

Written examination, TATM38 Mathematical Models in Biology

2021-08-23, 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. The interaction between two species  $x(t)$  and  $y(t)$  is modeled by the linear system

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

Determine the general solution to this system and draw a picture of the entire phase plane (including negative  $x$  and  $y$ ). Is the steady state (= equilibrium point)  $(0, 0)$  stable?

What is the limit of  $\frac{x(t)}{y(t)}$  as  $t \rightarrow \infty$  if  $x(0) > 0$  and  $y(0) > 0$ ?

What is the solution if  $x(0) = y(0) = 1$ ?

2. Consider the time discrete model

$$x_{n+1} = \frac{2x_n}{1 + x_n^2}, \quad n = 0, 1, 2, \dots$$

Find the steady states (= equilibrium points) and determine their stability. What happens to  $x_n$  as  $n \rightarrow \infty$  in the cases  $x_0 > 0$  and  $x_0 < 0$ ? Sketch a cobweb diagram for some  $x_0 > 0$ .

3. A model for interacting whale and krill populations in the sea is given by

$$\begin{cases} \frac{dx}{dt} = 4x \left(1 - \frac{x}{4}\right) - xy \\ \frac{dy}{dt} = \frac{y}{2} \left(1 - \frac{y}{2+x}\right) \end{cases}$$

Here  $x(t)$  is the whale population and  $y(t)$  the krill population (not measured in the same units!). Find all steady states and determine their stability. Draw, for  $x \geq 0$  and  $y \geq 0$ , a phase plane picture (with nullclines and directions of the vector field). What happens to the populations as  $t \rightarrow \infty$  if  $x(0) > 0$  and  $y(0) > 0$ ?

PLEASE TURN

4. A time discrete predator-prey model is given by the system

$$\begin{cases} x_{n+1} = x_n + 2x_n(1 - x_n) - 3x_n y_n \\ y_{n+1} = \frac{2}{3}y_n + x_n y_n \end{cases}$$

Here  $x_n$  and  $y_n$  are the numbers of prey and predators, respectively, at time  $n$ . Find all steady states and determine their stability.

5. For  $0 < x < 1$  and  $t > 0$ , solve the initial-boundary value problem (IBVP) for  $u(t, x)$

$$\begin{cases} u_t = u_{xx} - 2u_x \\ u(t, 0) = 0 \\ u(t, 1) = 0 \\ u(0, x) = e^x \sin 3\pi x \end{cases}$$

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

6. Let  $u(x, t)$  be activator concentration and  $v(x, t)$  inhibitor concentration in a Gierer-Meinhardt activator-inhibitor model for animal coat pattern formation, which for one space dimension is given by

$$\begin{cases} u_t = \frac{1}{9} - \frac{10}{9}u + \frac{u^2}{v} + D_1 u_{xx} \\ v_t = u^2 - v + D_2 v_{xx} \end{cases}$$

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  $D_1 = 1, D_2 = 9$ , that  $0 < x < L = 6\pi$ , and that perturbations near  $(\bar{u}, \bar{v})$  have the form  $e^{\sigma t} \cos qx$  with  $q = n\pi/L = n/6, n = 0, 1, 2, \dots$ . For what values of  $n$  can we have diffusive instabilities ( $\sigma > 0$ )? Sketch the resulting patterns.

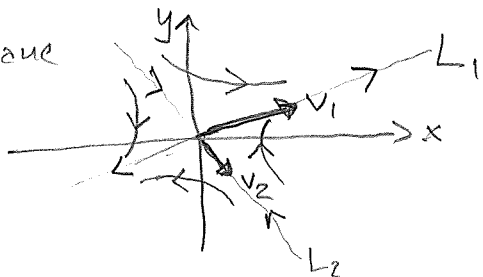
(1)  $\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 1 & 3 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$  Eigenvalues  $\begin{vmatrix} 1-\lambda & 3 \\ 1 & -1-\lambda \end{vmatrix} = \lambda^2 - 4 = 0 \Rightarrow \lambda_{1,2} = \pm 2$

