NATURAL SCIENCES TRIPOS **Part IA**

MATHEMATICAL BIOLOGY

Paper released: 1st June 2020 (9:00 am) **Upload until:** 30th June 2020 (12:00 noon)

Moodle site: Part IA Assessments 2020 MB

*You have **three hours** to answer this paper (plus any pre-agreed individual adjustments). Please treat this as a "closed book exam" and write your answers within the three hour time period. Do not include the downloading and uploading of files in the allocated time.*

*You must answer **eight** questions.*

*You must answer at least **one question from each of Sections A to E**.*

All questions carry equal weight.

The question in Section B that is marked with an asterisk (*) requires knowledge of the last six lectures in Michaelmas term.

Indicative proportions of marks are given for each question part.

You may use an approved calculator and the 2020 Mathematical Biology Formula Booklet.

*Begin each answer on a **separate** sheet of paper.*

*Answers should be **hand-written on blank paper**. Where relevant, formulae, equations, diagrams, graphs and sketches should be drawn by hand on blank paper, not prepared using a computer. Do not copy and paste any figures from other documents.*

After you have completed the assessment

(1) *Complete the cover sheet, clearly indicating which questions you have attempted.*

(2) *Scan the cover sheet and your answers for all attempted questions.*

(3) *Include all of the scans in a **single PDF file**, with the cover sheet as the first page, followed by answer sheets in the same order as the corresponding questions appear in the assessment paper.*

(4) *The PDF file should be named as follows: **your-crsid_MatBio.pdf***

(5) *Upload the PDF file to the **Submission of Papers** section of the **Part IA Assessments 2020 MB** Moodle site, following the guidance in the **Essential Information** section.*

SECTION A

A1

(a) A modeller wants to select a suitable dispersal kernel to include in a stochastic model for the spread of an invasive species. Field studies suggest that the pest lays its eggs between a minimum distance of 1 meter from its parental nest and a maximum of 5 meters. The modeller writes down the following probability density function to express the probability the pest lays its eggs a distance *x* from its parental nest:

$$f_X(x) = \begin{cases} c(25 - x^2) & \text{if } 1 < x < 5 \\ 0 & \text{otherwise} \end{cases}$$

(i) Calculate the value of *c* required to make f_X a valid probability density function.

(ii) What is the probability that a pest lays its eggs between 2 and 3 meters from the parental nest?

(iii) Calculate $E[X]$.

[~40% marks]

(b) Suppose nests are randomly distributed with a mean of 45 nests per 100 m^2.

(i) What is the probability that a surveyor laying down a 1 m^2 quadrant will find no nests?

(ii) What is the minimum size quadrant a surveyor should use to have a 75 % chance of finding at least one nest?

[~40% marks]

(c) Parasitic wasps are released into the infested area to control the pest. The parasites attack at random and in any given nest there is an 80 % chance that an egg will be parasitized. What is the probability that in a nest of 6 eggs at least 2 eggs will not be parasitized?

[~20% marks]

Note: workings must be shown to get full credit.

A2

(a) Show that the following expression is true for any 2 x 2 matrix $\boldsymbol{A}$:

$$\boldsymbol{A}^2 = \mathrm{tr}(\boldsymbol{A})\,\boldsymbol{A} - \det(\boldsymbol{A})\,\boldsymbol{I}$$

where $\boldsymbol{I}$ is the identity matrix.

