Examples sheets for Block C

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Modelling biological systems using differential equations
Discussion of these exercises should form the basis of the first four Mathematical Biology supervisions in Lent.
Students should complete one sheet per week, although supervisors might not expect students to attempt all questions on every sheet.
Questions have been designed such that Sheet A should be accessible after Lectures 1-3; Sheet B after Lectures 4-6; Sheet C after Lectures 7-9 and Sheet D after Lectures 10-12.
Final numeric/algebraic answers (where applicable) are provided for reference at the end of the document. Full worked solutions will be provided after supervisions have been completed.

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Sheet A. Basic skills and the exponential and monomolecular models

Question 1. Revision of calculus, sketching and logarithms

(a) Differentiate with respect to t:

(i) $y = t^{10}\sin 2t$; (ii) $y = \exp(3t^7)$; (iii) $y = t^2 e^{5t}$; (iv) $y = \frac{(2t-3)}{\sqrt{t}}$;
(v) $y = (2t^2 + \sin t + 2)^3$; (vi) $y = \frac{\cos(2t)+1}{t^2}$; (vii) $y = t^{2t}$; (viii) $y = \exp(e^{10t})$;
(ix) $y = \frac{t^2+1}{t+1}$; (x) $y = t^5 \log t + \cos t$.

(b) Obtain the following integrals:

(i) $\int t^{10} dt$; (ii) $\int \left(\frac{t^{12}+t^5}{t^{10}}\right) dt$; (iii) $\int t^{-8} dt$; (iv) $\int \frac{1}{2t} dt$;
(v) $\int \frac{1}{4t+3} dt$; (vi) $\int \frac{1}{t(t-1)} dt$ (vii) $\int e^{10t} dt$; (viii) $\int (3t+10)^3 dt$;
(ix) $\int \cos(5t+3) dt$; (x) $\int e^{2t+1} dt$.

(c) Sketch the following functions $y(t)$:

(i) $y = t^2 + 5t + 6$; (ii) $y = \frac{1}{t+2}$; (iii) $y = 2te^t$;
(iv) $y = 5(1 - e^{-10t})$; (v) $y = e^{t/4}\cos(6\pi t)$.

(d) Solve each of the following for t:

(i) $2^t = 32$; (ii) $2^{3t} = 15$; (iii) $2^t = 4^{3t}$; (iv) $5^{t-1} = 4^{1-3t}$.

Question 2. Exponential growth

A model used to represent the dynamics of a population of size $y(t)$ at time t is

$$\frac{dy}{dt} = \beta y,$$

where β is a positive parameter.

(a) Briefly explain the key biological assumption underlying this model.
(b) Solve the model, assuming that the initial population size is y_0.
(c) Sketch the solution of the model, illustrating carefully any effect(s) of changes to β and y_0.
(d) Find an expression for the time taken for the population to increase by a factor of 10.

Question 3. Radiocarbon dating

Write and solve a differential equation describing the decay of ^{14}C. A unit volume sample of an old piece of oak taken from a museum has an activity of ^{14}C that is one third that of a similar volume of a modern piece of oak. Given that the half-life for ^{14}C is 5730 years, how old is the museum piece?

Question 4. Immigration and birth or death

A group of organisms living in an isolated habitat is subject to immigration at constant rate α, reproduction at per capita rate β, and death at per capita rate γ, where α, β and γ are positive constants

(a) Write down an expression describing the evolution of $Y(t)$, the size of the population at time t.

(b) Solve your model to find $Y(t)$, given that the habitat was initially empty.

(c) Sketch your solution and biologically interpret the changes to your sketches as the values of the parameters are changed.

(d) What happens if $\beta = \gamma$?

Question 5. Newton's law of cooling

A body is found indoors at 16.00h. The temperature of the body (T) is 27^{o}C; by 19.00h, it has fallen to 24^{o}C. The room temperature is assumed to have remained constant at 10^{o}C and the original body temperature may be assumed to be 37^{o}C.