$\lambda_1 > 0$   
 $\lambda_2 < 0$  }  $\Rightarrow$  saddle point (unstable) at  $(0,0)$

Eigenvectors  $\lambda_1 = 2 \Rightarrow v_1 = \begin{pmatrix} 3 \\ 1 \end{pmatrix}$ ,  $\lambda_2 = -2 \Rightarrow v_2 = \begin{pmatrix} 1 \\ -1 \end{pmatrix} \Rightarrow$  general solution is

$$\begin{pmatrix} x \\ y \end{pmatrix} = c_1 e^{2t} \begin{pmatrix} 3 \\ 1 \end{pmatrix} + c_2 e^{-2t} \begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

Phase plane



Solutions with  $x(0) > 0, y(0) > 0$  will approach the line  $L_1$  parallel to  $v_1$  for large  $t$  ( $L_1$  is  $y=x/3$ )

$$e^{-2t} \rightarrow 0 \Rightarrow \begin{pmatrix} x \\ y \end{pmatrix} \approx c_1 e^{2t} \begin{pmatrix} 3 \\ 1 \end{pmatrix} \Rightarrow$$

$\frac{x(t)}{y(t)} \rightarrow 3, t \rightarrow \infty$  (unless  $c_1 = 0$  which is for initial values on  $L_2$ )

$$\begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = c_1 \begin{pmatrix} 3 \\ 1 \end{pmatrix} + c_2 \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \Rightarrow c_1 = \frac{1}{2}, c_2 = -\frac{1}{2} \Rightarrow \begin{pmatrix} x \\ y \end{pmatrix} = \frac{1}{2} e^{2t} \begin{pmatrix} 3 \\ 1 \end{pmatrix} - \frac{1}{2} e^{-2t} \begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

(2)  $x_{n+1} = \frac{2x_n}{1+x_n^2} = f(x_n)$

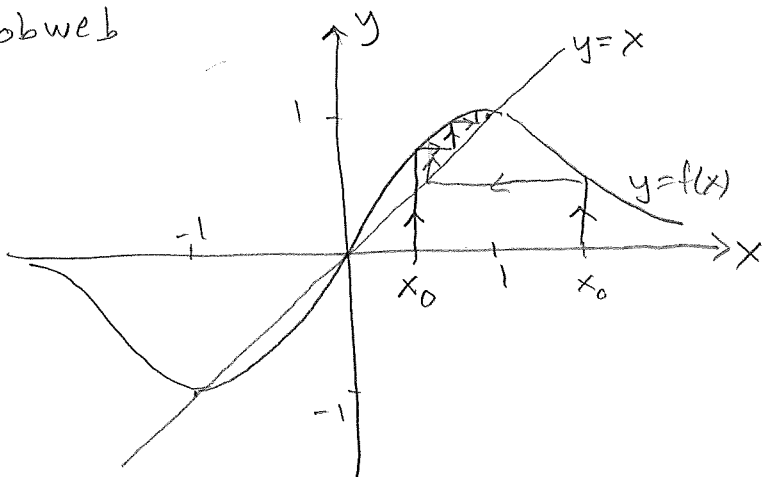
Steady states  $\bar{x} = f(\bar{x}) = \frac{2\bar{x}}{1+\bar{x}^2} \Rightarrow \bar{x}_1 = 0$  or  $1+\bar{x}^2 = 2 \Rightarrow \bar{x}_{2,3} = \pm 1$  3 steady states

$$f'(x) = \frac{2(1+x^2) - 2x \cdot 2x}{(1+x^2)^2} = \frac{2-2x^2}{(1+x^2)^2} \Rightarrow |f'(\bar{x}_1)| = |f'(0)| = 2 > 1 \text{ unstable}$$

