JANUARY 2006 EXAMINATIONS

Degree of Bachelor of Arts : Year 3
Degree of Bachelor of Science : Year 3
Degree of Bachelor of Science : Year 4
Degree of Master of Mathematics : Year 3
Degree of Master of Mathematics : Year 4
Degree of Master of Science : Year 1

NON-PHYSICAL APPLICATIONS II
(POPULATION DYNAMICS)

TIME ALLOWED : Two Hours and a Half

INSTRUCTIONS TO CANDIDATES

Full marks can be obtained for complete answers to FIVE questions.
Only the best FIVE answers will be counted.

1. *Saccharomyces cerevisiae* is one of the most commercialized species of bakers yeast. The dynamics of yeast population in a bioreactor with constant supply of nutrients can be approximately described by the Verhulst equation

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(1 - N/K), \tag{1}$$

where $N(t)$ is the yeast biomass at time t.

(a) Explain the biological significance of the parameters r and K. How will parameters r, K change if the volume of the bioreactor is increased tenfold, with the same composition of supplied nutrients?

(4 marks)

(b) Integrate the differential equation (1) by separation of variables or otherwise, and show that

$$N(t) = \frac{e^{rt}N(0)}{1 + N(0)\left(e^{rt} - 1\right)/K}.$$

(5 marks)

(c) Deduce from the result of part 1(b) the dependence of $N(t+\tau)$ on $N(t)$ for $\tau > 0$. Show that the mapping $N(t) \to N(t+\tau)$ is described by a Hassell equation

$$N(t+\tau) = \frac{RN(t)}{(1 + aN(t))^b}$$

and find the values of R, a and b in this equation in terms of the parameters r and K of the continuous-time model and the time interval τ.

(5 marks)

(d) The yeast biomass is harvested at discrete time intervals τ. The process is cyclic, i.e. the harvest H is equal to the increase of the population during one such interval, $H = N(t+\tau) - N(t)$. Using your previous results or otherwise, find the maximal harvest H achievable at fixed r, K and τ, and the value of $N(t)$ which will yield this maximum

(6 marks)

2. The model of outbreaks of spruce budworm *Choristoneura fumiferana* suggested by Ludwig (1978) can be written in the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right) - \frac{x^2 z}{x^2+1} \tag{2}$$

where x is budworm population density, z is the density of the population of birds preying on the budworms and r and K are constant parameters.

(a) Explain the biological significance of the two terms in the right-hand side of this equation, and of the parameters r and K. What is the Holling type of the predatory response of birds to the budworms?

(5 marks)

(b) Draw carefully the graph of the function $y = f(x) = x/(x^2+1)$ in the range $x \in [0, 15]$. Explain how it can be used to find graphically the equilibrium values of x in the above model, for given values of r, z and K? Use this method to demonstrate that at $K = 15$, $r = 1$ and $z = 2.5$, there are three positive equilibrium states, and roughly estimate their values.

(7 marks)

(c) Based on the graphical method discussed in part 2(b), or otherwise, derive conditions on parameters K, r, z and x for the bifurcation of double equilibria in this model. Solve these conditions for r and K as explicit functions of the double equilibrium position x.

(4 marks)

(d) For the specified values of parameters, $r = 1$, $K = 15$, $z = 2.5$, the budworm population was in an equilibrium with $x > 10$. This attracted more birds to the infested forest, which resulted in a gradual decline of the budworm density. When the budworm density decreased to $x \approx 7.4$, a collapse happened, i.e. a sudden decrease of the budworm density to a very low value $x < 1$. Use the result of part 2(c) to find, to 2 significant figures, what was the density of bird population at that moment.

(4 marks)

3. One of the most famous "feral" cat colonies lives in the Colosseum in Rome. An ecologist visiting Rome as a tourist has observed that females in that colony often help their daughters to raise their kittens. She has conjectured that dynamics of that population can be modelled using an appropriate modification of the discrete-time Ricker model:

$$N_{t+1} = RN_t \exp\left(-aN_t + bN_{t-T}\right) \tag{3}$$

where $N_t \geq 0$ is the size of the population of female cats of the reproductive age at time t measured in generations, and $T \geq 0$ and $a > b > 0$ are constant parameters, $t, T \in \mathbb{Z}$.