(a) Assuming that the rate of cooling of the body was proportional to the difference between room temperature and body temperature, construct a simple equation for $T(t)$ and solve it.

(b) Use the information about cooling between 16.00h and 19.00h to estimate the rate parameter for the cooling process and then estimate the time of death to the nearest hour.

Sheet B. Separation of variables, partial fractions, Bernoulli equations and the logistic model

Question 1. Separation of variables and verifying solutions

Solve the following four differential equations using separation of variables.

(a) $\frac{dy}{dt} = 4t^3$ with $y(0) = 1$; **(b)** $(t+1)\frac{dy}{dt} = y$ with $y(1) = 4$;
(c) $\frac{dy}{dt} = -\frac{2y}{(1+t)^3}$ with $y(0) = 20$; **(d)** $e^t \frac{dy}{dt} = \sqrt{y}$ with $y(0) = 4$.

In all cases verify your solution is correct by checking it in the differential equation and by verifying the expected value of y is obtained at $t = 0$ ((a), (c) and (d)) or $t = 1$ ((b)).

Question 2. Partial fractions

Express the following functions in partial fractions.

(a) $\frac{1}{(x-2)(x+3)}$ **(b)** $\frac{1}{x^3+5x^2+6x}$ **(c)** $\frac{3x+11}{x^2-x-6}$.

Use the partial fractions decomposition to write down the integral of each function with respect to x.

Question 3. Solving the logistic model

The logistic model is given by

$$\frac{dN}{dt} = \beta N \left(1 - \frac{N}{\kappa}\right),$$

with $N = N_0$ when $t = 0$ (where $N_0 < \kappa$).

(a) Suggest a plausible biological meaning of the equation.
(b) Solve this model via separation of variables
(c) Verify your solution is correct.
(d) Sketch the solution of the model.

Question 4. Treating the logistic model as a Bernoulli equation

The growth of root systems of wheat, *Triticum aestivum*, can be modelled using

$$\frac{dN}{dt} = \alpha N - \gamma N^2,$$

where α is the rate of growth and γ reflects the finite resources for the production of new roots.

(a) Using the (Bernoulli) substitution $Y = 1/N$, transform and solve this model (given that $N(0) = 1$).
(b) Compare your solution to (a) with your answer to Question 3 to verify it is correct.

Question 5. An extension to logistic growth

Chalara dieback is a disease of ash trees caused by the fungus *Chalara fraxinea*, first detected in the United Kingdom in 2012. Fungal spores can be blown in from Europe on the wind and cause primary infections. Infected ash trees within the United Kingdom then go on to cause further infections via secondary spread. The following model is proposed for the number of infected ash trees in the United Kingdom

$$\frac{dI}{dt} = (\alpha + \beta I)(N - I).$$

The positive parameters α, β and N are all constant.

(a) Explain the model, paying particular attention to the meaning of the parameters α, β and N.

(b) Solve the model to find $I(t)$ assuming no ash trees are infected at $t = 0$.

(c) Find the value of $I(t)$ when the number of infected trees is increasing most quickly.

(d) Sketch I as a function of t, distinguishing any cases that arise depending on values of α, β and N.

(e) Suggest three distinct ways in which the model might be too simplistic.

Sheet C. Qualitative analysis and extending the basic models

Question 1. Direction fields

Obtain sketches of the solutions to the following differential equations by sketching the direction field (where β and κ are positive constants):

$$\textbf{(a)}\quad \frac{dy}{dt} = \frac{1}{1+y};\quad \textbf{(b)}\quad \frac{dy}{dt} = ty;\quad \textbf{(c)}\quad \frac{dy}{dt} = \beta(\kappa - y).$$

Demonstrate that your sketches have the correct form by solving the equations.