$$|f'(\bar{x}_2)| = |f'(1)| = 0 < 1 \text{ stable}$$

$$|f'(\bar{x}_3)| = |f'(-1)| = 0 < 1 \text{ stable}$$

Cobweb



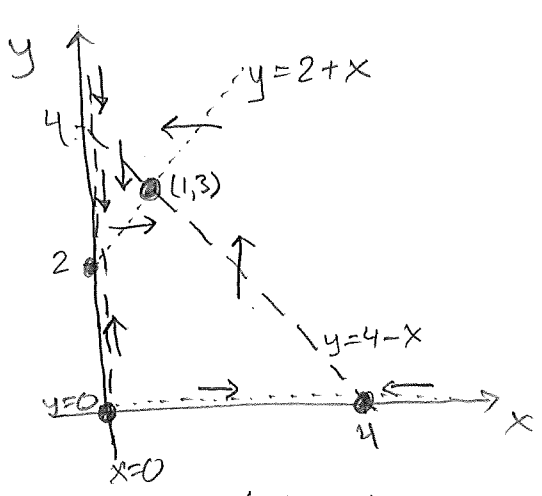
$x_n \rightarrow 1$  as  $n \rightarrow \infty$  if  $x_0 > 0$

(and  $x_n \rightarrow -1$  if  $x_0 < 0$ )

( $f' = 0$  at  $x = \pm 1, f \rightarrow 0, x \rightarrow \pm \infty$ )

③  $\begin{cases} x' = 4x(1-\frac{x}{4}) - xy = x(4-x-y) & x \text{ nullclines: } x=0, y=4-x \text{ 2 lines} \\ y' = \frac{y}{2}(1-\frac{y}{2+x}) & y \text{ nullclines: } y=0, y=2+x \text{ 2 lines} \end{cases}$

Phase plane (for  $x \geq 0, y \geq 0$ )



4 steady states  $(\bar{x}_1, \bar{y}_1) = (0,0), (\bar{x}_2, \bar{y}_2) = (4,0)$   
 $(\bar{x}_3, \bar{y}_3) = (1,3), (\bar{x}_4, \bar{y}_4) = (0,2)$

$J(x,y) = \begin{pmatrix} 4-2x-y & -x \\ \frac{y^2}{2(2+x)^2} & \frac{1}{2} - \frac{y}{2+x} \end{pmatrix}$   
 $J(0,0) = \begin{pmatrix} 4 & 0 \\ 0 & 1/2 \end{pmatrix}$   
 $\begin{cases} \lambda_1 = 4 > 0 \\ \lambda_2 = 1/2 > 0 \end{cases}$  unstable

$J(4,0) = \begin{pmatrix} -4 & -4 \\ 0 & 1/2 \end{pmatrix}$   
 $\begin{cases} \lambda_1 = -4 < 0 \\ \lambda_2 = 1/2 > 0 \end{cases}$  unstable (saddle)  
 $J(0,2) = \begin{pmatrix} 2 & 0 \\ 1/2 & -1/2 \end{pmatrix}$   
 $\begin{cases} \lambda_1 = 2 > 0 \\ \lambda_2 = -1/2 < 0 \end{cases}$  unstable (saddle)

$J_3 = J(1,3) = \begin{pmatrix} -1 & -1 \\ 1/2 & -1/2 \end{pmatrix}$   
 $\text{Tr } J_3 = -3/2 < 0$   
 $\text{det } J_3 = 1 > 0$   
 $\Rightarrow$  stable  
 [or  $\lambda^2 + \frac{3}{2}\lambda + 1 = 0 \Rightarrow \lambda_{1,2} = -\frac{3}{4} \pm i\frac{\sqrt{7}}{4}$   
 $\text{Re } \lambda_{1,2} < 0 \Rightarrow$  stable (spiral)]

The populations approach the stable steady state  $(\bar{x}_3, \bar{y}_3) = (1,3)$  as  $t \rightarrow \infty$

