Durham University

EXAMINATION PAPER

Examination Session:	Year:	Exam Code:
May/June	2022	MATH3171-WE01

Title: Mathematical Biology III

Time:	3 hours	
Additional Material provided:		
Materials Permitted:		
Calculators Permitted:	No	Models Permitted: Use of electronic calculators is forbidden.

Instructions to Candidates:	Answer all questions. Section A is worth 40% and Section B is worth 60%. Within each section, all questions carry equal marks. Students must use the mathematics specific answer book.

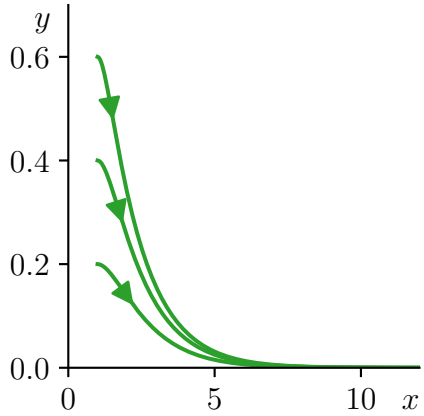
Revision:	

SECTION A

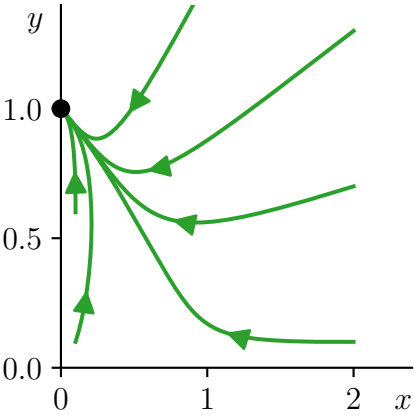
Q1 Variations on Lotka–Volterra The following graphs show the phase portraits of two species, $x(t)$ and $y(t)$, over time, t. Each graph, labelled **(G1)**–**(G4)**, shows sample trajectories and corresponds to one of the nondimensionalised models listed below, labelled **(M1)**–**(M4)**. Giving a good reason in each case, match the graphs to the models.

Graphs:

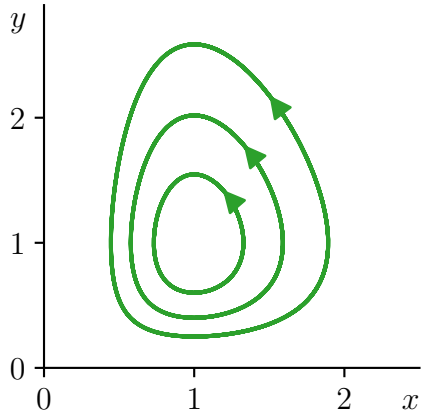
(G1)



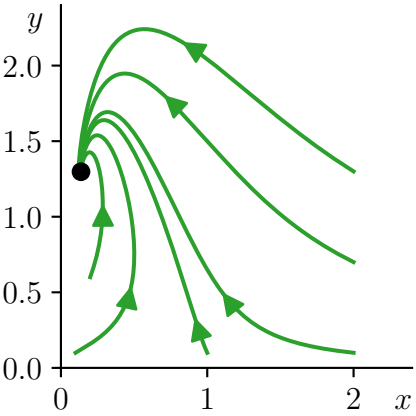
(G2)



(G3)



(G4)



Models:

$$\textbf{(M1)}\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t} = x - xy \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = \gamma(-y + xy)\end{cases} \qquad \textbf{(M2)}\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t} = x - xy \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = \gamma(-y - xy)\end{cases}$$

$$\textbf{(M3)}\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t} = x(1-x) - \gamma xy \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = \delta y(1-y) + \beta xy\end{cases} \qquad \textbf{(M4)}\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t} = x(1-x) - \gamma xy \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = \delta y(1-y) - \beta xy\end{cases}$$

where the constants $\beta, \gamma, \delta > 0$ wherever they appear, although they are not necessarily equal between graphs.