Question 2. An extension to the monomolecular model

A model of an epidemic of a soil-borne disease allows the amount of inoculum in the soil to decrease over time. The number of plants infected at time t, $Y(t)$, then changes according to the differential equation

$$\frac{dY}{dt} = \beta e^{-\alpha t}(\kappa - Y),$$

where α, β and κ are positive constants.

(a) Suggest plausible biological meanings for the parameters α, β and κ.
(b) Solve the equation assuming that $Y(0) = 0$.
(c) Verify your solution is correct.
(d) What is the long term size of the population?
(e) When is the population size increasing most quickly? Explain why this is.
(f) Use your answers to (d) and (e) to sketch the number of infected plants over time.
(g) Check your answer to (f) is consistent with the differential equation's direction field.

Question 3. Another extension to logistic growth

The number of students in a Cambridge college, $R(t)$, who are aware of a certain scurrilous rumour, may be modelled by

$$\frac{dR}{dt} = \beta R(N - R),$$

where N is the total number of students in the college, t is the time since the start of the academic year, and β is a positive parameter.

(a) Explain the right hand side of the model, paying careful attention to the meaning of β.
(b) Solve the model, assuming 1% of students know the rumour at the start of the year.

Like all rumours, this one becomes less interesting with time. An updated model is proposed

$$\frac{dR}{dt} = \beta e^{-\gamma t} R(N - R),$$

where γ is a positive parameter.

(c) Explain the alteration to the model, carefully explaining the meaning of the parameter γ.
(d) Solve the updated model.

(e) Given that no more than 75% of the student body ever become aware of the rumour, assuming again that 1% of students initially know it, prove that γ must satisfy

$$\gamma > \frac{\beta N}{\ln(297)}.$$

Explain why, to ensure no more than a certain fraction of students ever hear the rumour, the inequality specifies a *lower* bound on the admissible set of values of γ.

Question 4. A von Bertalanffy model

The area at time t of a single circular *Phytophthora infestans* lesion growing across the surface of a leaf, $A(t)$, is modelled using the von Bertalanffy equation

$$\frac{dA}{dt} = \lambda\sqrt{A} - \mu A,$$

in which λ and μ are positive constants. The initial lesion area, A_0, is very small.

(a) Suggest a plausible mechanistic basis for the model.

(b) Find all equilibrium values of A, and examine their stability by sketching $\frac{dA}{dt}$ as a function of A.

(c) Determine an expression for $A(t)$ (Hint: you may find substitution $v = \sqrt{A}$ to be of use).

(d) Find the value of $A(t)$ as $t \to \infty$ according to (c). Comment in the light of (b).

(e) Find the value of A at which the area is increasing most rapidly. Determine the corresponding time.

(f) Sketch your solution for $A(t)$.

Question 5. An extension to exponential growth

A model for the number of undifferentiated cells in a plant meristem (N) as a function of time (t) is

$$\frac{dN}{dt} = \mu N.$$

The relative growth rate (μ) is itself a function of t

$$\frac{d\mu}{dt} = -D\mu_0.$$

The constants D and μ_0 are both positive, and μ_0 is the initial value of μ.

(a) Assuming that the meristem contains N_0 cells initially, show that

$$N = N_0 \exp\left(\mu_0\left(t - \frac{Dt^2}{2}\right)\right).$$

(b) Show that the number of cells in the meristem is changing most rapidly when

$$(1 - Dt)^2 = \frac{D}{\mu_0}.$$

(c) Sketch your solution for N as a function of t.

Sheet D. Series expansions, analytic tests for stability and linking the models

Question 1. Maclaurin and Taylor series

(a) Obtain the first three non-zero terms of the Maclaurin series of the following functions

$$\text{(i)}\quad y = e^{2t};\quad \text{(ii)}\quad y = \tfrac{1}{1+t};\quad \text{(iii)}\quad y = \tfrac{1}{1+t^2}.$$

(b) For the functions in (aii) and (aiii), above, instead obtain Taylor series about the point $t = 1$.

