IMPERIAL

MATH70014

BSc, MSci and MSc EXAMINATIONS (MATHEMATICS)
Summer 2025

This paper is also taken for the relevant examination for the
Associateship of the Royal College of Science

Mathematical Biology

Date: Thursday, May 15, 2025

Time: Start time 10:00 – End time 12:30 (BST)

Time Allowed: 2.5 hours

This paper has 5 Questions.

Please Answer All Questions in 1 Answer Booklet

This is a closed book examination.

Candidates should start their solutions to each question on a new sheet of paper.

Supplementary books may only be used after the relevant main book(s) are full.

Any required additional material(s) will be provided.

Credit will be given for all questions attempted.

Allow margins for marking.

DO NOT OPEN THIS PAPER UNTIL THE INVIGILATOR TELLS YOU TO DO SO

1. Researchers have developed a strain of *Wolbachia* bacteria that can infect mosquitos carrying the dengue virus so that virus transmission is blocked. Bacterial infection is spread from the female to its eggs, regardless of whether or not the male is infected. On the other hand if the female is uninfected but the male is infected then no viable eggs are produced. Infected female mosquitos die at a faster rate and lay fewer eggs. Uninfected and infected mosquitos also die due to competition.

(a) Consider the following population model of u uninfected and v infected females:

$$\frac{du}{dt} = ru\frac{u}{u+v} - \gamma u - \sigma u(u+v),$$
$$\frac{dv}{dt} = r\lambda v - \mu\gamma v - \sigma v(u+v),$$

where $\mu > 1$ and $\lambda < 1$. Assuming that the fraction of infected males is identical to the fraction of infected females, namely $u/(u+v)$, interpret the various terms on the right-hand side of these equations. (4 marks)

(b) Consider the non-dimensionalized equations

$$\frac{dx}{d\tau} = f(x,y) \equiv x\left[\frac{x}{x+y} - \frac{\gamma}{r} - (x+y)\right],$$
$$\frac{dy}{d\tau} = g(x,y) \equiv y\left[\lambda - \mu\frac{\gamma}{r} - (x+y)\right]$$

and assume that $r > \mu\gamma/\lambda$.

(i) Derive the nondimensionalised equations from the original model in part (a). (3 marks)

(ii) Show that there are four non-negative fixed points of the form

$$(0,0), \quad (x_0,0), \quad (0,y_0), \quad (x_1,y_1),$$

and determine the values x_0, y_0, x_1, y_1. (4 marks)

(iii) Determine the nullclines and sketch a phase portrait. Hence, deduce that $(0,0)$ is unstable and (x_1,y_1) is a saddle. [Hint: The x-nullcline is defined implicitly. Find the intercepts with the x-axis and show that the nullcline has a single positive maximum.] (5 marks)

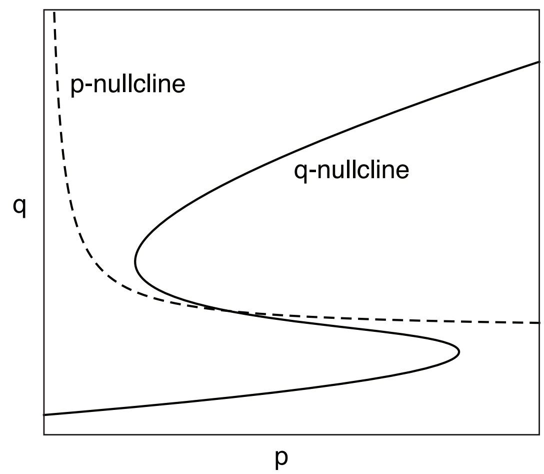
(iv) By adding trajectories to the phase portrait, explain how a sufficiently large number of infected mosoquitos needs to be introduced to an uninfected population $x(0)$ in order to ensure that all mosquitos are eventually infected. How is this result affected by reducing μ or increasing λ? (4 marks)

(Total: 20 marks)

2. Consider a simplified two-gene activator-repressor model of circadian rhythms. Let $p(t)$ and $q(t)$ denote the concentrations of the two protein products at time t. After eliminating the explicit dynamics of mRNA, one obtains the following two-dimensional ODE:

$$\frac{dp(t)}{dt} = -k_p p(t) + \frac{k_1}{q(t) + k_2},$$
$$\epsilon \frac{dq(t)}{dt} = -k_q q(t) + \frac{q^2(t)}{q^2(t) + k_4} p(t) + k_3,$$

where k_p, k_q and k_j, $j = 1, \ldots, 4$, are positive constants and $0 < \epsilon \ll 1$. The nullclines for a given choice of parameters are sketched in the figure below.



(a) Identify which protein acts as a repressor and which acts as an activator. Briefly explain your answer. (3 marks)

(b) Denote the unique fixed point on the middle branch of the q-nullcline by (p^*, q^*). Calculate the Jacobian in terms of p^* and q^*. Show that it takes the form

$$\mathbf{J} = \frac{1}{\epsilon} \begin{pmatrix} \epsilon a & \epsilon b \\ c & d \end{pmatrix},$$

with $a < 0$, $b < 0$ and $c > 0$. Based on the slopes of the nullclines at the fixed point in the phase-plane plot, deduce that $d > 0$ and $\det \mathbf{J} > 0$. Hence show that the fixed point is unstable for sufficiently small ϵ. (6 marks)

(c) Use the phase-plane diagram to sketch the approximate trajectory of a limit cycle oscillation for small ϵ. Identify the regions of slow and fast dynamics, and the direction of motion around the limit cycle. (3 marks)

(d) (i) Explain how the slow dynamics can be understood by taking the singular limit $\epsilon \to 0$ in the model equations. (4 marks)

(ii) Write down the rescaled model equations obtained by setting $t = \epsilon\tau$. Explain how taking the limit $\epsilon \to 0$ now determines the fast dynamics. (4 marks)

(Total: 20 marks)

3. Consider the reaction-diffusion (RD) system

$$\frac{\partial u}{\partial t} = -u + u^2 v + \frac{\partial^2 u}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = b - u^2 v + d\frac{\partial^2 v}{\partial x^2},$$

with $x \in \mathbb{R}$ and $t \geq 0$.