Q2 Nondimensionalisation & model simplifications Consider the dimensional Fisher–Kolmogorov equation modelling an invasive species:

$$\frac{\partial \tilde{u}}{\partial \tilde{t}} = D\frac{\partial^2 \tilde{u}}{\partial \tilde{x}^2} + r\tilde{u}\left(1 - \frac{\tilde{u}}{K}\right), \quad \tilde{x} \in [0, L],$$

where $D, r, K > 0$ and we assume Neumann boundary conditions.

2.1 Not including the initial conditions, describe what every parameter in this model represents.

2.2 Nondimensionalise the model to reduce it to the equation,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \alpha u(1 - \beta u), \quad x \in [0, 1], \tag{1}$$

stating clearly how the new and old variables are related. Without introducing additional parameters (that is, keeping the coefficients of 1 in front of the derivative terms and the same scale for x), can you find a nondimensionalisation for which we also have $\beta = 1$? What about $\alpha = 1$? Explain why or why not in each case.

2.3 Solve equation (1) with $\beta = 0$, for a general initial condition. Interpret what this solution represents. Under what mathematical restrictions does the approximation of $\beta = 0$ make biological sense? Hint: Consider the limit $t \to \infty$. You may find the following relation useful for $m, n \in \mathbb{Z}$:

$$\int_0^L \cos\left(\frac{n\pi x}{L}\right)\cos\left(\frac{m\pi x}{L}\right)\mathrm{d}x = \begin{cases} L & \text{if } m = n = 0, \\ L/2 & \text{if } m = n > 0, \\ 0 & \text{if } m \neq n. \end{cases}$$

Q3 Chemotaxis in a Petri dish A chemotactic bacteria is kept in a circular Petri dish, and moves according to self-generated gradients of a chemoattractant. A model for this on the timescale neglecting bacterial growth or death is given by

$$\frac{\partial n}{\partial t} = D\nabla^2 n - \boldsymbol{\nabla} \cdot (g(n,c)\boldsymbol{\nabla} c),$$
$$\frac{\partial c}{\partial t} = \nabla^2 c + f(n) - ac,$$

where a, D are positive parameters, and the solution is solved in the domain (using polar coordinates (r, θ)) $0 \leq r \leq R$ and $0 \leq \theta < 2\pi$. We assume both species satisfy no-flux conditions on the domain boundary $r = R$.

3.1 Give a biological interpretation to the parameters as well as the two arbitrary functions.

3.2 Is the no-flux boundary condition on both species the same as Neumann boundary conditions? Clearly show why or why not.

3.3 Find all equilibria of this model, and state any conditions necessary for these equilibria to be stable in the absence of transport terms.

3.4 Linearise the PDE system, and determine an equation for the growth rates of a perturbation, λ_k, in terms of spatial eigenvalues ρ_k of the Laplacian (you do not need to solve for λ_k but should have an explicit algebraic equation that it satisfies). What equation and boundary conditions do these spatial eigenvalues satisfy? You do not need to solve this spatial eigenvalue problem, but should describe what kinds of functions satisfy it.

Q4 Patterns in predator–prey Consider the nondimensionalised predator–prey Lotka–Volterra equations in a general spatial domain $\Omega \subset \mathbb{R}^n$:

$$\frac{\partial u}{\partial t} = u(1-u) - auv + \nabla^2 u,$$
$$\frac{\partial v}{\partial t} = -v + buv + D\nabla^2 v,$$

with Neumann boundary conditions, and a, b, D positive constants.

4.1 Find the spatially homogeneous equilibria, noting for what ranges of parameters they are feasible. For what values of a and b are each of these equilibria stable?

4.2 Which of the equilibria does it make sense to perform a Turing-type analysis for diffusion-driven instability around? Explain your reasoning.

4.3 Show that this system can not undergo a diffusion-driven instability. Hint: Does the sign structure of the Jacobian at the equilibrium have the form needed for a diffusion-driven instability?