[~30% marks]

(b) Find an inverse for the following matrix, if one exists:

$$\begin{pmatrix} 2 & 4 & 1 \\ -1 & 1 & -1 \\ 1 & -4 & 0 \end{pmatrix}$$

[~35% marks]

(c) Find a complete set of eigenvalues and eigenvectors for the following matrix:

$$\begin{pmatrix} 4 & 0 & -2 \\ 2 & 5 & 4 \\ 0 & 0 & 5 \end{pmatrix}$$

[~35% marks]

SECTION B

B3

(a) A population biologist is interested in the rate of population change (λ, the log of the ratio of population sizes at t+1 and t) of male and female red deer. She collects estimates for 10 different populations:

Male λ	Female λ	difference
0.5	−0.9	1.4
−0.8	1.3	−2.1
0.1	−1.0	1.1
−0.5	−1.4	0.9
0.3	−0.4	0.7
−0.1	−0.3	0.2
−1.0	0.0	−1.0
1.3	1.2	0.1
−0.7	0.8	−1.5
−0.6	0.0	−0.6

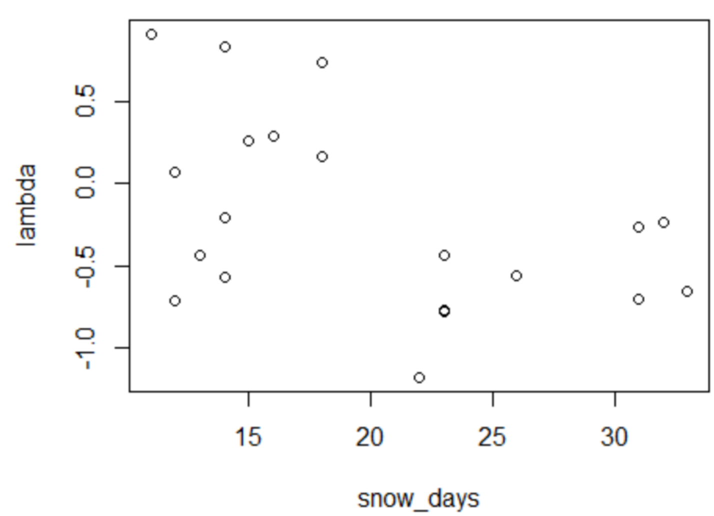
Given that the mean difference, $\bar{x}$, is –0.08, and $\sum_{i=1}^{n}(x_i - \bar{x})^2$ is 12.48, does the rate of population change differ between males and females?

[~15% marks]

(b) Provide a sentence that you could use to report your results for part ***(a)*** in a scientific paper.

[~10% marks]

(c) In a follow-up study, the population biologist decides to focus on the rate of population change, λ, of males only, expanding her dataset to 20 locations and collecting additional information on the number of days with snow cover (which might limit access to food):



B3 (CONTINUED)

If SS_{Model} = 1.41 and SS_{Total} = 6.59, does the number of days with snow cover predict the rate of population change, λ?

[~35% marks]

