

Written examination, TATM38 Mathematical Models in Biology
2021-10-30, 8.00 - 13.00

Each problem is worth 4 points. To obtain a grade 3, 4 or 5, you need 10, 14 or 18 points, respectively. You must not use any aids (no textbooks, notes, calculators or other electronic tools).

1. (a) The interaction between two species $x(t)$ and $y(t)$ is modeled by the linear system

$$\begin{pmatrix} x'(t) \\ y'(t) \end{pmatrix} = \begin{pmatrix} -1/3 & \alpha \\ \alpha & -1/3 \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix},$$

where $\alpha > 0$ is a constant. For what values of α is the steady state (= equilibrium point) $(0, 0)$ stable? Determine the general solution to this system.

- (b) Consider the linear system of difference equations with the same matrix (and again $\alpha > 0$ constant)

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} -1/3 & \alpha \\ \alpha & -1/3 \end{pmatrix} \begin{pmatrix} x_n \\ y_n \end{pmatrix}.$$

For what values of α is $(0, 0)$ stable in this case? Give the general solution to the system.

2. A population $N(t)$ is described by a logistic equation with a fishing term $4N(1 - N)^2$:

$$\frac{dN}{dt} = 2N(1 - N) - 4N(1 - N)^2$$

Find all steady states (= equilibrium points) and determine their stability. Sketch the phase line for $N \geq 0$. What happens to the population as $t \rightarrow \infty$ for different initial values $N(0)$?

3. Two populations $N(t)$ and $P(t)$ compete for the same resources, and their time evolution is given by

$$\begin{cases} \frac{dN}{dt} = N(1 - N - 3P) \\ \frac{dP}{dt} = 2P(1 - P - 2N) \end{cases}$$

Find all steady states and determine their stability. Draw a phase plane picture with nullclines and directions of the vector field. What can happen to the populations as $t \rightarrow \infty$? Give an interpretation of what the result means for the possibility of coexistence.

PLEASE TURN

4. Let S_n , I_n and R_n be the number of susceptibles, infective, and removed, respectively, at time $n \geq 0$ in a time discrete SIRS epidemic model. The total population N is constant, $N = 900$, and with $R_n = N - S_n - I_n$ one has a two-dimensional system for S_n and I_n :

$$\begin{cases} S_{n+1} = S_n - \frac{S_n I_n}{1000} + \frac{1}{10}(900 - S_n - I_n) \\ I_{n+1} = I_n + \frac{S_n I_n}{1000} - \frac{2I_n}{5} \end{cases}$$

Find all steady states (= equilibrium points) and determine their stability.

5. For $0 < x < \pi/2$ and $t > 0$, solve the initial-boundary value problem (IBVP) for $u(t, x)$

$$\begin{cases} 2u_t = u_{xx} + 2u \\ u_x(t, 0) = 0 \\ u_x(t, \pi/2) = 0 \\ u(0, x) = 3 \cos 4x - \cos 2x \end{cases}$$

Hint: put $u(t, x) = v(t, x)e^{\alpha t}$.

6. A substrate depletion (or positive feedback) model for two chemical concentrations $u(x, t)$ and $v(x, t)$ of a type originally studied by Alan Turing is given by

$$\begin{cases} u_t = uv - u - 2 + D_1 u_{xx} \\ v_t = 4 - uv + D_2 v_{xx} \end{cases}$$

Find the spatially uniform steady state (\bar{u}, \bar{v}) , and show that it is stable if there is no diffusion ($D_1 = D_2 = 0$).

With diffusion present ($D_1 > 0, D_2 > 0$), find the condition for Turing diffusive instability. Suppose now that $D_1 = 1/30$, $D_2 = 1/2$, that $0 < x < L = \sqrt{3}\pi$, and that perturbations near (\bar{u}, \bar{v}) have the form $e^{\sigma t} \cos qx$ with $q = n\pi/L = n/\sqrt{3}$, $n = 0, 1, 2, \dots$. For what values of n can we have diffusive instabilities ($\sigma > 0$)? Sketch the resulting patterns.