(a) Show that the spatially homogeneous system has a single fixed point $(u^*, v^*) = (b, b^{-1})$. (2 marks)

(b) Linearize the full RD system about the fixed point using the perturbations

$$u(x,t) = u^* + U(x,t), \quad v(x,t) = v^* + V(x,t).$$

Substituting the solution

$$U(x,t) = U\mathrm{e}^{\lambda t}\cos kx, \quad V(x,t) = V\mathrm{e}^{\lambda t}\cos kx$$

into the linearized RD system, derive the k-dependent eigenvalue equation

$$\lambda \begin{pmatrix} U \\ V \end{pmatrix} = \mathbf{J}(k) \begin{pmatrix} U \\ V \end{pmatrix},$$

and determine the k-dependent elements of the Jacobian $\mathbf{J}$. Interpret λ and k. (5 marks)

(c) (i) Show that Tr$\mathbf{J}(0) = 1 - b^2$ and Det$\mathbf{J}(0) = b^2$. Hence, deduce that the fixed point of the homogeneous system is stable when $b > 1$. (2 marks)

(ii) Show that Tr$\mathbf{J}(k) < 0$ for all k when $b > 1$. Also show that Det$\mathbf{J}(k) < 0$ for a band of modes $k \in [k_-, k_+]$ with $k_\pm^2 = \mu_\pm$ provided that there are two real positive roots $\mu_\pm$ of the characteristic equation

$$d\mu^2 - (d - b^2)\mu + b^2 = 0.$$

Hence obtain the following necessary and sufficient conditions for the existence of a band of unstable modes:

$$b > 1, \quad \frac{d}{b^2} > 3 + \sqrt{8}.$$

(5 marks)

(iii) Use part (ii) to show that the critical wavenumber k_c for a Turing instability is given by

$$k_c^2 = \sqrt{b^2/d},$$

which occurs on the Turing bifurcation curve $d = (3 + \sqrt{8})b^2$. (3 marks)

(c) Sketch the regions in the (b, d)-parameter plane where the homogeneous fixed point is (i) unstable to homogeneous perturbations and (ii) stable to homogeneous perturbations but unstable to spatially varying patterns. (3 marks)

(Total: 20 marks)

4. Consider the following master equation for a birth-death-immigration process $X(t)$ with $p_n(t) = \text{Prob}[X(t) = n]$:

$$\frac{dp_0}{dt} = \mu p_1(t) - ap_0(t),$$
$$\frac{dp_n}{dt} = -[(\lambda+\mu)n + a]p_n(t) + \mu(n+1)p_{n+1}(t) + [\lambda(n-1)+a]p_{n-1}(t).$$

Assume the initial condition $p_n(0) = P_{nN}(0) = \delta_{n,N}$.

(a) (i) Multiplying the n-th equation by n and summing over n, derive the following ODE for the expectation $m(t) = \sum_{n=1}^{\infty} np_n(t)$:

$$\frac{dm}{dt} = a + (\lambda - \mu)m.$$

(5 marks)

(ii) Briefly explain what happens to the mean $m(t)$ in the limit $t \to \infty$ when $\lambda \geq \mu$ (3 marks)

(b) Now suppose $a = 0$ so that $n = 0$ is an absorbing state.

(i) Let π_m denote the probability of absorption at zero given that the system is initially at state m. Since the transitions $m \to m+1$ and $m \to m-1$ occur with probability $\lambda/(\lambda+\mu)$ and $\mu/(\lambda+\mu)$, respectively, we have the iterative equation

$$\pi_m = \frac{\lambda}{\lambda+\mu}\pi_{m+1} + \frac{\mu}{\lambda+\mu}\pi_{m-1},$$

with $\pi_0 = 1$ and $0 \leq \pi_m \leq 1$ for $m \geq 1$. Show that $\pi_m = \mu^m/\lambda^m$ when $\mu < \lambda$ and $\pi_m = 1$ when $\mu \geq \lambda$ for all $m \geq 1$. [HINT: Consider the trial solution $\pi_n = \Gamma^n$.] (6 marks)

(ii) The generating function $\mathcal{P}(z,t) = \sum_{n=0}^{\infty} z^n p_n(t)$ satisfies the first-order PDE

$$\frac{\partial \mathcal{P}}{\partial t} = (z-1)(\lambda z - \mu)\frac{\partial \mathcal{P}}{\partial z},$$

with initial condition $\mathcal{P}(z,0) = z^N$. Use the method of characteristics to obtain the solution

$$\mathcal{P}(z,t) = \left(\frac{e^{(\mu-\lambda)t}(\lambda z - \mu) - \mu(z-1)}{e^{(\mu-\lambda)t}(\lambda z - \mu) - \lambda(z-1)}\right)^N, \quad \lambda \neq \mu.$$

Hence, recover the result of part (i) by setting $p_0(t) = \mathcal{P}(0,t)$ and taking the limit $t \to \infty$.

(6 marks)

(Total: 20 marks)

5. Consider a protein that exists either as a monomer with concentration $x_1(t)$ or a dimer with concentration $x_2(t)$. The law of mass action yields the pair of ODEs

$$\frac{dx_1}{dt} = k_3 - kx_1 - 2k_1x_1^2 + 2k_2x_2,$$
$$\frac{dx_2}{dt} = k_1x_1^2 - k_2x_2.$$

(a) (i) Write down the set of chemical reactions.