Question 2. Analytic determination of stability properties of equilibria

Find all equilibria of the following models, and characterise the stability of the equilibria by using the analytical technique described in Lecture 11.

(a) $\frac{dY}{dt} = Y(1-Y)(Y-10)$; **(b)** $\frac{dY}{dt} = \sin Y$ **(c)** $\frac{dY}{dt} = (3Y^2 - 2Y - 1)e^{2Y}$.

Confirm your results using the graphical method from Lecture 7.

Question 3. A model of fishing

Population dynamics of cod in the absence of fishing can be described by a logistic equation

$$\frac{dY}{dt} = G(Y) = \beta Y \left(1 - \frac{Y}{\kappa}\right).$$

where β and κ are positive parameters. If the population is also fished, then

$$\frac{dY}{dt} = G(Y) - C(Y),$$

in which $C(Y)$ is the rate at which fish are caught when the population size is Y. A model of fishing assumes fish are removed at a rate proportional to the size of the fish population

$$C(Y) = \alpha Y$$

where α is a positive parameter. However, if the catch rate is too high, the fish population can collapse.

(a) Find the equilibria of the model with fishing

(b) Verify that the positive equilibrium is stable if $\alpha < \beta$. What is the biological basis of this condition?

(c) Find the rate at which fish are caught at the positive equilibrium population.

A modified formula for the catch is proposed

$$C(Y) = \frac{\alpha Y}{1 + \omega Y}.$$

(d) Suggest a plausible interpretation of the new catch rate.

(e) Show that the updated model possesses three equilibria

$$\left(\omega + \frac{1}{\kappa}\right)^2 > \frac{4\omega\alpha}{\kappa\beta}.$$

(note you are *not* required to determine whether the equilibria are: i) distinct; ii) non-negative).

Question 4. Levins' metapopulation model

A metapopulation is a collection of spatially-separated but interacting populations. A particularly influential model simplifies within-patch dynamics so that only the presence or absence of the species is considered. Populations in occupied patches lead to colonisation of empty patches, but occupied patches can lose their population due to local extinction. The total number of patches is assumed to be very large. The model is used to track the proportion of occupied patches, p, in a particular region, and the dynamics are governed by

$$\frac{dp}{dt} = cp(1-p) - ep,$$

where c and e are positive parameters.

(a) Explain the model, paying particular attention to the meaning of c and e.

(b) Give a condition on c and e that ensures that the non-zero equilibrium proportion of occupied patches is positive, and give a short biological explanation of this condition.

An extension to the model additionally represents immigration from a very large population external to the region under consideration. The proportion of occupied patches then follows

$$\frac{dp}{dt} = (m+cp)(1-p) - ep,$$

where m is an additional positive parameter.

(c) Explain the updated model, paying particular attention to the meaning of m.

(d) Demonstrate that the new model always has two equilibria, and that these equilibria are always of opposite sign (i.e. one is positive and one is negative).

(e) By sketching the graph of dp/dt as a function of p, examine the stability of the positive equilibrium.

(f) Confirm this result analytically (i.e. by using the techniques of Lecture 11).

(g) Sketch a graph of the proportion of occupied patches in the region as a function of time, assuming that the region is entirely empty initially.

Question 5. Using the output of one model as the input to another

A given population has seasonal reproduction, and the rate of change in population growth is given by

$$\begin{aligned} \frac{dN}{dt} &= -\beta_1 N \qquad 0 \le t < \frac{3T}{4}, \\ &= \beta_2 N \qquad \frac{3T}{4} \le t < T, \end{aligned}$$

where T is the total season length, and β_1 and β_2 are both positive.

(a) Solve the model for an entire season, given that the population was N_0 when $t = 0$.

(b) Prove that the condition for the population to be N_0 at the end of the season is $\beta_2 = 3\beta_1$.

(c) Comment on the biological meaning of the condition from (b).