① a) $\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} -1/3 & \alpha \\ \alpha & -1/3 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$ Eigenvalues $\begin{vmatrix} -1/3-\lambda & \alpha \\ \alpha & -1/3 \end{vmatrix} = (\lambda + 1/3)^2 - \alpha^2 = 0 \Rightarrow \lambda_{1,2} = -1/3 \pm \alpha$ (real)

(0,0) stable if $\lambda_{1,2} < 0$ $\begin{cases} -1/3 + \alpha < 0 \Rightarrow \alpha < 1/3 \\ -1/3 - \alpha < 0 \text{ for all } \alpha > 0 \end{cases} \Rightarrow$ stable if $\alpha < 1/3$ ($\alpha > 0$ was assumed)

[can also check $\begin{cases} \text{Tr} A = -2/3 < 0 \\ \det A = 1/9 - \alpha^2 > 0 \Rightarrow \alpha^2 < 1/9 \Rightarrow \alpha < 1/3 \end{cases}$]

Eigenvectors

$\lambda_1: \begin{pmatrix} -\alpha & \alpha \\ \alpha & -\alpha \end{pmatrix} \sim \begin{pmatrix} -1 & 1 \\ 0 & 0 \end{pmatrix} \Rightarrow \bar{v}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$, $\lambda_2: \begin{pmatrix} \alpha & \alpha \\ \alpha & \alpha \end{pmatrix} \sim \begin{pmatrix} 1 & 1 \\ 0 & 0 \end{pmatrix} \Rightarrow \bar{v}_2 = \begin{pmatrix} 1 \\ -1 \end{pmatrix}$

General solution is $\begin{pmatrix} x \\ y \end{pmatrix} = c_1 e^{\lambda_1 t} \bar{v}_1 + c_2 e^{\lambda_2 t} \bar{v}_2 = c_1 e^{(-1/3 + \alpha)t} \begin{pmatrix} 1 \\ 1 \end{pmatrix} + c_2 e^{(-1/3 - \alpha)t} \begin{pmatrix} 1 \\ -1 \end{pmatrix}$

b) $\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = A \begin{pmatrix} x_n \\ y_n \end{pmatrix}$, (0,0) stable if $|\lambda_{1,2}| < 1$ $\begin{cases} |-1/3 + \alpha| < 1 \Rightarrow -1 < -1/3 + \alpha < 1 \Rightarrow -2/3 < \alpha < 4/3 \\ |-1/3 - \alpha| = |1/3 + \alpha| < 1 \Rightarrow -1 < 1/3 + \alpha < 1 \Rightarrow -4/3 < \alpha < 2/3 \end{cases}$
 \Rightarrow stable if $\alpha < 2/3$ ($\alpha > 0$ assumed)

[or check with Jury test $\begin{cases} |\text{Tr} A| < 1 + \det A < 2 \\ \det A < 1 \end{cases}$ satisfied
 $\Rightarrow 2/3 < 1/9 - \alpha^2 \Rightarrow \alpha^2 < 8/9 \Rightarrow \alpha < 2/3$]

General solution is $\begin{pmatrix} x_n \\ y_n \end{pmatrix} = c_1 \lambda_1^n \bar{v}_1 + c_2 \lambda_2^n \bar{v}_2 = c_1 (-1/3 + \alpha)^n \begin{pmatrix} 1 \\ 1 \end{pmatrix} + c_2 (-1/3 - \alpha)^n \begin{pmatrix} 1 \\ -1 \end{pmatrix}$

② $\frac{dN}{dt} = f(N) = 2N(1-N) - 4N(1-N)^2 = 2N(1-N)[1 - 2(1-N)] = 2N(1-N)(2N-1)$

Steady states: $f(\bar{N}) = 0 \Rightarrow \bar{N}_1 = 0, \bar{N}_2 = 1/2, \bar{N}_3 = 1$, stable if $f'(\bar{N}_j) < 0$

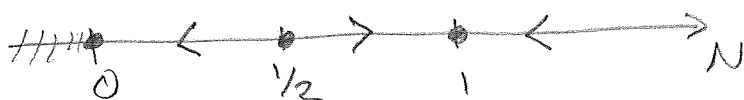
$f'(N) = 2(1-N)(2N-1) - 2N(2N-1) + 4N(1-N) \Rightarrow$

