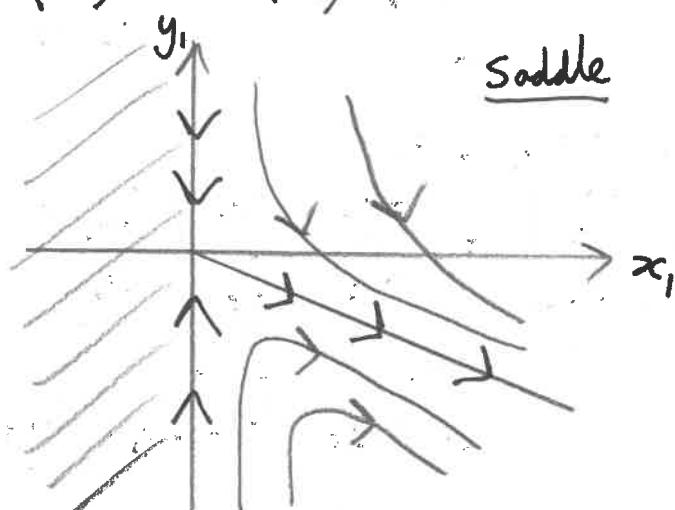
$$(3) (x_0, y_0) = (0, 1)$$

This will be qualitatively identical to $(1, 0)$.

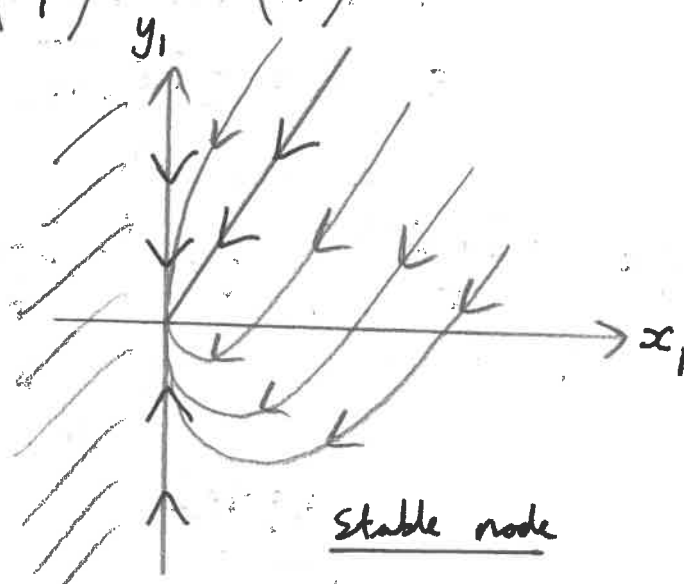
$$\lambda_1 = \alpha - 1, \lambda_2 = -\beta,$$

$$v_1 = \begin{pmatrix} 1 - \alpha - \beta \\ 1 \end{pmatrix}, v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$$

(i). $\lambda_1 = 1, \lambda_2 = -3$
 $v_1 = \begin{pmatrix} -4 \\ 1 \end{pmatrix}, v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$



(ii). $\lambda_1 = -\frac{1}{2}, \lambda_2 = -\frac{1}{3}$
 $v_1 = \begin{pmatrix} \frac{1}{6} \\ 1 \end{pmatrix}, v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$



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$$(4) (x_0, y_0) = \left(\frac{\beta(\alpha-1)}{\alpha\beta-1}, \frac{\alpha(\beta-1)}{\alpha\beta-1} \right)$$

$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} \frac{\alpha\beta(1-\alpha)}{\alpha\beta-1} & -\frac{\beta(\alpha-1)}{\alpha\beta-1} \\ -\frac{\alpha(\beta-1)}{\alpha\beta-1} & \frac{\alpha\beta(1-\beta)}{\alpha\beta-1} \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix}$$

$$(i). \alpha=2, \beta=3 \rightarrow (x_0, y_0) = \left(\frac{3}{5}, \frac{4}{5} \right)$$

$$\Rightarrow \begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} -\frac{6}{5} & -\frac{3}{5} \\ -\frac{4}{5} & -\frac{12}{5} \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix}$$

$$e.\text{values: } \left(-\frac{6}{5} - \lambda \right) \left(-\frac{12}{5} - \lambda \right) - \left(-\frac{4}{5} \right) \left(-\frac{3}{5} \right) = 0$$