(4 marks)

(ii) Let $a = 1, 2$ denote the production and degradation of monomers, and let $a = 3, 4$ label dimerization and its reverse reaction. Rewrite the kinetic equations in the general form

$$\frac{dx_j}{dt} = \sum_{a=1}^{4} S_{ja} f_a(\mathbf{x}), \quad j = 1, 2,$$

with $\mathbf{x} = (x_1, x_2)^\top$ Identify the stoichiometric coefficients S_{ja} and the propensities $f_a(\mathbf{x})$. (4 marks)

(b) Consider a stochastic version of the chemical process with $N_1(t)$and $N_2(t)$ the number of monomers and dimers at time t, respectively. Let $P_{n_1n_2}(t) = \text{Prob}[N_1(t) = n_1, N_2(t) = n_2]$.

(i) Construct the chemical master equation for $P_{n_1n_2}(t)$ in terms of the coefficients S_{ja} and the propensities written as $f_a(\mathbf{n}/\Omega)$ where Ω is the system size and $\mathbf{n} = (n_1, n_2)^\top$. (6 marks)

(ii) Perform a system size expansion of the master equation to derive up to $O(1/\Omega)$ the Fokker-Planck equation

$$\frac{\partial p}{\partial t} = -\sum_{i=1,2} \frac{\partial [A_i(\mathbf{x})p(\mathbf{x}, t)]}{\partial x_i} + \frac{1}{2\Omega} \sum_{i,j=1,2} \frac{\partial [D_{ij}(\mathbf{x})p(\mathbf{x}, t)]}{\partial x_i \partial x_j}$$

and give the explicit expressions for $A_i(\mathbf{x})$ and $D_{ij}(\mathbf{x})$. (6 marks)

(Total: 20 marks)

BSc and MSci EXAMINATIONS (MATHEMATICS)

May 2025

This paper is also taken for the relevant examination for the Associateship.

M70014

Mathematical Biology (Solutions)

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1. (a) Consider the following population model of u uninfected and v infected females: unseen $\Downarrow$

$$\frac{du}{dt} = ru\frac{u}{u+v} - \gamma u - \sigma u(u+v),$$
$$\frac{dv}{dt} = r\lambda v - \mu\gamma v - \sigma v(u+v),$$

where $\mu > 1$ and $\lambda < 1$.

• Uninfected females produce uninfected eggs at a rate r when paired with uninfected males. The probability of encountering an uninfected male is $u/(u+v)$ so that the uninfected birth rate is $ru^2/(u+v)$.

• Infected females produce infected eggs at a reduced rate λr, $\lambda < 1$, irrespective of the state of males. Hence, infected birth rate is $r\lambda v$.

• Intrinsic uninfected death rate is γu

• Intrinsic infected death rate is $\mu\gamma u$ with $\mu > 1$

• $\sigma u(u+v)$ and $\sigma v(u+v)$ are the death rates due to competition 4, B

(b) (i) Introduce the nondimensionalized time $\tau = rt$ and rescale the population variables according to $x = \sigma u$ and $y = \sigma y$. Dividing the model equatons by $r\sigma$ then yields meth seen $\Downarrow$

$$\frac{dx}{d\tau} = f(x,y) \equiv x\left[\frac{x}{x+y} - \frac{\gamma}{r} - (x+y)\right],$$
$$\frac{dy}{d\tau} = g(x,y) \equiv y\left[\lambda - \mu\frac{\gamma}{r} - (x+y)\right]$$

3, A

(ii) There are four non-negative fixed points when $r > \mu\gamma/\lambda$:

$$(0,0), \quad (x_0,0), \quad (0,y_0), \quad (x_1,y_1)$$

with

$$x_0 = 1 - \frac{\gamma}{r}, \quad y_0 = \lambda - \frac{\mu\gamma}{r} < x_0, \quad x_1 = y_0(1-x_0+y_0), \quad y_1 = y_0(x_0-y_0).$$

In the last case, first note that $x_1 + y_1 = y_0$ and substitute into the first equation to give $x_1 = (1-x_0)y_0 + y_0^2$ etc. 3, A

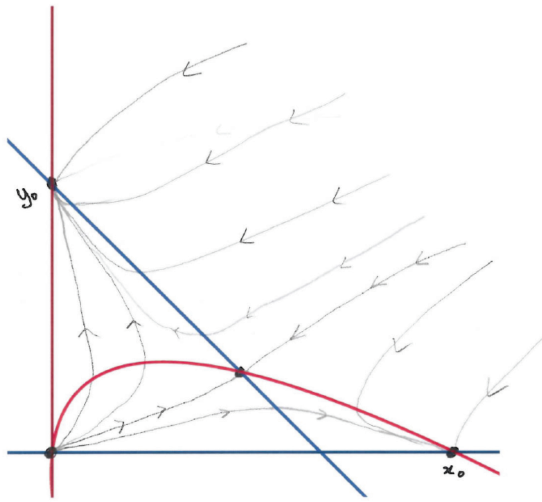
(iii) The x-nullcline ($\dot{x} = 0$) is given by the union of the y-axis and the implicitly defined curve