SECTION B

Q5 'Furrier' transforms A population of lemmings live along the edge of a cliff. A team of conservationists model the population of lemmings over one-dimensional space and time, $u(x,t)$, by

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + v\frac{\partial u}{\partial x} + \alpha u, \quad u(x,0) = \begin{cases} 0 & \text{if } x < -1 \\ 1 & \text{if } -1 \le x \le 1 \\ 0 & \text{if } x > 1 \end{cases}, \quad u(\pm\infty, t) = 0, \tag{2}$$

where $\alpha, D, v \ge 0$ are constants and $x \in \mathbb{R}$.

5.1 Interpret the terms in this equation and the boundary conditions in the context of the lemmings and their environment. What sort of behaviour do you expect to see from this model?

5.2 The total number of lemmings in the population, M, is

$$M = \int_{-\infty}^{\infty} u(x,t)\,\mathrm{d}x.$$

Consider $\mathrm{d}M/\mathrm{d}t$. Assuming additionally that $\partial u/\partial x = 0$ at $x = \pm\infty$, work out a condition for which the total population does not grow in time.

5.3 Using Fourier transforms, solve the fundamental problem for (2) and then solve the full problem. You may find the following useful:

$$\mathcal{F}(k)[f(x)] = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} \mathrm{e}^{-\mathrm{i}kx} f(x)\,\mathrm{d}x,$$
$$\mathcal{F}^{-1}(x)[g(k)] = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} \mathrm{e}^{\mathrm{i}kx} g(k)\,\mathrm{d}k,$$
$$\int_{-\infty}^{\infty} \mathrm{e}^{-ax^2+bx+c}\,\mathrm{d}x = \sqrt{\frac{\pi}{a}}\mathrm{e}^{c}\mathrm{e}^{b^2/(4a)},$$
$$\mathrm{erf}(z) = \frac{2}{\sqrt{\pi}}\int_0^z \mathrm{e}^{-t^2}\mathrm{d}t.$$

5.4 Suppose now that the cliff edge is modelled instead to have finite length, $x \in [-10, 10]$. When a lemming reaches an edge of the cliff, it jumps off and dies.

(i) Which boundary conditions on u would you specify for this new problem?

(ii) Now consider $\mathrm{d}M/\mathrm{d}t$ again, as you did in question **5.2**. Work out a condition (in terms of D, v, α, as well as $\partial u/\partial x$ evaluated at the boundary points) for which the population in this new model does not grow indefinitely in time.

Q6 Allee population dynamics with spatial variations

6.1 Consider a population $u(t)$ evolving according to

$$\frac{\mathrm{d}u}{\mathrm{d}t} = ru\left(\frac{u}{A} - 1\right)\left(1 - \frac{u}{K}\right),$$

with the parameters $r > 0$, $K > 0$ and $0 < A < K$. Explain the biological interpretation of the three parameters. Using linear stability analysis and/or a graphical representation of the phase space, explain the behaviour of the population for different initial conditions.

6.2 Consider the spatial model for $u(x, t)$,

$$\frac{\partial u}{\partial t} = D\nabla^2 u + ru\left(\frac{u}{A} - 1\right)\left(1 - \frac{u}{K}\right), \quad x \in \Omega = [0, L], \tag{3}$$

where u satisfies no-flux conditions on its boundaries. Can this model exhibit pattern-forming instabilities of homogeneous equilibria? Can *stable* spatially inhomogeneous equilibria exist for this equation which are not due to pattern-forming instabilities? What about if Ω were a simply connected two-dimensional domain?

6.3 Now consider (3) with Dirichlet conditions of the form $u = u_B$ for $x = 0, L$, for some constant value u_B. For what values of u_B do spatially homogeneous equilibria exist? For all cases where they do, use a linear stability analysis to determine their stability as a function of the model parameters. For any of these cases where the spatial model can give a different stability prediction from the ODE, compute the critical domain length, L_c, where the stability of a spatially homogeneous equilibrium changes.

Q7 Travelling waves in skin repair A model of wound healing in one spatial dimension is given by

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - u \log\left(\frac{u+a}{K}\right), \tag{4}$$

where $u(x,t)$ is the density of healthy tissue at position x and time t; and where a and K are positive constants, with $0 < a < K$.