$$\Rightarrow (5\lambda + 6)(5\lambda + 12) - 12 = 0$$

$$\Rightarrow 25\lambda^2 + 90\lambda + 60 = 0$$

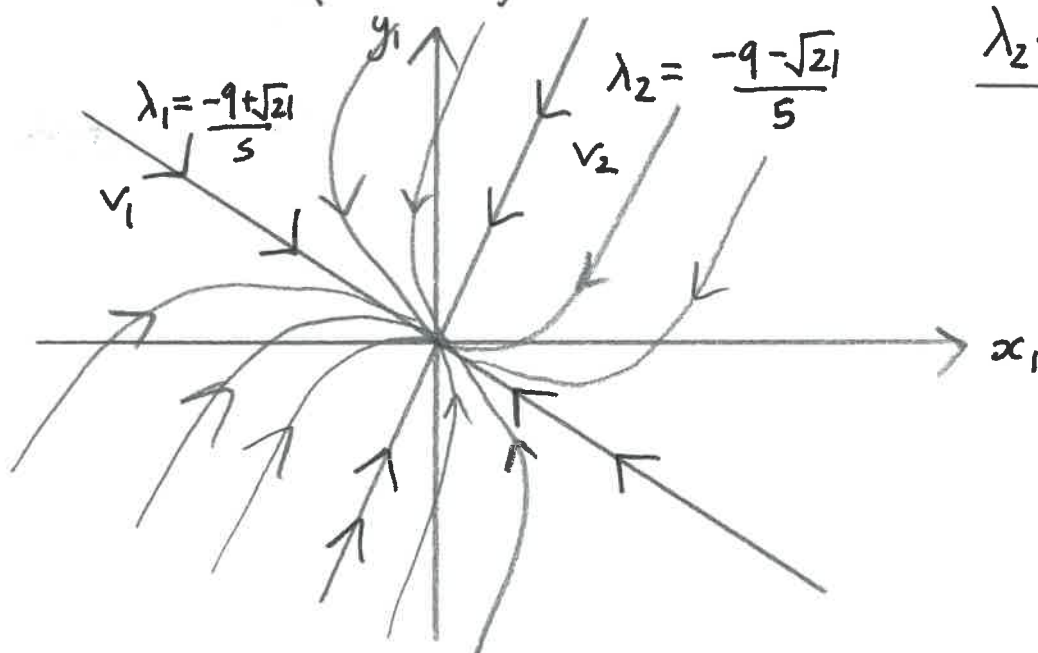
$$\Rightarrow 5\lambda^2 + 18\lambda + 12 = 0$$

$$\Rightarrow \lambda = \frac{-9 \pm \sqrt{21}}{5}$$

$$\Rightarrow \lambda_1, \lambda_2 < 0$$

\Rightarrow Attracting or stable node.

$$V_1 = \begin{pmatrix} -\frac{(3+\sqrt{21})}{4} \\ 1 \end{pmatrix}, V_2 = \begin{pmatrix} -\frac{(3-\sqrt{21})}{4} \\ 1 \end{pmatrix}$$



$$\underline{\lambda_2 < \lambda_1 < 0}$$

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(ii). $\alpha = \frac{1}{2}, \beta = \frac{1}{3} \rightarrow (x_0, y_0) = \left(\frac{1}{5}, \frac{2}{5}\right)$

$$\begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \end{bmatrix} = \begin{bmatrix} -\frac{1}{10} & -\frac{1}{5} \\ -\frac{2}{5} & -\frac{2}{15} \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \end{bmatrix}$$

e. values: $\left(-\frac{1}{10} - \lambda\right)\left(-\frac{2}{15} - \lambda\right) - \left(-\frac{2}{5}\right)\left(-\frac{1}{5}\right) = 0$