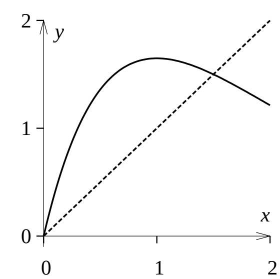
(a) Suggest an interpretation of the biological significance of the parameters R, a and b. What should be the value of parameter T, if cats only help to raise their grandchildren but do not care about more distant generations?

(4 marks)

(b) Find any nonzero equilibria in this model and the ranges of parameter values at which they exist and are biologically feasible. Investigate their stability.

(7 marks)

(c) Consider the case of $T = 0$, $a = 2$, $b = 1$ and $R = e^{3/2}$. Using the graphs of functions $y = x\exp(\frac{3}{2} - x)$ and $y = x$ shown on the right, sketch a cobweb/stepladder diagram for model (3), with the initial condition $x_0 = 0.1$. Deduce from it whether or not the nontrivial equilibrium in this model is stable. Is this equilibrium monotonic or oscillatory?



(3 marks)

(d) Consider the case of $T = 1$, $a = 2$, $b = 1$ and $R = e^{3/2}$. Using the substitution $N_t = N^* + h_t$, where N^* is the nontrivial equilibrium, and $|h_t|$ is small, verify that the behaviour of the system close to this equilibrium is described by

$$h_{t+1} + 2h_t - \frac{3}{2}h_{t-1} = 0.$$

Hence conclude, whether the grandmothers' contribution has stabilizing or destabilizing effect on this population's dynamics.

(6 marks)

4. The spotted knapweed *Centaurea biebersteinii*, whose natural habitat stretches from Central Europe to Western Siberia, is now a serious problem weed in North America where it was accidentally introduced in 1880s. The population of plants consists of seeds (age group 0), seedlings (age group 1), young adults (age group 2), medium adults (age group 3) and old adults (age group 4). Each year,
   - a fraction $B_0 \in (0,1)$ of seeds remain in the soil, and a fraction $P_0 \in (0,1)$ germinates into seedlings,
   - a fraction $P \in (0,1)$ of seedlings become young adults,
   - the same fraction P of young adults become medium adults,
   - the same fraction P of medium adults become old adults,
   - young, medium and old adults each produce $B > 0$ seeds on average; seedlings do not produce any seeds. The dynamics of this population can be described by Leslie model

   $$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t \tag{4}$$

   where $\mathbf{N}_t = (N_t^0, \ldots N_t^4)^T$ is the column-vector describing the population in year t, and N_t^j is the size of the j-th age group at that year.

   (a) Write down the system of discrete time evolution equations for the plant age groups. Thus construct the Leslie transition matrix $\mathbf{L}$.

   (4 marks)

   (b) Find the characteristic polynomial $p(\mu)$ for $\mathbf{L}$. By considering the function $f(\mu) = p(\mu)/\mu^5$ for positive μ, show that for $P_0 > 0$, $B_0 > 0$, $P > 0$ and $B > 0$, this polynomial always has exactly one positive root.

   (7 marks)

   (c) Observations have shown that an unchecked population of spotted knapweed increases by 25% each year. Assuming that $P_0 = B_0 = 1/4$ and $P = 1/2$, estimate, to 1 decimal place, the average value B of seeds produced by an adult plant.

   (5 marks)

   (d) Two species of seed head flies, *Urophora affinis* and *U. quadrifasciata*, are well-established on spotted knapweed. The larvae of these species reduce seed production by 50% by feeding on spotted knapweed seed heads. Determine if using these flies would alone be an effective method of biocontrol of the knapweed population, for the values of parameters specified in part 4(c).

   (4 marks)

5. The snowshoe hare *Lepus americanus* is nearly the only prey of the Canadian lynx *Lynx lynx*. Their population dynamics are so closely linked that they exhibit stable synchronous oscillations with the period of several years, evidence of which can be seen in the records of pelts obtained by Hudson Bay company. Consider a modification of the Lotka-Volterra model describing the dynamics of the two populations:

$$\begin{aligned} \mathrm{d}H/\mathrm{d}t &= H\left(a - \alpha L^2\right) \\ \mathrm{d}L/\mathrm{d}t &= L\left(-b + \beta H^2\right) \end{aligned} \tag{5}$$

where H is the hare population size, L is the lynx population size, both estimated by thousands of pelts obtained, time t is measured in years, and a, b, α, β are positive coefficients.

(a) Describe the biological significance of the parameters a, α, b and β.

(4 marks)

(b) Find all biologically feasible equilibria in this model and classify their stability in the linear approximation.