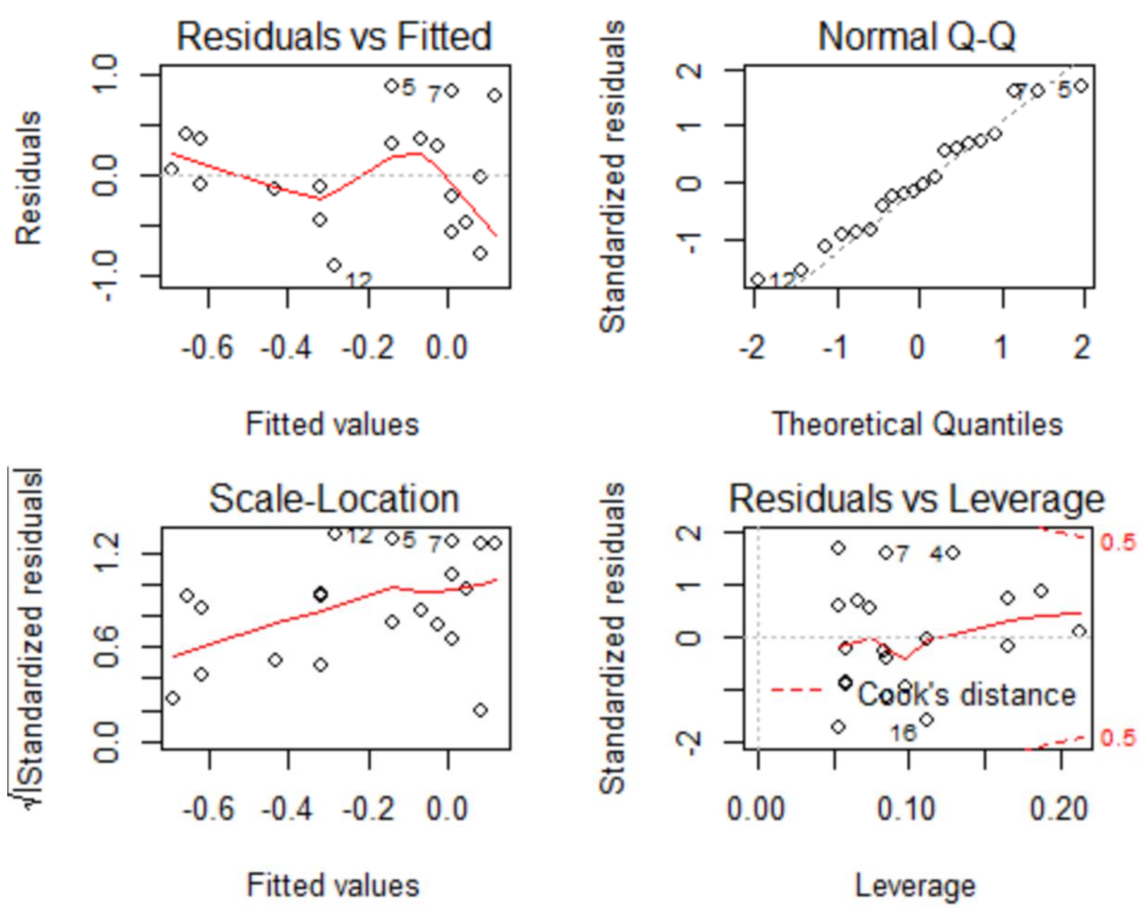
(d) Provide a sentence that you could use to report your results for part ***(c)*** in a scientific paper.

[~10% marks]

(e) Given that SS_x = 1036.95, $SS_{xy} = -38.26$, $\bar{x}$ = 20.05, and $\bar{y} = -0.21$, estimate the line of best fit and predict the value of λ for 27 days of snow cover.

[~10% marks]

(f) Comment on the following diagnostic plots:



[~20% marks]

B4 *

(a) A freshwater biologist wants to investigate the predictors of abundance of three-spine sticklebacks (a fish) in 31 Canadian streams. At each location, he captures fish by laying a trap for 12 hrs and measures dissolved oxygen (mg/L), the type of substrate (mud or gravel), and the extent of vegetation on the banks (low, medium or tall). He then fits a General Linear Model with a Poisson error structure:

```
Call:
glm(formula = abundance ~ oxygen + substrate + vegetation,
    family = poisson, data = fish)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.8085  -1.8210  -0.4219   0.4162   6.9669

Coefficients:
                 Estimate  Std. Error  z value  Pr(>|z|)
(Intercept)       1.34559     0.79873    1.685    0.0921 .
oxygen           -0.04349     0.09144   -0.476    0.6343
substratemud     -0.56864     0.22874   -2.486    0.0129 *
vegetationmedium  1.07554     0.25577    4.205  2.61e-05 ***
vegetationtall    1.01229     0.26009    3.892  9.94e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 157.90  on ??  degrees of freedom
Residual deviance: 117.62  on ??  degrees of freedom
AIC: 222.97

Number of Fisher Scoring iterations: 5
```

What are the degrees of freedom for the Null and Residual Deviance?

[~10% marks]

(b) Given the coefficients, how many sticklebacks would you predict would be caught (again, using a trap for 12 hrs) in a stream with 8.2 mg/L oxygen, a muddy substrate and short vegetation? And how many for a stream with 9.7 mg/L oxygen, a gravel substrate and tall vegetation?