(d) The model may be applied to a population over more than one season. Sketch the form of the population over three seasons in each of the cases (i) $\beta_2 < 3\beta_1$; (ii) $\beta_2 = 3\beta_1$; (iii) $\beta_2 > 3\beta_1$.

Numerical and algebraic answers

Sheet A, Question 1

a)

(i)	$2t^9(t\cos(2t)+5\sin(2t))$	(ii)	$21t^6e^{3t^7}$
(iii)	$te^{5t}(5t+2)$	(iv)	$\frac{1}{2t\sqrt{t}}(2t+3)$
(v)	$3(4t+\cos t)(2t^2+\sin t+2)^2$	(vi)	$-\frac{2}{t^3}(t\sin(2t)+\cos(2t)+1)$
(vii)	$2(\log t+1)t^{2t}$	(viii)	$10\exp(10t+e^{10t})$
(ix)	$\frac{t^2+2t-1}{(t+1)^2}$	(x)	$y=t^4(5\log t+1)-\sin t$

b) (Note: all answers include an arbitrary constant of integration, which has been omitted below)

(i)	$\frac{1}{11}t^{11}$	(ii)	$\frac{t^3}{3}-\frac{1}{4t^4}$	(iii)	$-\frac{1}{7t^7}$	(iv)	$\frac{1}{2}\log t$	(v)	$\frac{1}{4}\log(4t+3)$
(vi)	$\log\left(\frac{t-1}{t}\right)$	(vii)	$\frac{1}{10}e^{10t}$	(viii)	$\frac{1}{12}(3t+10)^4$	(ix)	$\frac{1}{5}\sin(5t+3)$	(x)	$\frac{1}{2}e^{2t+1}$

d)

(i) $t=5$ (ii) $t=\frac{\log(15)}{\log(8)}$ (iii) $t=0$ (iv) $t=\frac{\log(20)}{\log(320)}$

Sheet A, Question 2

b) $y(t)=y_0e^{\beta t}$.
d) $T_{10}=\frac{1}{\beta}\log(10)$

Sheet A, Question 3

Just over $9,000$ years.

Sheet A, Question 4

a) $\frac{dY}{dt}=\alpha+(\beta-\gamma)Y$.
b) If $\omega=\gamma-\beta$ then $Y(t)=\frac{\alpha}{\omega}(1-e^{-\omega t})$.
d) $\frac{dY}{dt}=\alpha$ and so $Y(t)=\alpha t$.

Sheet A, Question 5

a) $\frac{dT}{dt}=-\gamma(T-10)$. If we take $t=0$ to correspond to time of death, then $T=10+27e^{-\gamma t}$ (other choices of $t=0$ would lead to different constants in front of the exponential term).
b) The rate parameter is $\gamma=\frac{1}{3}\log\left(\frac{17}{14}\right)\approx 0.0647$ hr^{-1}. The time of death is just before 9am.

Sheet B, Question 1

a) $y(t)=t^4+1$
b) $y(t)=2(t+1)$
c) $y(t)=20\exp\left(\frac{1}{(1+t)^2}-1\right)$
d) $y(t)=\frac{(5-e^{-t})^2}{4}$

Sheet B, Question 2

a) Since

$$\frac{1}{(x-2)(x+3)} = \frac{1}{5}\left(\frac{1}{x-2} - \frac{1}{x+3}\right),$$

it must be that

$$\int \frac{1}{(x-2)(x+3)}dx = \frac{1}{5}\left(\log(x-2) - \log(x+3)\right) + C.$$

b) Since

$$\frac{1}{x^3+5x^2+6x} = \frac{1}{6x} - \frac{1}{2(x+2)} + \frac{1}{3(x+3)},$$

it must be that

$$\int \frac{1}{x^3+5x^2+6x}dx = \frac{1}{6}\log x - \frac{1}{2}\log(x+2) + \frac{1}{3}\log(x+3) + C.$$

c) Since

$$\frac{3x+11}{x^2-x-6} = \frac{4}{x-3} - \frac{1}{x+2},$$

it must be that

$$\int \frac{3x+11}{x^2-x-6}dx = 4\log(x-3) - \log(x+2).$$

Sheet B, Question 3

b) $N = \frac{\kappa}{1+Je^{-\beta t}}$ with $J = \frac{\kappa - N_0}{N_0}$ (or equivalent).