$f'(0) = -2 < 0 \Rightarrow \bar{N}_1 = 0$ stable

$f'(1/2) = 1 > 0 \Rightarrow \bar{N}_2 = 1/2$ unstable

$f'(1) = -2 < 0 \Rightarrow \bar{N}_3 = 1$ stable

Phase line for $N \geq 0$

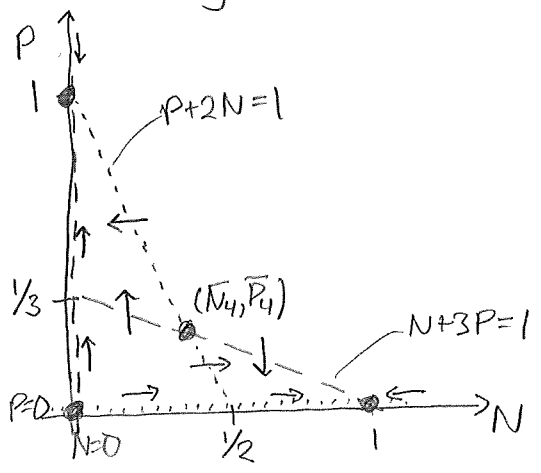


$N(t) \rightarrow \begin{cases} 0 & \text{if } N(0) < 1/2 \\ 1/2 & \text{if } N(0) = 1/2 \\ 1 & \text{if } N(0) > 1/2 \end{cases}$

③ $\begin{cases} N' = N(1-N-3P) & \text{N-nullclines } N=0 \text{ and } N+3P=1 \text{ (dashed)} \\ P' = 2P(1-P-2N) & \text{P-nullclines } P=0 \text{ and } P+2N=1 \text{ (dotted)} \end{cases}$

steady states $N=0$ in $\textcircled{*} \Rightarrow P(1-P)=0 \Rightarrow P=0$ or $P=1$
 $N=1-3P$ in $\textcircled{*} \Rightarrow P(5P-1)=0 \Rightarrow P=0, N=1$ or $P=1/5, N=2/5$

Four steady states $(\bar{N}_1, \bar{P}_1) = (0,0), (\bar{N}_2, \bar{P}_2) = (1,0), (\bar{N}_3, \bar{P}_3) = (0,1), (\bar{N}_4, \bar{P}_4) = (2/5, 1/5)$



$$J(N,P) = \begin{pmatrix} 1-2N-3P & -3N \\ -4P & 2-4P-4N \end{pmatrix} \Rightarrow$$

$$J(0,0) = \begin{pmatrix} 1 & 0 \\ 0 & 2 \end{pmatrix} \begin{matrix} \lambda_1 = 1 > 0 \\ \lambda_2 = 2 > 0 \end{matrix} \Rightarrow (0,0) \text{ unstable}$$

$$J(1,0) = \begin{pmatrix} -1 & -3 \\ 0 & -2 \end{pmatrix} \begin{matrix} \lambda_1 = -1 < 0 \\ \lambda_2 = -2 < 0 \end{matrix} \Rightarrow (1,0) \text{ stable}$$

$$J(0,1) = \begin{pmatrix} -2 & 0 \\ -4 & -2 \end{pmatrix} \begin{matrix} \lambda_1 = -2 < 0 \\ \lambda_2 = -2 < 0 \end{matrix} \Rightarrow (0,1) \text{ stable}$$

$$J(2/5, 1/5) = \begin{pmatrix} -2/5 & -6/5 \\ -4/5 & -2/5 \end{pmatrix} \Rightarrow \lambda_{1,2} = -\frac{2}{5} \pm \frac{\sqrt{24}}{5} \begin{cases} \lambda_1 > 0 \\ \lambda_2 < 0 \end{cases} \Rightarrow \text{saddle, unstable}$$

[or check $\det J = \frac{4}{25} - \frac{24}{25} = -\frac{4}{5} < 0 \Rightarrow$ saddle]

As $t \rightarrow \infty$, (N,P) can approach either $(1,0)$ or $(0,1)$, which one depends on initial values $(N(0), P(0))$. Only one population survives, coexistence is not possible.