$$y = x_0(x+y) - (x+y)^2.$$

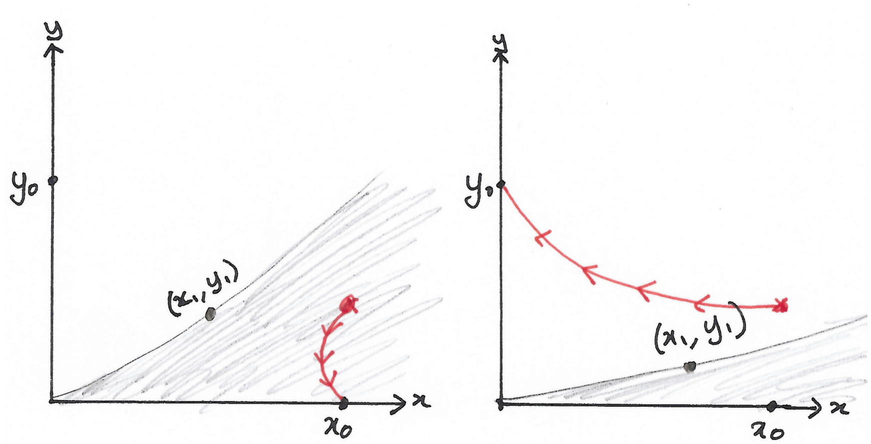
The curve intercepts the x-axis when $x_0 x = x^2$, that is, $x = 0, x_0$. In addition,

$$\frac{dy}{dx} = x_0 + x_0\frac{dy}{dx} - 2(x+y)\left(1 + \frac{dy}{dx}\right).$$

It follows that $dy/dx = 0$ if and only if $(x+y) = x_0/2$. Substituting for $x+y$ in the implicit equation for the nullcline shows that the latter has a single critical point at $(x_0/2 - x_0^2/4, x_0^2/4)$.
The y-nullcline ($\dot{y} = 0$) is given by the union of the x-axis and $x + y = y_0$. 5, B



(iv) The initial point must lie above the separatrix separating the basins of attraction of the two stable fixed points so that $(x(t), y(t)) \to (0, y_0)$ as $t \to \infty$ The separatrix is given by the stable manifold of the saddle (x_1, y_1). Hence, we require that a sufficiently large number of infected mosoquitos is introduced in order to ensure that all mosquitos are eventually infected. Reducing μ or increasing λ will lower the threshold for converging to the fully infected population since the death rate of the infected population is reduced whereas the corresponding birth rate is increased.



$\boxed{5,\ \mathrm{D}}$

2. (a) • Protein Q represses the synthesis of protein P since the rate of synthesis $k_1/(q+k_2)$ is a decreasing function of the concentration q. unseen ⇓

• Protein P activates the synthesis of protein Q since the rate of synthesis $pq^2/(q^2+k_4)$ is an increasing function of the concentration p 3, A

(b) Evaluating the first derivatives of f, g at a point (p, q) we have meth seen ⇓

$$\frac{\partial f}{\partial p} = -k_p, \quad \frac{\partial f}{\partial q} = -\frac{k_1}{(q+k_2)^2}$$
$$\frac{\partial g}{\partial p} = \frac{1}{\epsilon}\frac{q^2}{q^2+k_4}, \quad \frac{\partial f}{\partial q} = \frac{1}{\epsilon}\left[-k_q + \frac{2qp}{q^2+k_4} - \frac{2q^3p}{(q^2+k_4)^2}\right].$$

Hence, the Jacobian at the fixed point (p^*, q^*) takes the form

$$\mathbf{J} = \frac{1}{\epsilon}\begin{pmatrix} \epsilon a & \epsilon b \\ c & d \end{pmatrix},$$

with

$$a = -k_p < 0, \quad b = -\frac{k_1}{(q^*+k_2)^2} < 0, \quad c = \frac{q^{*2}}{q^{*2}+k_4} > 0$$

and

$$d = -k_q + \frac{2k_4q^*p^*}{(q^{*2}+k_4)^2}.$$

At the fixed point (p^*, q^*) the slope of the p-nullcline $f(p,q) = 0$ (blue curve) is $-a/b$ whereas the slope of the q-nullcline $g(p,q) = 0$ (orange curve) is $-c/d$. It can be seen from the figure that

$$-\frac{c}{d} < -\frac{a}{b} < 0.$$

Since $a, b < 0$ and $c > 0$ it follows that $d > 0$. We can thus rearrange the inequality to deduce that

$$bc < ad.$$

Hence

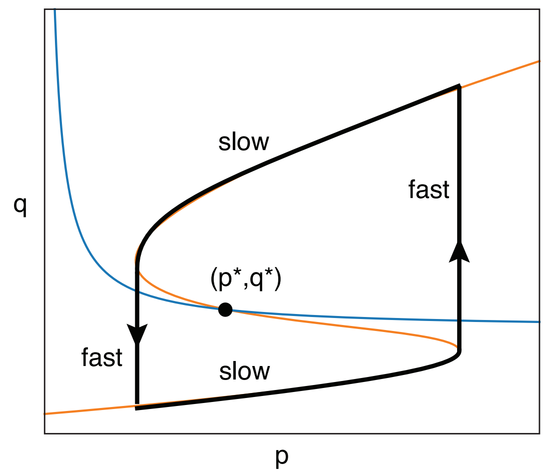
$$\text{Det}\,\mathbf{J} \equiv \frac{1}{\epsilon}(ad - bc) > 0.$$

Recall that the eigenvalues of a 2-matrix are

$$\lambda_\pm = \frac{1}{2}\left[\text{Tr}\mathbf{J} \pm \sqrt{(\text{Tr}\mathbf{J})^2 - 4\text{Det}\mathbf{J}}\right].$$

with Tr$\mathbf{J} = a + d/\epsilon$. Since $a < 0$ and $d > 0$ it follows that Tr$\mathbf{J} > 0$ for sufficiently small ϵ. We have also shown that Det$\mathbf{J} > 0$. Hence, the fixed point is an unstable node or spiral for sufficiently small ϵ. 6, B

(c) The following figure shows the approximate trajectory of a limit cycle oscillation for small ϵ. unseen ⇓



3, A

(d) (i) Setting $\epsilon = 0$ in the model equations gives

meth seen ⇓

$$\frac{dp(t)}{dt} = f(p,q), \quad g(p,q) = 0.$$

This defines the slow system in which the fast variable q lies on one of the stable branches of the q-nullcline. That is, we can set $q = q(p)$ with $g(p, q(p)) = 0$ and $q(p)$ lying on either the top or bottom branch of the nullcline. The slow dynamics along a stable branch is determined by the closed equation

$$\frac{dp}{dt} = f(p, q(p)).$$

Since $f(p, q(p) < 0$ on the top branch we have $dp/dt < 0$. On the other hand, $f(p, q(p)) > 0$ on the bottom branch so that $dp/dt > 0$. This explains the direction of motion around the limit cycle. When the slow dynamics reaches the end of a stable branch, the system rapidly jumps to the remaining stable branch.