Hint: the link function for a Poisson model is the natural logarithm, ln.

[~30% marks]

B4* (CONTINUED)

(c) If we drop single predictors from the full model, we get:

```
Single term deletions

Model:
abundance ~ oxygen + substrate + vegetation
              Df  Deviance      AIC
<none>              117.62   222.97
oxygen        ??    117.85   221.19
substrate     ??    124.46   227.81
vegetation    ??    140.43   241.77
```

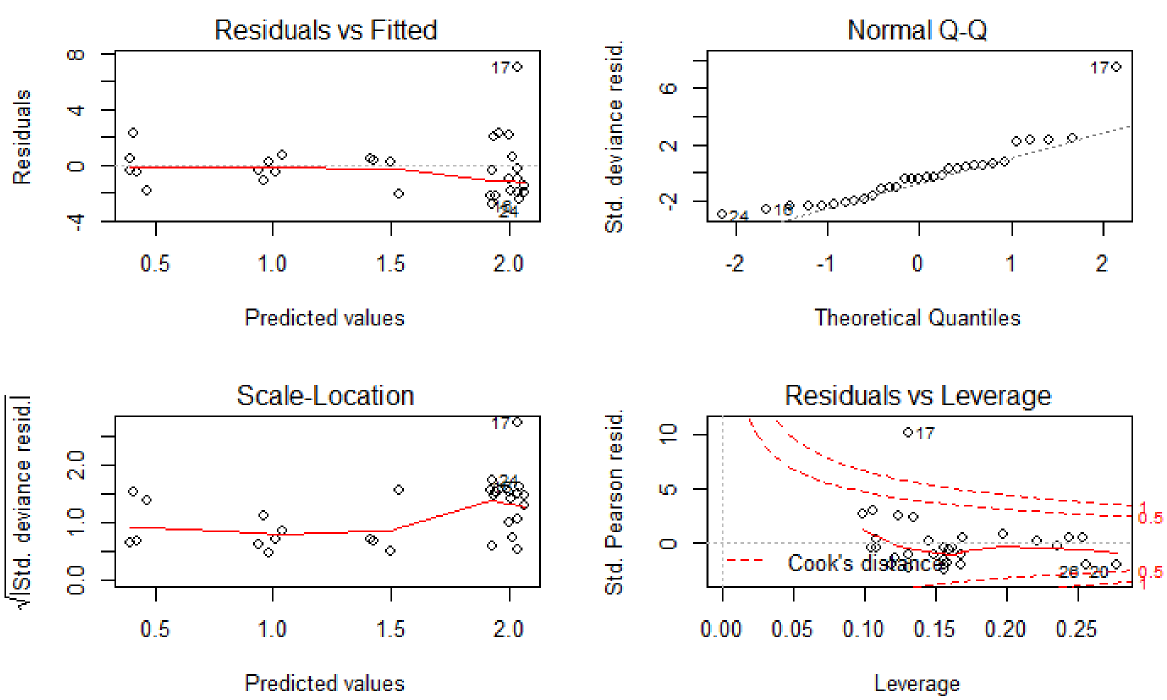
Which variables (if any) should we remove, based on the AIC values?

[~15% marks]

(d) Use a χ^2 test to support your answer to ***(c)***.

[~25% marks]

(e) The diagnostic plots for the model are:



Are the assumptions of a General Linear Model satisfied?

[~20% marks]

SECTION C

C5

A salmon farm has a stock of salmon fish. Their growth rate in the absence of harvesting is modelled by the following differential equation

$$\frac{\mathrm{d}Y}{\mathrm{d}t} = 2AY - A\frac{Y^2}{N},$$

where Y is the population of salmon, t is the time in days and A and N are positive constants.

(a) Find the equilibrium values of Y and analyse their stability.

[~15% marks]

(b) Find, with justification, the population at which the maximum population growth rate occurs.

[~15% marks]

(c) Sketch the graph of Y against t, given that the starting population is small.