④ $\begin{cases} S_{n+1} = S_n - \frac{S_n I_n}{1000} + \frac{1}{10}(900 - S_n - I_n) \\ I_{n+1} = I_n + \frac{S_n I_n}{1000} - \frac{2}{5} I_n \end{cases}$

steady states
 $\bar{S} = S_{n+1} = S_n, \bar{I} = I_{n+1} = I_n$

$$\Rightarrow \begin{cases} \bar{S} = \bar{S} - \frac{\bar{S}\bar{I}}{1000} + \frac{1}{10}(900 - \bar{S} - \bar{I}) & \textcircled{*} \\ \bar{I} = \bar{I} + \frac{\bar{S}\bar{I}}{1000} - \frac{2}{5}\bar{I} \Rightarrow \bar{I}(\frac{\bar{S}}{1000} - \frac{2}{5}) = 0 \end{cases} \Rightarrow \bar{I} = 0 \text{ or } \bar{S} = 400$$

$\bar{I} = 0$ in $\textcircled{*} \Rightarrow \bar{S} = 900, \bar{S} = 400$ in $\textcircled{*} \Rightarrow \bar{I} = 100 \Rightarrow$ Two steady states:
 $(\bar{S}_1, \bar{I}_1) = (900, 0)$ and $(\bar{S}_2, \bar{I}_2) = (400, 100)$ (with $\bar{R}_1 = 0$ and $\bar{R}_2 = 400$ resp.)

$$J(S,I) = \begin{pmatrix} 1 - \frac{I}{1000} - \frac{1}{10} & -\frac{S}{1000} - \frac{1}{10} \\ \frac{I}{1000} & 1 + \frac{S}{1000} - \frac{2}{5} \end{pmatrix} \Rightarrow J(900,0) = \begin{pmatrix} 0.9 & -1 \\ 0 & 1.5 \end{pmatrix} \Rightarrow \begin{cases} \lambda_1 = 0.9 \\ \lambda_2 = 1.5 \end{cases}$$

$|\lambda_2| = 1.5 > 1 \Rightarrow (\bar{S}_1, \bar{I}_1) \text{ unstable}$

$$J(400,100) = \begin{pmatrix} 0.8 & -0.5 \\ 0.1 & 1 \end{pmatrix} \Rightarrow \lambda^2 - 1.8\lambda + 0.85 = 0 \Rightarrow \lambda_{1,2} = 0.9 \pm \sqrt{0.81 - 0.85} = 0.9 \pm 0.2i$$

$\Rightarrow |\lambda_{1,2}| = \sqrt{0.9^2 + 0.2^2} = \sqrt{0.85} < 1 \Rightarrow (\bar{S}_2, \bar{I}_2) \text{ stable}$

[or use Jury test $\frac{|Tr J|}{1.8} < 1 + \frac{\det J}{0.85} < 2$, satisfied \Rightarrow stable]

⑤ $u(t,x) = v(t,x)e^{\alpha t} \Rightarrow u_t = (v_t + \alpha v)e^{\alpha t}, u_x = v_x e^{\alpha t}, u_{xx} = v_{xx} e^{\alpha t} \Rightarrow$
 $2u_t = u_{xx} + 2u \Leftrightarrow \underline{2(v_t + \alpha v)}e^{\alpha t} = (v_{xx} + \underline{2v})e^{\alpha t}$. Take $2\alpha = 2 \Rightarrow \alpha = 1 \Rightarrow$
 $2v_t = v_{xx}$

IBVP for $v(t,x)$:

$$\begin{cases} 2v_t = v_{xx} \\ v_x(t,0) = u_x(t,0)e^{-t} = 0 \\ v_x(t,\pi/2) = u_x(t,\pi/2)e^{-t} = 0 \\ v(0,x) = u(0,x)e^{-0} = u(0,x) = 3\cos 4x - \cos 2x \end{cases}$$