4, A

(ii) Setting $t = \epsilon\tau$ we obtain the fast system

$$\frac{dp(\tau)}{d\tau} = \epsilon f(p,q), \quad \frac{dq(\tau)}{d\tau} = g(p,q),$$

In the limit $\epsilon \to 0$ we can take p to be a constant p_0 and we have the effective 1D system

$$\frac{dq}{d\tau} = g_0(q), \quad g_0(q) \equiv g(p_0, q).$$

For a given p_0 the fast variable will rapidly converge to a stable fixed point satisfying $g_0(q) = 0$ and $g_0'(q) < 0$. Using the fact that the slope of a given branch of the q-nullcline is $-\partial_q g/\partial_p g$ and $\partial_p g > 0$ everywhere, it follows that $g_0'(q) < 0$ on any branch whose slope is positive, namely, the top and bottom branches.

4, A

3. (a) The spatially homogeneous system is

seen $\Downarrow$

$$\frac{du}{dt} = -u + u^2 v, \quad \frac{dv}{dt} = b - u^2 v.$$

At a fixed point (u^*, v^*) we have $(u^*)^2 v^* = b$ which implies that $u^* = b$ and hence $v^* = 1/b$. Hence, by explicit construction there exists a unique homogeneous fixed point

$$(u^*, v^*) = (b, b^{-1}).$$

2, A

(b) Linearizing the RD system about the fixed point (u^*, v^*) using the perturbations

meth seen $\Downarrow$

$$u(x,t) = u^* + U(x,t), \quad v(x,t) = v^* + V(x,t).$$

gives

$$\begin{aligned}
\frac{\partial U}{\partial t} &= (-1 + 2u^* v^*)U(x,t) + u^{*2} V(x,t) + \frac{\partial^2 U(x,t)}{\partial x^2} \\
&= U(x,t) + b^2 V(x,t) + \frac{\partial^2 U(x,t)}{\partial x^2} \\
\frac{\partial V}{\partial t} &= -2u^* v^* U(x,t) - u^{*2} V x,t) + d\frac{\partial^2 V(x,t)}{\partial x^2} \\
&= -2U(x,t) - b^2 V(x,t) + \frac{\partial^2 V(x,t)}{\partial x^2}.
\end{aligned}$$

Setting

$$U(x,t) = U\mathrm{e}^{\lambda t}\cos kx, V(x,t) = V\mathrm{e}^{\lambda t}\cos kx,$$

yields the eigenvalue equation

$$\lambda \begin{pmatrix} U \\ V \end{pmatrix} = \left[\begin{pmatrix} 1 & b^2 \\ -2 & -b^2 \end{pmatrix} - \begin{pmatrix} k^2 & 0 \\ 0 & k^2 d \end{pmatrix}\right]\begin{pmatrix} U \\ V \end{pmatrix} \equiv \mathbf{J}(k)\begin{pmatrix} U \\ V \end{pmatrix}.$$

We have used the identities

$$\frac{d\mathrm{e}^{\lambda t}}{dt} = \lambda \mathrm{e}^{\lambda t}, \quad \frac{d^2\cos(kx)}{dx^2} = -k^2\cos(kx),$$

and cancelled the common factor $\mathrm{e}^{\lambda t}\cos(kx)$. Re$[\lambda]$ is the rate of growth or decay of the perturbation, whereas k is the wavenumber of the spatially periodic perturbation.

5, A

(c) (i) Given

meth seen $\Downarrow$

$$\mathbf{J}(0) = \begin{pmatrix} 1 & b^2 \\ -2 & -b^2 \end{pmatrix},$$

it follows that Tr$\mathbf{J}(k) = 1 - b^2$ and Det$\mathbf{J}(k) = b^2$. Since the eigenvalues of the Jacobian satisfy

$$\lambda_\pm(0) = \frac{1}{2}\left[\mathrm{Tr}[\mathbf{J}(0)] \pm \sqrt{\mathrm{Tr}[\mathbf{J}(0)]^2 - 4\mathrm{Det}[\mathbf{J}(0)]}\right],$$

we deduce that the eigenvalues have negative real parts when $b > 1$ and the fixed point is stable with respect to homogeneous perturbations.

2, A

unseen $\Downarrow$

(ii) We see that

$$\text{Tr}\mathbf{J}(k) = 1 - b^2 - k^2(1+d) < 0 \text{ for all } k \text{ when } b > 1.$$

In addition,

$$\text{Det}\mathbf{J}(k) = (k^2-1)(b^2+dk^2) + 2b^2 = dk^4 - (d-b^2)k^2 + b^2.$$