[~10% marks]

(d) State one way in which this model is a simplification of the biological situation.

[~5% marks]

Note: a harvest will be sustainable if a positive equilibrium value can be achieved.

Daniel, a biologist, suggests that salmon are harvested at a rate of k per day.

(e) Adapt the original model to include Daniel's suggested model of harvesting. Show that, based on Daniel's model, the harvest is sustainable only if $k \leq AN$. Explain the biological significance of the equilibrium population size occurring at the maximum possible harvest rate.

[~30% marks]

(f) If $k = 3AN/4$, find with justification the smallest initial salmon population which will allow a sustainable harvest to occur, according to Daniel's model.

[~15% marks]

(g) Alessia, another biologist, suggests a new model for salmon harvesting in which the salmon are harvested at a rate of pY per day, where p is a positive constant. Find a condition on p and A that would allow the harvest to be sustainable.

[~10% marks]

C6

Coccidiosis is a disease in chickens caused by the parasite *Eimeria tenella*. The rate equation for the number of parasites in a particular chicken, N, is modelled by:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha e^{-\gamma t} - \beta N$$

where α, β and γ are positive constants, and $\beta \neq \gamma$.
Initially, there are no parasites in the chicken.

(a) Suggest a plausible biological interpretation for each term in the differential equation.

[~10% marks]

(b) Show that a solution of the form

$$N = \frac{\alpha}{\beta - \gamma}\left(e^{-\gamma t} - f(t)\right)$$

leads to a differential equation for $f(t)$. Solve the differential equation for $f(t)$.

[~30% marks]

(c) Find the time, t_{max}, at which the parasitic infection is a maximum. (You may assume that any stationary point that you find is a maximum.) Show that $t_{max} > 0$.

[~20% marks]

(d) Show that the graph of N against t possesses a point of inflexion at $t = 2t_{max}$.

[~15% marks]

(e) Show that when t is small N is approximately proportional to t. Write the constant of proportionality in terms of the parameters of the model in a simplified form.

[~10% marks]

(f) Sketch a graph of N against t. You do not need to label the N coordinates of any points, but you should label the t coordinates of any significant points.

[~15% marks]

SECTION D

D7

Consider the system represented by the following pair of simultaneous first-order non-linear differential equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = y - x^2 + 4x - 3$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = xy - 2x^2 + 5x$$

(a) Find and classify the equilibrium points.

[~45% marks]

(b) Sketch the null clines and then the phase plane for this system, including the equilibrium points, direction field and some generic trajectories showing the behaviour around the equilibrium points.

Note: *all sketches should be drawn on blank paper by hand, not on a computer.*

[~25% marks]

(c) For the initial conditions $x(0) = 2$ and $y(0) = -1.5$, mark clearly on the phase plane the trajectory associated with this initial condition, and sketch the corresponding graphs for $x(t)$ and $y(t)$.

[~15% marks]

(d) What happens for the initial conditions $x(0) = 1.5$ and $y(0) = -1.5$? Explain why this small change leads to such different long-term behaviour for $x(t)$ and $y(t)$.

[~15% marks]

D8

The following equations represent the dynamics of juveniles, $J(t)$, and adults, $A(t)$, in a closed population:

$$\frac{\mathrm{d}J}{\mathrm{d}t} = bA - (m + \mu J)J - \alpha J$$

$$\frac{\mathrm{d}A}{\mathrm{d}t} = \alpha J - mA$$

where b is the birth rate, α the mutation rate, m the adult death rate, and $(m + \mu J)$ the juvenile death rate per capita.

(a) Propose an interpretation for the form of the juvenile death rate in this model.

[~10% marks]

(b) Calculate the nullclines of this system.

[~10% marks]

(c) Calculate the stationary points and show that a non-zero equilibrium can only exist when $(b/m) > 1 + (m/\alpha)$.

[~20% marks]

(d) Using the following numerical values, show that the non-zero equilibrium is a stable node: $b = 1$, $m = 0.2$, $\alpha = 2$, $\mu = 0.2$.