$$\Rightarrow (10\lambda + 1)(15\lambda + 2) - 12 = 0$$

$$\Rightarrow 150\lambda^2 + 35\lambda - 10 = 0$$

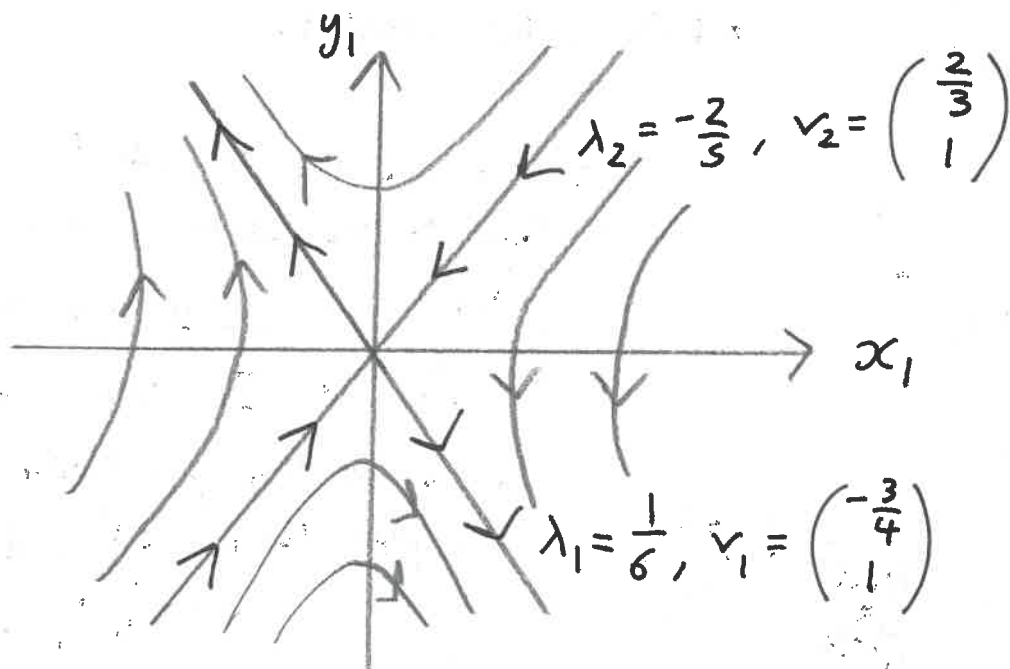
$$\Rightarrow 30\lambda^2 + 7\lambda - 2 = 0$$

$$\Rightarrow \lambda_1 = \frac{1}{6} \text{ or } \lambda_2 = -\frac{2}{5}$$

$$\lambda_1 > 0, \lambda_2 < 0$$

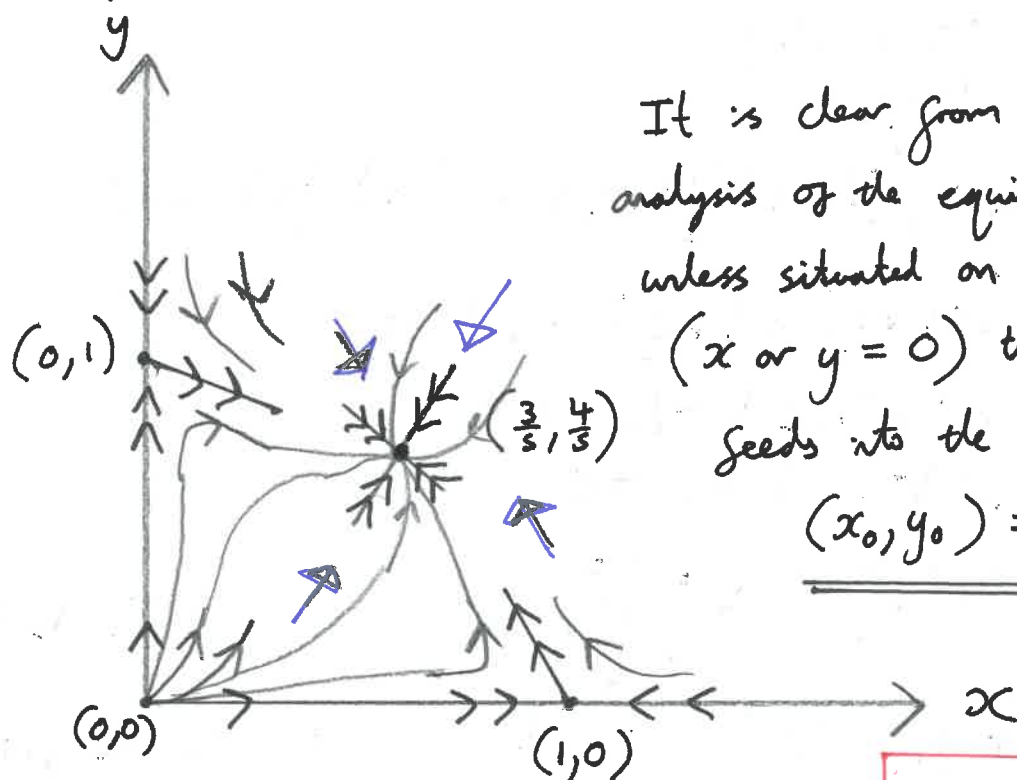
$$\Rightarrow v_1 = \begin{pmatrix} -\frac{3}{4} \\ 1 \end{pmatrix}, v_2 = \begin{pmatrix} \frac{2}{3} \\ 1 \end{pmatrix}$$