④  $\begin{cases} x_{n+1} = x_n + 2x_n(1-x_n) - 3x_n y_n \\ y_{n+1} = \frac{2}{3}y_n + x_n y_n \end{cases}$  Steady states  $\begin{cases} \bar{x} = x_{n+1} = x_n \\ \bar{y} = y_{n+1} = y_n \end{cases} \Rightarrow$

$\begin{cases} \bar{x} = \bar{x} + 2\bar{x}(1-\bar{x}) - 3\bar{x}\bar{y} \\ \bar{y} = \frac{2}{3}\bar{y} + \bar{x}\bar{y} \end{cases} \Rightarrow \begin{cases} \bar{x}(2-2\bar{x}-3\bar{y}) = 0 & (1) \\ \bar{y}(\bar{x}-\frac{1}{3}) = 0 & (2) \end{cases}$   
 $\Rightarrow \bar{y} = 0 \text{ or } \bar{x} = \frac{1}{3}$   
 $\Downarrow (1)$   
 $\bar{x} = 0 \text{ or } \bar{x} = 1$   
 $\Rightarrow \bar{y} = \frac{4}{9}$

$\Rightarrow$  3 steady states  $(\bar{x}_1, \bar{y}_1) = (0,0), (\bar{x}_2, \bar{y}_2) = (1,0), (\bar{x}_3, \bar{y}_3) = (\frac{1}{3}, \frac{4}{9})$

$J(x,y) = \begin{pmatrix} 3-4x-3y & -3x \\ y & x+\frac{2}{3} \end{pmatrix}$   
 $J(0,0) = \begin{pmatrix} 3 & 0 \\ 0 & 2/3 \end{pmatrix}$   
 $|\lambda_1| = |3| > 1 \Rightarrow$  unstable  
 $(|\lambda_2| = |2/3| < 1)$

$J(1,0) = \begin{pmatrix} -1 & -3 \\ 0 & 5/3 \end{pmatrix}$   
 $|\lambda_1| = |-1| = 1$   
 $|\lambda_2| = |5/3| = 5/3 > 1 \Rightarrow$  unstable

$J_3 = J(\frac{1}{3}, \frac{4}{9}) = \begin{pmatrix} 1/3 & -1 \\ 4/9 & 1 \end{pmatrix}$   
 $\lambda^2 - \frac{4}{3}\lambda + \frac{7}{9} = 0, \lambda_{1,2} = \frac{2}{3} \pm \sqrt{\frac{4}{9} - \frac{7}{9}} = \frac{2 \pm i\sqrt{3}}{3} \Rightarrow |\lambda_{1,2}| = \sqrt{(\frac{2}{3})^2 + (\frac{\sqrt{3}}{3})^2} =$

$= \sqrt{\frac{7}{9}} < 1 \Rightarrow$  stable (with Jury test  $|\text{Tr } J_3| < 1 + \text{det } J_3 < 2$  satisfied!)  
 $\Rightarrow$  stable

(5)  $u(t,x) = v(t,x)e^{\alpha t + \beta x} \Rightarrow u_t = (v_t + \alpha v)e^{\alpha t + \beta x}$ ,  $u_x = (v_x + \beta v)e^{\alpha t + \beta x}$ ,  
 $u_{xx} = (v_{xx} + 2\beta v_x + \beta^2 v)e^{\alpha t + \beta x}$ . Substitute into  $u_t = u_{xx} - 2u_x \Rightarrow$   
 $(v_t + \alpha v)e^{\alpha t + \beta x} = (v_{xx} + 2\beta v_x + \beta^2 v - 2v_x - 2\beta v)e^{\alpha t + \beta x}$  with  $\beta = 1$  and  
 $\alpha = \beta^2 - 2\beta = -1$  we get  $v_t = v_{xx}$  and IBVP for  $v(t,x)$ :

$$\begin{cases} v_t = v_{xx} \\ v(t,0) = u(t,0)e^{-\alpha t - \beta \cdot 0} = 0 \\ v(t,1) = u(t,1)e^{-\alpha t - \beta \cdot 1} = 0 \\ v(0,x) = u(0,x)e^{-\beta x} = e^x \sin 3\pi x \cdot e^{-x} = \sin 3\pi x \end{cases}$$