Separation of variables
 $v(t,x) = T(t)X(x) \Rightarrow$
 $\frac{2T'(t)}{T(t)} = \frac{X''(x)}{X(x)} = \lambda = \text{constant}$
 $\Rightarrow T(t) = e^{xt/2}$

$v_x(t,0) = v_x(t,\pi/2) = 0 \Rightarrow X'(0) = X'(\pi/2) = 0$

$$\begin{cases} X''(x) - \lambda X(x) = 0 \\ X'(0) = X'(\pi/2) = 0 \end{cases} \Rightarrow X_n(x) = \cos \frac{n\pi x}{\pi/2} = \cos 2nx, n=0,1,2,\dots \quad \lambda = -4n^2$$

($n=0$ from $\lambda=0$, $X_0(x)$ constant)

$\Rightarrow v(t,x) = \sum_{n=0}^{\infty} \alpha_n e^{-2n^2 t} \cos 2nx$ (or $\frac{\alpha_0}{2} + \sum_{n=1}^{\infty} \alpha_n e^{-2n^2 t} \cos 2nx$)

$v(0,x) = \sum_{n=0}^{\infty} \alpha_n \cos 2nx = 3\cos 4x - \cos 2x$, identify $\alpha_1 = -1, \alpha_2 = 3$, all other $\alpha_n = 0$
 ($n=1$) ($n=2$)

$\Rightarrow v(t,x) = -e^{-2t} \cos 2x + 3e^{-8t} \cos 4x \Rightarrow$
 $u(t,x) = v(t,x)e^t = \underline{-e^{-t} \cos 2x + 3e^{-7t} \cos 4x}$

⑥ $\begin{cases} u_t = uv - u - 2 + D_1 u_{xx} \\ v_t = 4 - uv + D_2 v_{xx} \end{cases}$ Spatially uniform steady state (\bar{u}, \bar{v}) :

$\begin{cases} \bar{u}\bar{v} - \bar{u} - 2 = 0 \\ 4 - \bar{u}\bar{v} = 0 \end{cases} \Rightarrow (\bar{u}, \bar{v}) = (2, 2)$

Stability for $D_1 = D_2 = 0$

$J(u,v) = \begin{pmatrix} v-1 & u \\ -v & -u \end{pmatrix} \Rightarrow J(2,2) = \begin{pmatrix} 1 & 2 \\ -2 & -2 \end{pmatrix} \stackrel{A}{=} \text{Tr} A = -1 < 0$
 $\det A = 2 > 0 \Rightarrow \text{stable}$ (or $\lambda_{1,2} = \frac{-1 \pm i\sqrt{7}}{2}$ have $\text{Re}(\lambda_{1,2}) < 0$)

Condition for Turing instability:

$a_{11}D_2 + a_{22}D_1 > 2\sqrt{D_1 D_2 \det A} \Leftrightarrow D_2 - 2D_1 > 2\sqrt{2D_1 D_2}$

With $D_1 = \frac{1}{30}, D_2 = \frac{1}{2}$: $\frac{1}{2} - \frac{2}{30} = \frac{13}{30}$, $2\sqrt{2/60} = \frac{2}{\sqrt{30}} = \frac{2\sqrt{30}}{30} < \frac{13}{30}$ OK ($\sqrt{30} < 6$)

Unstable perturbations ($q = n/\sqrt{3}$): $0 > \det(A - q^2 D) = \begin{vmatrix} 1 - \frac{q^2}{30} & 2 \\ -2 & -2 - \frac{q^2}{2} \end{vmatrix} =$

$= \frac{q^4}{60} - \frac{13q^2}{30} + 2 = \frac{1}{60}(q^4 - 26q^2 + 120) = \frac{1}{60}[(q^2 - 13)^2 - 49] \Leftrightarrow (q^2 - 13)^2 < 49 \Leftrightarrow$

$-7 < q^2 - 13 < 7 \Leftrightarrow 6 < q^2 < 20 \Leftrightarrow 6 < \frac{n^2}{3} < 20 \Leftrightarrow 18 < n^2 < 60 \Rightarrow \underline{n=5, 6, 7}$

Patterns 