[~25% marks]

(e) Using the same numerical values, sketch the phase plane (nullclines, stationary points, direction field).

Note: *all sketches should be drawn on blank paper by hand, not on a computer.*

[~25% marks]

(f) Without performing any calculation, explain how the dynamics would differ if μ was set equal to 0.

[~10% marks]

SECTION E

E9

The following reaction scheme describes the mechanism of an enzyme, E, that cleaves a single substrate, S, into two different products, P (which detaches from the enzyme first) and Q (which detaches from the enzyme subsequently).

$$\mathrm{E + S} \underset{k_2}{\overset{k_1}{\rightleftharpoons}} \mathrm{ES} \xrightarrow{k_3} \mathrm{EQ + P} \xrightarrow{k_4} \mathrm{E + P + Q}$$

(a) Construct a mass balance equation for the total concentration of enzyme present at time zero, $[\mathrm{E}]_0$.

[~10% marks]

(b) Write down two differential equations that describe the rates of change of [ES] and [EQ] as a function of time. Then show how the steady state approximation can be applied to both ES and EQ.

[~15% marks]

(c) Using your results from part ***(b)***, construct an expression for $[\mathrm{E}]_0$ in terms of rate constants, the current concentration of free enzyme, [E], and the current concentration of the enzyme-substrate complex, [ES].

[~10% marks]

(d) Using your results from part ***(c)***, construct an expression for [E] in terms of rate constants, $[\mathrm{E}]_0$ and the current concentration of free substrate, [S].

[~15% marks]

(e) Using your results from part ***(d)***, construct an expression for the rate of change in the concentration of product P in terms of rate constants, $[\mathrm{E}]_0$ and [S].

[~20% marks]

(f) Using your results from part ***(e)***, show that $K_\mathrm{M}^{\mathrm{eff}}$, the effective Michaelis constant for the production of product P, can be written in the form:

$$K_\mathrm{M}^{\mathrm{eff}} = \frac{k_2}{k_1} \cdot \frac{(1 + k_3/k_2)}{(1 + k_3/k_4)}$$

[~15% marks]

E9 (CONTINUED)

(g) If K_D, the dissociation constant for the enzyme-substrate complex, is defined as the ratio k_2/k_1, describe the conditions under which:

(i) $K_M^{eff} = K_D$;

(ii) $K_M^{eff} > K_D$; and

(iii) $K_M^{eff} < K_D$.

[~15% marks]

E10

Two wild dogs must each simultaneously decide whether to pursue or to ignore a potential prey. Pursuit entails an energetic expenditure of c, while the prey is of total energetic value b. If both dogs pursue, they are certain to capture the prey, and will divide it equally between them. If only one dog pursues, then it captures the prey with probability p and consumes it all, while the other dog obtains nothing. If neither dog pursues, then neither gains anything. Measuring the payoff to each dog in terms of expected energetic gain yields the following payoff matrix:

		Other's strategy: Pursue	Other's strategy: Ignore
Own strategy:	Pursue	$(b/2)-c$	$pb-c$
	Ignore	0	0

(a) Under what conditions is each strategy evolutionarily stable?

[~30% marks]

(b) Determine the conditions (if any) for which the game yields a mixed evolutionarily stable strategy (ESS) and determine the probability of pursuit at this ESS (if it exists).

[~25% marks]

(c) Suppose that one dog is adult and the other juvenile, and that the adult's chance of capturing the prey if it pursues alone, denoted p_A, is greater than the juvenile's chance of capturing the prey if it pursues alone, denoted p_J. Write out a new payoff matrix for the game, and determine the conditions under which the strategy "pursue if adult, but not if juvenile" is evolutionarily stable.

[~30% marks]

(d) Suggest three ways in which you might modify the assumptions of the model to create a more realistic analysis of prey pursuit behaviour.

[~15% marks]

(END OF PAPER)