$v(t,x) = T(t)X(x) \Rightarrow$   
(separation of variables)  
 $\frac{T'}{T} = \frac{X''}{X} = \text{constant} = \lambda$   
and  $X(0) = X(1) = 0$

Solutions to  $X$ -eq.  $X_n(x) = \sin n\pi x$ ,  $n=1,2,3,\dots$

$\lambda = -n^2\pi^2$ .  $T$ -eq  $T' = -n^2\pi^2 T \Rightarrow T_n(t) = e^{-n^2\pi^2 t} \Rightarrow v(t,x) = \sum_{n=1}^{\infty} a_n e^{-n^2\pi^2 t} \sin n\pi x$

$v(0,x) = \sum_{n=1}^{\infty} a_n e^0 \sin n\pi x = \sin 3\pi x \Rightarrow a_3 = 1, a_n = 0$  for  $n \neq 3 \Rightarrow$

$v(t,x) = e^{-9\pi^2 t} \sin 3\pi x \Rightarrow u(t,x) = v(t,x)e^{-t+x} = e^{-(1+9\pi^2)t} e^x \sin 3\pi x$

(6)  $\begin{cases} u_t = \frac{1}{9} - \frac{10}{9}u + \frac{u^2}{9} + D_1 u_{xx} \\ v_t = u^2 - v + D_2 v_{xx} \end{cases}$  Spatially uniform steady state  $(\bar{u}, \bar{v})$ :  
 $\begin{cases} \frac{1}{9} - \frac{10}{9}\bar{u} + \frac{\bar{u}^2}{9} = 0 \\ \bar{u}^2 - \bar{v} = 0 \end{cases} \Rightarrow (\bar{u}, \bar{v}) = (1, 1)$

Stability for  $D_1 = D_2 = 0$ :

Jacobian  $J(u,v) = \begin{pmatrix} -\frac{10}{9} + \frac{2u}{9} & -\frac{u^2}{v^2} \\ 2u & -1 \end{pmatrix} \Rightarrow J(1,1) = \begin{pmatrix} \frac{8}{9} & -1 \\ 2 & -1 \end{pmatrix} = J$   $\begin{cases} \text{Tr } J = -\frac{1}{9} < 0 \\ \det J = \frac{10}{9} > 0 \end{cases} \Rightarrow$  stable

Turing condition  $J_{11}D_2 + J_{22}D_1 > 2\sqrt{D_1D_2 \det J} \Leftrightarrow \frac{8}{9}D_2 - D_1 > 2\sqrt{10D_1D_2/9}$

With  $D_1 = 1, D_2 = 9$   $8 - 1 > 2\sqrt{10}$  (satisfied)

Unstable perturbations ( $q = \frac{n}{6}$ ):  $0 > \det(J - q^2 D) = \begin{vmatrix} \frac{8}{9} - 1 \cdot q^2 & -1 \\ 2 & -1 - 9q^2 \end{vmatrix} =$

$= 9q^4 - 7q^2 + \frac{10}{9} = (3q^2 - \frac{7}{6})^2 - \frac{9}{36} \Leftrightarrow |3q^2 - \frac{7}{6}| < \sqrt{\frac{9}{36}} = \frac{1}{2} \Leftrightarrow -\frac{1}{2} < 3q^2 - \frac{7}{6} < \frac{1}{2}$

$\Leftrightarrow \frac{4}{6} < 3q^2 < \frac{10}{6} \Leftrightarrow \frac{2}{9} < q^2 < \frac{5}{9} \Leftrightarrow \frac{2}{9} < \frac{n^2}{36} < \frac{5}{9} \Leftrightarrow 8 < n^2 < 20$

$\Rightarrow n = 3$  or  $n = 4$

Patterns



$n = 3, \cos \frac{3\pi x}{L}$



$n = 4, \cos \frac{4\pi x}{L}$