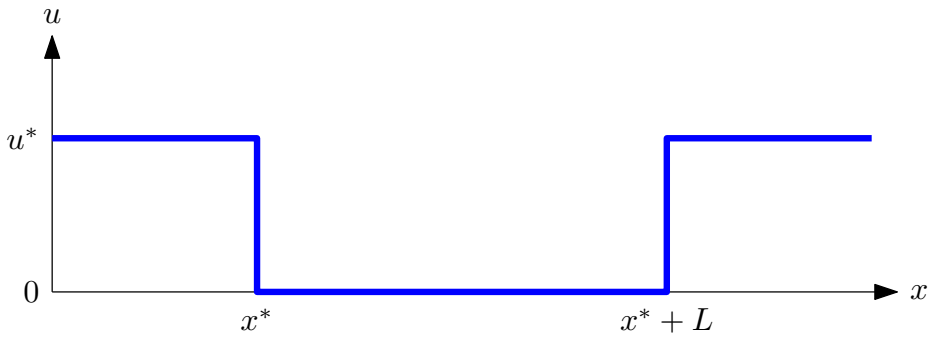
7.1 Consider first the homogeneous form of (4). Find the equilibria and determine their stability in this case.

7.2 Describe qualitatively the full model, (4). In what way is it different to that described by the Fisher–Kolmogorov equation?

7.3 We are going to look for travelling wave solutions, i.e. solutions of the form $u(z)$, where $z = x - ct$ and $c > 0$. Given the stability of the equilibria in the homogeneous system, suggest suitable boundary conditions for $u(z)$ at $z = \pm\infty$, explaining your choice.

7.4 Now write (4) for $u(z)$, and by performing a linear stability analysis, determine the stability of the homogeneous equilibria. Given that waves travel at their lowest possible speed, determine the wavespeed, c.

7.5 Consider now a wound which is initially of length L, i.e. as in the diagram below, where u^* is the value of the nonzero homogeneous equilibrium of (4):



Illustrating your answer with sketches of $u(x,t)$ for increasing t, explain what you expect to happen for subsequent times and determine approximately how long it will take for the wound to heal.

Q8 Disease modelling with vaccination Consider the following extension of the SIR model for an infectious disease, where susceptible individuals are vaccinated at a rate ν,

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \alpha R - \beta IS - \nu S, \tag{5}$$
$$\frac{\mathrm{d}I}{\mathrm{d}t} = \beta IS - \gamma I, \tag{6}$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = \gamma I - \alpha R + \nu S,$$

where $\alpha, \beta, \gamma, \nu$ are all positive constants, and $S(t), I(t), R(t) \geq 0$ to be feasible.

8.1 Show that $N = S + I + R$ is constant and use this to eliminate R from (5). Explain why, from now on, we only need to consider the subsystem formed of equations (5) and (6).

8.2 Give an interpretation of the constants α, β, γ, N. What would be suitable units for these constants?

8.3 It is proposed that this could be an appropriate model for the spread of Covid-19. Is this a suitable model for this problem? Give three clear arguments, which can be in favour of this as a suitable model, or against its suitability. Your three arguments do not have to argue the same way.

8.4 (i) Find the values of S and I at the two equilibria of the system.

(ii) The disease is eradicated if the disease-free equilibrium is the only possible stable equilibrium and the endemic equilibrium does not exist. Perform a linear stability analysis on both equilibria of the system and show that the disease is eradicated if $R^* < 1$, where you should define the constant R^*.

(iii) Define R_0 as the value of R^* in the absence of vaccination (i.e. when $\nu = 0$): in this way, R_0 can be seen as an inherent property of the disease. Rearrange the statement $R^* < 1$ to find the condition on the vaccination rate, ν, for the disease to be eradicated in terms of R_0.

8.5 You are now asked to present the same argument graphically. Draw a phase portrait of I against S and, by moving the nullclines on your portrait, show how the existence of the endemic equilibrium depends on the vaccination rate, ν, and the value of R_0. You do not need to explicitly draw trajectories to make this argument.