Saddle point



So piecing everything together:

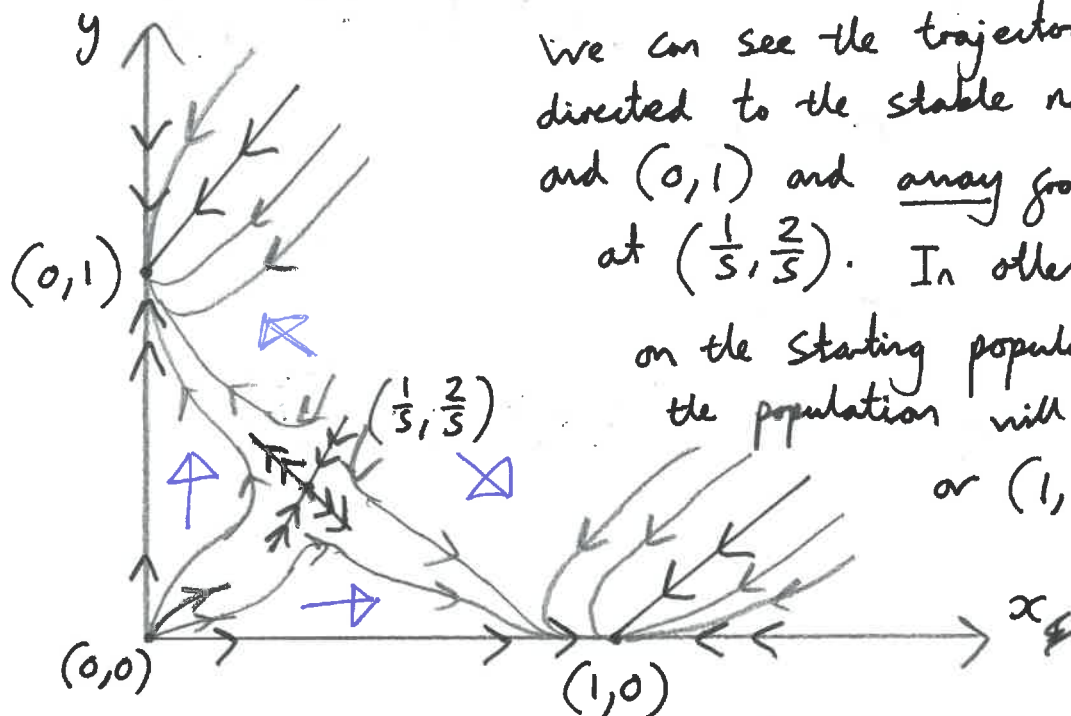
(i). $\alpha = 2, \beta = 3$



It is clear from our local analysis of the equilibria that unless situated on the boundary (x or $y = 0$) that everything seeds into the point $(x_0, y_0) = (\frac{3}{5}, \frac{4}{5})$.

\Rightarrow Long-run population distribution tends to $(x, y) = (\frac{3}{5}, \frac{4}{5})$
 • Both species coexist.

(ii). $\alpha = \frac{1}{2}, \beta = \frac{1}{3}$



We can see the trajectories are directed to the stable nodes at $(1,0)$ and $(0,1)$ and away from the saddle at $(\frac{1}{3}, \frac{2}{3})$. In other words depending on the starting population distribution the population will tend to $(1,0)$ or $(0,1)$.

\Rightarrow Long-run population distribution is $(x, y) = (1,0)$ or $(0,1)$
 • One species extinct, other thrives.