(5 marks)

(c) Find the orbit derivative of function V defined as

$$V(H, L) = \frac{\alpha}{2}L^2 - a\ln(L) + \frac{\beta}{2}H^2 - b\ln(H)$$

and show that this derivative is identically zero for all solutions of (5). What does this result mean for (i) possibility of periodic solution in this model, (ii) asymptotic stability of the coexistence equilibrium, (iii) its Lyapunov stability.

(6 marks)

(d) Using your results, estimate, to 1 significant figure, the average sizes of the two populations and the period of their mutual oscillations for $a = b = 0.32$ and $\alpha = \beta = 2 \times 10^{-4}$. Sketch the phase portrait of the system at these parameters, by designating on the (H, L) plane the equilibria, the null-clines $\dot{H} = 0$ and $\dot{L} = 0$ and a few typical trajectories.

(5 marks)

6. The accidental release of cats to Amsterdam Island in the southern Indian Ocean has considerably increased ecological pressure on endemic bird species. Eradication of cats has been considered. However the plan raised concerns that such eradication will lead to an increase of the island's population of rats, which are prey to cats but predators to birds, and thus make the birds' situation worse. In 1999, Courchamp et al. constructed a mathematical model of the ecosystem, which in a simplified form can be represented in a Lotka-Volterra-Gause form,

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= B(\alpha - \beta B - \gamma R - \delta C) \\ \frac{\mathrm{d}R}{\mathrm{d}t} &= R(\epsilon + \zeta B - \eta R - \theta C) \\ \frac{\mathrm{d}C}{\mathrm{d}t} &= C(\kappa + \lambda B + \mu R - \nu C). \end{aligned} \tag{6}$$

where all constant coefficients $\alpha \ldots \nu$ are assumed positive.

(a) Explain how, based on the signs of the terms in the right-hand sides, one can deduce that B describes the population of birds, R describes the population of rats and C describes the population of cats.

(3 marks)

(b) From now on, assume $\alpha = 3$, $\epsilon = \theta = \nu = 4$, $\kappa = 2$, and all other coefficients $= 1$. Show that $R = B = C = 1$ is an equilibrium Investigate its stability. *Hint: one of the eigenvalues is equal to* -1.

(6 marks)

(c) Consider the model at the values of parameters specified in the previous part, in the absence of cats, $C = 0$. On the phase plane (B, R), sketch the phase portrait by drawing the null-clines, finding equilibria, designating the crude directions of trajectories in parts of the phase plane separated by null-clines and sketching some typical trajectories.

(8 marks)

(d) Give the interpretation of your results in parts 6(b) and 6(c) in terms of benefits and damages to the bird population. In reality, after all consideration, the plan to eradicate cats has been abandoned. Would this be a correct decision if the system was described by equations 6 with the specified values of parameters?

(3 marks)

7. To describe Bombay plague epidemic of 1905-6, Kermack and McKendrick (1927) have suggested the following model

$$\begin{aligned} \mathrm{d}S/\mathrm{d}t &= -\beta SI \\ \mathrm{d}I/\mathrm{d}t &= \beta SI - \nu I \end{aligned} \tag{7}$$

where S is the number of susceptible, I the number of infective individuals of the population, and β and ν are non-negative parameters.

(a) Explain the biological meaning of the terms in these equations, and what biological assumptions have been used in this model.

(6 marks)

(b) Perform the phase-plane analysis of the model (7): draw the null-clines, indicate equilibria, show the general direction of trajectories in different parts of the phase plane, and sketch a typical trajectory representing an epidemic.

(6 marks)

(c) Consider function $V(S, I) = I + S - \frac{\nu}{\beta}\ln(S)$. Calculate its orbit derivative due to system (7). Thus show that any trajectory of (7) satisfies equation $I = \frac{\nu}{\beta}\ln(S) - S + \text{const}$. Deduce from here an equation, relating the population S_0 before an epidemic and population S_∞ after the epidemic. Prove that S is a Lyapunov function of (7), and state what this means for the possibility of periodic solutions in this model.

(5 marks)

(d) There was an outbreak of plague in the village of Eyam in England from 1665 to 1666. The village sealed itself off when the plague was discovered. In the epidemic, the population of the village decreased from 350 to 83. Assume that the mortality rate for infectives was approximately 1/day. Estimate from these data the value of the coefficient β in (7).

(3 marks)