From the fundamental theorem of algebra we can factorize the determinant according to

$$\text{Det}\mathbf{J}(k) = d(k^2-\mu_+)(k^2-\mu_-).$$

where $\mu_\pm$ are the roots of the characteristic equation $d\mu^2 - (d-b^2)\mu + b^2 = 0$. If $\mu_\pm$ are real and positive with $\mu_+ \geq \mu_-$, say, then $\text{Det}\mathbf{J}(k) < 0$ for all $k \in (k_-, k_+)$ with $k_\pm = \sqrt{\mu_\pm}$. From the characteristic equation we find that

$$\mu_\pm = \frac{1}{2d}\left[d - b^2 \pm \sqrt{(d-b^2)^2 - 4db^2}\right]$$

The roots $\mu_\pm$ will be real and positive provided that $d > b^2$ and

$$d^2 - 6db^2 + b^4 > 0 \implies \left(\frac{d}{b^2}\right)^2 - 6\frac{d}{b^2} + 1 > 0 \implies (d-d_+)(d-d_-) > 0,$$

with $d_\pm = 3 \pm \sqrt{8}$. Combining with the condition $d/b^2 > 1$ we deduce that $\mu_\pm$ are real and positive provided that $d > d_+$. In summary, the condition $b > 1$ ensures that the fixed point of the homogeneous system is stable and that $\text{Tr}[\mathbf{J}(k)] < 0$ for all k. Since the eigenvalues of the Jacobian satisfy

$$\lambda_\pm(k) = \frac{1}{2}\left[\text{Tr}[\mathbf{J}(k)] \pm \sqrt{\text{Tr}[\mathbf{J}(k)]^2 - 4\text{Det}[\mathbf{J}(k)]}\right],$$

we see that the band of modes $k \in (k_-, k_+)$ are unstable provided that $d > d_+$. We thus obtain the following necessary and sufficient conditions:

$$b > 1, \quad \frac{d}{b^2} > 3 + \sqrt{8}.$$

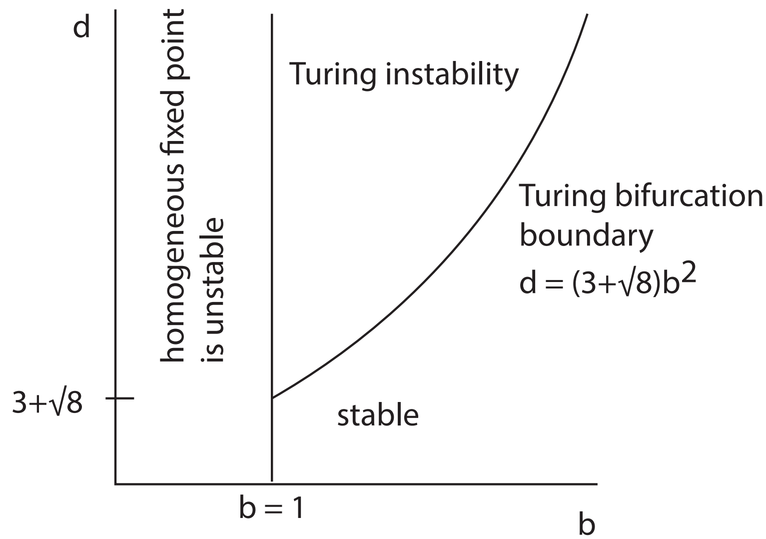
5, D

(iii) The critical wavenumber k_c for a Turing instability occurs when $k_+ = k_-$, that is, when $(d-b^2)^2 = 4db^2$ or equivalently $d = (3+\sqrt{8})b^2$. Hence unseen $\Downarrow$

$$k_c^2 = \mu_\pm = \frac{d-b^2}{2d} = \frac{2\sqrt{db^2}}{2d} = \sqrt{b^2/d} = \sqrt{\frac{1}{3+\sqrt{8}}}.$$

3, C

(d) Diagram shows the regions in the (b, d)-parameter plane where the homogeneous fixed point is (i) unstable to homogeneous perturbations and (ii) stable to homogeneous perturbations but unstable to spatially varying unseen $\Downarrow$



patterns. $\boxed{3, \text{C}}$

4. Consider the master equation

$$\frac{dp_0}{dt} = \mu p_1(t) - a p_0(t),$$
$$\frac{dp_n}{dt} = -[(\lambda+\mu)n + a]p_n(t) + \mu(n+1)p_{n+1}(t) + [\lambda(n-1)+a]p_{n-1}(t).$$

with $p_n(0) = P_{nN}(0) = \delta_{n,N}$. $\boxed{\text{meth seen} \Downarrow}$

(a) (i) Multiplying the n-th equation by n and summing over n gives

$$\sum_{n=0}^{\infty} n\frac{dp_n}{dt} = \sum_{n=0}^{\infty} n[\lambda(n-1)+a]p_{n-1} + \sum_{n=0}^{\infty} n[\mu(n+1)p_{n+1} - \sum_{n=0}^{\infty} n[(\lambda+\mu)n + a]p_n.$$

Since,

$$\sum_{n=0}^{\infty} np_{n-1} = \sum_{n=0}^{\infty}(n+1)p_n. \quad \sum_{n=0}^{\infty} n(n-1)p_{n-1} = \sum_{n=0}^{\infty} n(n+1)p_n,$$
$$\sum_{n=0}^{\infty} n(n+1)p_{n+1} = \sum_{n=0}^{\infty} n(n-1)p_n$$

we have

$$\sum_{n=0}^{\infty} n\frac{dp_n}{dt} = \frac{d}{dt}\sum_{n=0}^{\infty} nP_n = a\sum_{n=0}^{\infty} p_n + (\lambda-\mu)\sum_{n=0}^{\infty} np_n.$$

Finally, setting $m(t) = \sum_{n=N}^{\infty} np_n(t)$ we obtain the following ODE for the mean:

$$\frac{dm}{dt} = a + (\lambda-\mu)m.$$

$\boxed{5, \text{B}}$

(ii) If $\lambda > \mu$ then $m(t)$ grows exponentially as $\mathrm{e}^{(\lambda-\mu)t}$, whereas if $\lambda = \mu$ then it grows linearly as at. $\boxed{3, \text{A}}$