Sheet B, Question 5

b) The solution is anything equivalent to

$$I = \frac{\alpha N(1-\exp(-(\beta N+\alpha)t))}{\beta N\exp(-(\beta N+\alpha)t)+\alpha},$$

c) $I = \frac{1}{2}\left(N - \frac{\alpha}{\beta}\right)$.

Sheet C, Question 1

a) $t = y + y^2/2 - C$ (where C is a constant).
b) $y = A\exp(t^2/2)$ (where A is a constant).
c) $y = \kappa(1-Je^{-\beta t})$ (where J is a constant).

Sheet C, Question 2

b) $Y = \kappa\left(1 - \exp\left(-\frac{\beta}{\alpha}(1-e^{-\alpha t})\right)\right)$.
d) $Y \to \kappa(1-e^{-\beta/\alpha})$.

Sheet C, Question 3

b) $R = \frac{N}{1+99e^{-\beta N t}}$.

d) $R = \frac{N}{1+99\exp\left(-\frac{\beta N}{\gamma}(1-e^{-\gamma t})\right)}$.

Sheet C, Question 4

b) $\bar{A} = 0$ and $\bar{A} = (\lambda/\mu)^2$

c) $A = \left(\frac{\lambda}{\mu}\right)^2 \left(1 - Je^{-\mu t/2}\right)^2$ where $J = 1 - \frac{\mu\sqrt{A_0}}{\lambda}$.

d) As $t \to \infty$, $A \to (\lambda/\mu)^2$.

e) $A = \frac{1}{4}\left(\frac{\lambda}{\mu}\right)^2$, when $t = \frac{2}{\mu}\log\left(2\left(1 - \frac{\mu\sqrt{A_0}}{\lambda}\right)\right)$.

Sheet D, Question 1

ai) $y(t) = 1 + 2t + 2t^2 + \cdots$.

aii) $y(t) = 1 - t + t^2 + \cdots$.

aiii) $y(t) = 1 - t^2 + t^4 + \cdots$.

bii) Either

$$y(1+h) = 1/2 - h/4 + h^2/8 + \cdots,$$

or

$$y(t) = 1/2 - (t-1)/4 + (t-1)^2/8 + \cdots.$$

biii) Either

$$y(1+h) = 1/2 - h/2 + h^2/4 + \cdots,$$

or

$$y(t) = 1/2 - (t-1)/2 + (t-1)^2/4 + \cdots.$$

Sheet D, Question 2

a) $\bar{Y} = 0$ (stable); $\bar{Y} = 1$ (unstable); $\bar{Y} = 10$ (stable).

b) For any $k \in \mathbb{Z}$ (i.e. an integer), $\bar{Y} = 2k\pi$ (unstable) and $\bar{Y} = (2k+1)\pi$ (stable).

c) $\bar{Y} = 1$ (unstable) and $\bar{Y} = -1/3$ (stable).

Sheet D, Question 3

a) $\bar{Y} = 0$ and $\bar{Y} = \kappa\left(1 - \frac{\alpha}{\beta}\right)$ (if $\alpha < \beta$).

c) $C = \alpha\kappa\left(1 - \frac{\alpha}{\beta}\right)$.

Sheet D, Question 4

b) $c > e$.

Sheet D, Question 5

a) For $t < 3T/4$, the solution is

$$N = N_0 e^{-\beta_1 t};$$

whereas for $t \geq 3T/4$, the solution is

$$N = N_0 \exp\left(\beta_2 t - \frac{3T}{4}(\beta_1 + \beta_2)\right).$$