C6a — Lent Term 2012

Mathematical Tripos Part II — P.H. Haynes

Mathematical Biology – Examples Sheet 1

[This examples sheet covers the first major section of the course – **Systems without spatial structure: deterministic equations** – which will be completed at about the end of lecture 10. Please communicate any errors in this sheet to `phh@damtp.cam.ac.uk`. Some further course material is available at `http://www.damtp.cam.ac.uk/user/phh/mathbio.html`.]

1. *Rabbits* (Fibonacci, 1202). Suppose that every pair of rabbits can reproduce only twice, when they are one and two months old, and that each time they produce exactly one new pair of rabbits. Assume that all rabbits survive. Starting with a single pair in the first generation, how many pairs will there be after n generations?

   (a) To solve this problem, define

   R_n^0 = number of newborn pairs after n months
   R_n^1 = number of one-month-old pairs after n months
   R_n^2 = number of two-month-old pairs after n months

   Show that R_n^0 satisfies the equation

   $$R_{n+1}^0 = R_n^0 + R_{n-1}^0.$$

   (b) Suppose that Fibonacci initially had one pair of newborn rabbits, i.e., that $R_0^0 = 1$ and $R_1^0 = 1$. Find the numbers of newborn, one-month-old, and two-month-old rabbits he had after n generations.

2. *Red Blood Cells.* Circulating red blood cells (RBCs) are destroyed in the spleen and created in the bone marrow in proportion to the number destroyed on the previous day. Treat days as discrete time units, and let R_n be the number of RBCs in circulation on day n, let M_n be the number produced by marrow on day n, let f be the fraction of RBCs removed by the spleen every day, and let γ be the number produced on day n for each cell lost on day $n-1$.

   Write down equations for R_{n+1} and M_{n+1} in terms of R_n and M_n, and show that

   $$R_n = A\lambda_1^n + \beta\lambda_2^n,$$

   where

   $$\lambda_{1,2} = \frac{1 - f \pm \sqrt{(1-f)^2 + 4\gamma f}}{2}.$$

   Deduce that the RBC count may fluctuate, but that it will remain constant at large times if and only if $\gamma = 1$. [No surprise there].

3. Reformulate the equation for RBC count in problem 2 as a delay differential equation for $R(t)$, where the production of new cells is proportional to $R(t-T)$. Show that there exists a solution of the form $R(t) = Ce^{\lambda ft}$ if

$$\frac{1}{\gamma}(\lambda + 1) = e^{-\lambda fT}. \qquad (*)$$

Show graphically that equation $(*)$ has a positive real root if and only if $\gamma > 1$, and interpret this result. By considering complex roots of $(*)$, show that there are no other solutions with $Re(\lambda) > 0$, if $\sqrt{\gamma^2 - 1}fT \leq \pi/2$

4. Consider the difference equation with delay:

$$x_{n+1} = rx_n(1 - x_{n-1}).$$

(This is the discrete equivalent of the delay differential equation for population discussed in lectures). Show that the fixed point $x_e = 1 - r^{-1}$ is unstable if r is sufficiently large. Show that when r takes its marginal value for instability, the linearised stability problem has a periodic solution (to be determined).

5. Consider the 'normal mode' solution $e^{\gamma t}r(a)$ for the age distribution model

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n$$

discussed in lectures. Suppose that the birth rate $b(a) = B$ for $a_1 < a < a_2$ and is zero otherwise. Derive an expression for the growth rate γ in the cases (i) that all deaths occur after age a_2, (ii) that the death rate $\mu(a) = \nu \times a^m$, for $m > 0, \nu \ll 1$, and give (approximately in case (ii)) the values of β for zero growth. Sketch the function $r(a)$ in each case for growing populations. (Note that in case (i) $\mu(a)$ is not specified uniquely. Where does this non-uniqueness appear in your answers?)

6. *A model of insect outbreak.* The population of a certain insect, $N(t)$, is modelled by the ODE

$$\frac{\partial N}{\partial t} = rN\left(1 - \frac{N}{K}\right) - p(N)$$

where $p(N)$ is the sigmoidal function $p(N) = BN/(A + N)$.

(i) Give suggestions as to the meaning of the terms in this equation.
(ii) Show by rescaling that the dynamics depends only on the two parameters $\alpha = A/K, \beta = B/rK$.
(iii) Show that depending on the values of α, β there can be either zero, one or two positive steady states, and sketch the corresponding regions on the $(\alpha, \beta,)$ plane.

What is the number of *stable* solutions, including the fixed point at $N = 0$, in each region?

7. Consider the 'harvesting' model introduced in lectures:

$$\dot{u} = u(1 - v) - \epsilon u^2 - f$$
$$\dot{v} = -\alpha v(1 - u),$$

with constants $\alpha > 0, f > 0$ and $0 < \epsilon < 1/2$.

Find all the fixed points of this system, and investigate their stability, distinguishing between different ranges of f (i.e. $0 < f < \epsilon, \epsilon < f < 1 - \epsilon, 1 - \epsilon < f$). In each case, sketch trajectories in the $u-v$ phase-plane in the neighbourhood of the fixed points, and discuss what would happen to the predator and prey populations in practice.

8. A simple model of two competing populations eating the same food takes the form

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_2}\right),$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_1}\right).$$

(i) Nondimensionalise the equations, and show that the solutions depend only on $\rho = r_2/r_1, b_{12}$ and b_{21}.
(ii) Now assume that $\rho, b_{12}, b_{21} > 0$. Find all the physically relevant fixed points and determine their stability. Give conditions on the coefficients such that there is a stable state of *coexistence*, with $N_1, N_2 \neq 0$.

9. Consider a model of a non-fatal infectious disease in which recovered individuals (R) become susceptible again at a rate γR; otherwise the model is the same as that considered in lectures. Reduce the system of equations to two, for S and I (the populations of susceptibles and infectives respectively), and sketch trajectories of the system in the $S-I$ plane. Show in particular that the system has a stable fixed point - i.e. the disease will remain endemic in the population - as long as $Nr/a > 1$, where N is the total population, and r, a represent the infection and recovery rates (as in lectures).

10. *An excitable medium model for plankton blooms.*

Let P, Z be the populations of phytoplankton P (prey) and zooplankton Z (predators) respectively. The system is modelled by the following differential equations, where all constants are positive:

$$\frac{dP}{dt} = rP(1-P/K) - SZ\frac{P^2}{a^2+P^2}$$
$$\frac{dZ}{dt} = \gamma SZ\frac{P^2}{a^2+P^2} - \mu Z.$$

Discuss the meaning of each term in these equations. Show that the variables can be rescaled so that the equations become

$$\frac{du}{dt} = \beta u(1-u) - v\frac{u^2}{\alpha^2+u^2} = f(u,v)$$

$$\frac{dv}{dt} = \gamma\left(\frac{u^2}{\alpha^2+u^2} - \lambda\right)v = g(u,v).$$

Assume that $0 < \lambda < 1/2, 0 < \alpha \ll 1$ and sketch the null-clines of this sytem, showing that there is one fixed-point at which neither u nor v is zero. Show that the null-cline $\dot{u} = 0$ has a minimum, M, at a value of u larger than $\alpha[\lambda/(1-\lambda)]^{1/2}$, and hence show that the fixed-point is stable.

The system is perturbed by the intrinsic growth rate r increasing as a result of a temperature rise. Demonstrate (or assume if you cannot) that this causes the value of v at M to rise. Deduce the possibility of excitable behaviour in which u can experience a large, rapid increase, followed by a gradual decline. Discuss the biological basis for these predictions.