(b) (i) Now suppose $a = 0$ so that $n = 0$ is an absorbing state. Let π_m denote the probability of absorption at zero given that the system is initially at state m. Since the transitions $m \to m+1$ and $m \to m-1$ occur with probability $\lambda/(\lambda+\mu)$ and $\mu/(\lambda+\mu)$, respectively, we have the iterative equation $\boxed{\text{unseen} \Downarrow}$

$$\pi_m = \frac{\lambda}{\lambda+\mu}\pi_{m+1} + \frac{\mu}{\lambda+\mu}\pi_{m-1},$$

with $\pi_0 = 1$ and $0 \le \pi_m \le 1$ for $m \ge 1$. Plugging in the trial solution $\pi_m = \Gamma^m$ we have

$$\Gamma^m = \frac{\lambda}{\lambda+\mu}\Gamma^{m+1} + \frac{\mu}{\lambda+\mu}\Gamma^{m-1}.$$

Dividing through by Γ^{m-1} and rearranging yields the quadratic equation

$$\frac{\lambda}{\lambda+\mu}\Gamma^2 - \Gamma + \frac{\mu}{\lambda+\mu} = 0 \implies \lambda\Gamma^2 - (\lambda+\mu)\Gamma + \mu = 0$$
$$\implies (\lambda\Gamma - \mu)(\Gamma - 1) = 0$$

We thus have the two roots $\Gamma = \mu/\lambda, 1$. The general solution is

$$\pi_m = A\left(\frac{\mu}{\lambda}\right)^m + B.$$

If $\mu > \lambda$ then $A = 0$ (otherwise $\pi_m > 1$ for large m) and $B = 1$. If $\lambda = \mu$ then there is a single solution $\Gamma = 1$. We deduce that

$$\pi_m = 1 \text{ for all } m \geq 0 \text{ if } \mu \geq \lambda$$

On the other hand, we have the solution $B = 0$ and $A = 1$ when $\lambda > \mu$ (so that $\pi_0 = 1$) and

$$\pi_m = \left(\frac{\mu}{\lambda}\right)^m \text{ for all } m \geq 0 \text{ if } \mu < \lambda.$$

$\boxed{6, \text{D}}$

$\boxed{\text{seen} \Downarrow}$

(ii) The generating function $\mathcal{P}(z,t) = \sum_{n=0}^{\infty} z^n p_n(t)$ satisfies the first-order PDE

$$\frac{\partial \mathcal{P}}{\partial t} = (z-1)(\lambda z - \mu)\frac{\partial \mathcal{P}}{\partial z},$$

with initial condition $\mathcal{P}(z,0) = z^N$. We solve this equation using the method of characteristics. Along the curves of constant s, we have

$$\frac{d\mathcal{P}}{d\tau} = 0, \quad \frac{dt}{d\tau} = 1, \quad \frac{dz}{d\tau} = (1-z)(\lambda z - \mu)$$

and therefore,

$$\mathcal{P} = c_1, \quad t = \tau + c_2, \quad \frac{z - \mu/\lambda}{1-z} = c_3 e^{(\lambda-\mu)\tau}.$$

The intial data along the Cauchy curve along is

$$t(s,0) = 0, \quad z(s,0) = s, \quad P(s,0) = s^N$$

and therefore, $t = \tau$ ($c_2 = 0$), and

$$c_3 = \frac{s - \mu/\lambda}{1-s}.$$

It follows that

$$s = \frac{e^{(\mu-\lambda)t}(\lambda z - \mu) - \mu(z-1)}{e^{(\mu-\lambda)t}(\lambda z - \mu) - \lambda(z-1)}$$

and thus,

$$\mathcal{P}(z,t) = \left(\frac{e^{(\mu-\lambda)t}(\lambda z - \mu) - \mu(z-1)}{e^{(\mu-\lambda)t}(\lambda z - \mu) - \lambda(z-1)}\right)^N, \quad \lambda \neq \mu.$$

Finally,

$$p_0(t) = \mathcal{P}(0,t) = \left(\frac{\mu - \mu e^{(\mu-\lambda)t}}{\lambda - \mu e^{(\mu-\lambda)t}}\right)^N.$$

so that

$$\lim_{t\to\infty} p_0(t) = \begin{cases} 1, & \text{if } \lambda \leq \mu \\ \left(\frac{\mu}{\lambda}\right)^N, & \text{if } \lambda > \mu. \end{cases}$$

$\boxed{6, \text{C}}$

5. (a) (i) The set of chemical reactions is as follows:

$$\emptyset \xrightarrow{k_3} X_1, \quad X_1 \xrightarrow{k} \emptyset$$
$$X_1 + X_1 \xrightarrow{k_1} X_2, \quad X_2 \xrightarrow{k_2} X_1 + X_1.$$

$\boxed{4, \text{M}}$

(ii) Rewrite the kinetic equations as

$$\frac{dx_1}{dt} = k_3 - kx_1 - 2k_1x_1^2 + 2k_2x_2 \equiv \sum_{a=1}^{4} S_{1a}f_a(\mathbf{x}).$$

and

$$\frac{dx_2}{dt} = 2k_1x_1^2 - 2k_2x_2 \equiv \sum_{a=1}^{4} S_{2a}f_a(\mathbf{x}).$$

We see that

$S_{11} = 1,\ S_{12} = -1,\ S_{13} = -2,\ S_{14} = 2,\ S_{21} = 0,\ S_{22} = 0,\ S_{23} = 2,\ S_{24} = -2$

and

$$f_1(\mathbf{x}) = k_3,\ f_2(\mathbf{x}) = kx_1,\ f_3(\mathbf{x}) = k_1x_1^2,\ f_4(\mathbf{x}) = k_2x_2.$$

$\boxed{4, \text{M}}$

(b) (i) First rewrite the kinetic equations in terms of (mean) numbers $n_j = \Omega x_j$ where Ω denotes the system size:

$$\frac{dn_1}{dt} = \Omega\left(k_3 - \frac{kn_1}{\Omega} - 2\frac{k_1n_1^2}{\Omega^2} + \frac{2k_2n_2}{\Omega}\right) = \Omega\sum_{a=1}^{4} S_{1a}f_a(\mathbf{n}/\Omega)$$

and

$$\frac{dn_2}{dt} = \Omega\left(2\frac{k_1n_1^2}{\Omega^2} - 2\frac{k_2n_2}{\Omega}\right) = \Omega\sum_{a=1}^{4} S_{2a}f_a(\mathbf{n}/\Omega).$$

Let $N_i(t)$ denote the stochastic number of molecules of species i at time t and introduce the probability distribution for $\mathbf{n} = (n_1, n_2)$:

$$P(\mathbf{n}, t) = \text{Prob}[N_1(t) = n_1, N_2(t) = n_2].$$

In an infinitesimal time interval Δt, one of the following events can occur

1. $N_i(t + \Delta t) = N(t) + S_{ia}$ for $i = 1, 2$ and a single reaction $a = 1, \ldots, 4$, which occurs with probability $\Omega f_a(\mathbf{N}(t)/\Omega)\Delta t$.
2. $N_i(t + \Delta t) = N_i(t)$ for $i = 1, 2$ with probability $1 - \Omega\sum_a f_a(\mathbf{N}(t)/\Omega)\Delta t$.

Hence, introducing the vector $\mathbf{S}_a = (S_{1a}, S_{2a})$, we have

$$P(\mathbf{n}, t + \Delta t) = \sum_{a=1}^{4}\left[\Omega\Delta t f_a([\mathbf{n} - \mathbf{S}_a]/\Omega)P(\mathbf{n} - \mathbf{S}_a, t)\right.$$
$$\left. + P(\mathbf{n}, t)\left(1 - \Omega\sum_a f_a(\mathbf{n}/\Omega)\Delta t\right)\right].$$

Subtracting $P(\mathbf{n},t)$ from both sides, dividing by Δt and taking the limit $\Delta t \to 0$ yields the chemical master equation

$$\frac{dP(\mathbf{n},t)}{dt} = \Omega \sum_{a=4}^{R} \Big(f_a([\mathbf{n}-\mathbf{S}_a]/\Omega) P(\mathbf{n}-\mathbf{S}_a,t) - f_a(\mathbf{n}/\Omega)P(\mathbf{n},t) \Big).$$

$\boxed{6, \text{M}}$

(ii) The first step is to set $f_a(\mathbf{n}/\Omega)P(\mathbf{n},t) \to f_a(\mathbf{x})p(\mathbf{x},t)$ with $\mathbf{x} = \mathbf{n}/\Omega$ treated as a continuous vector. Carrying out a Taylor expansion of the master equation to second order in $1/\Omega$ using and Taylor expand terms of the form

$$h(\mathbf{x}-\mathbf{S}_a/\Omega) = h(\mathbf{x}) - \Omega^{-1} \sum_{i=1,2} S_{ia} \frac{\partial h}{\partial x_i} + \frac{1}{2\Omega^2} \sum_{i,j=1,2} S_{ia}S_{ja} \frac{\partial^2 h(\mathbf{x})}{\partial x_i \partial x_j} + O(\Omega^{-3})$$

etc. gives

$$\frac{\partial p}{\partial t} = -\sum_{i=1,2} \frac{\partial A_i(\mathbf{x})p(\mathbf{x},t)}{\partial x_i} + \frac{1}{2\Omega} \sum_{i,j=1,2} \frac{\partial^2 D_{ij}(\mathbf{x})p(\mathbf{x},t)}{\partial x_i \partial x_j},$$

where

$$A_i(\mathbf{x}) = \sum_{a=1}^{4} S_{ia} f_a(\mathbf{x}), \quad D_{ij}(\mathbf{x}) = \sum_{a=1}^{4} S_{ia}S_{ja} f_a(\mathbf{x}).$$

Using part (a.ii),

$$\begin{aligned} A_1(\mathbf{x}) &= k_3 - kx_1 - 2k_1x_1^2 + 2k_2x_2, \quad A_2(\mathbf{x}) = k_1x_1^2 - k_2x_2, \\ D_{11}(\mathbf{x}) &= k_3 + kx_1 + 4k_1x_1^2 + 4k_2x_2, \quad D_{22} = k_1x_1^2 + k_2x_2 \\ D_{12}(\mathbf{x}) &= -4k_1x_1^2 - 4k_2x_2. \end{aligned}$$

$\boxed{6, \text{M}}$

Review of mark distribution:
Total A marks: 32 of 32 marks
Total B marks: 20 of 20 marks
Total C marks: 12 of 12 marks
Total D marks: 16 of 16 marks
Total Mastery marks: 20 of 20 marks

MATH70014 Mathematical Biology Markers Comments

Question 1	Most students obtained full marks in part (a), even though there was a typo stating that the fraction of "infected males" is u/(u+v), when it should have been "uninfected males". Students struggled to implement the phase-plane analysis in (biii,biv).
Question 2	Students should have noted that both the q and p nullclines are negative, and that the q-nullcline has a greater negative slope. This was how to establish that set(J) is positive. A similar example was presented in the lectures.
Question 3	Most students did well in this question. A few forgot to explicitly mention the decomposition into eigenfunctions (Fourier modes).
Question 4	Students generally struggled to answer the unseen question (bi). However, if the hint had been followed explicitly, then the answer would have been clear.
Question 5	Not many students completed this question, possibly because they ran out of time. Part (a) was covered in the lecture course, whereas parts (b,c) involved reproducing part of the extra material.