Homework 2

Due Friday, July 7 2017

Problem 1 (10 points)

We studied the logistic equation in class as a model of population growth. It is given by

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

with $N(0) = N_0$.

(a) Make the substitutions $x = N/K$ and $\tau = rt$. Show that (1) becomes

$$\frac{\mathrm{d}x}{\mathrm{d}\tau} = x(1 - x), \tag{2}$$

with $x(0) = N_0/K \equiv x_0$. Notice that neither x nor τ has units. This equation is a nondimensionalized version of (1).

(b) Solve equation (2). (The technique of partial fractions may come in handy.)

(c) Substitute $x = N/K$ and $\tau = rt$ in your solution to find an equation for $N(t)$.

Problem 2 (10 points)

The Gompertz equation, given by

$$\frac{\mathrm{d}N}{\mathrm{d}t} = re^{-\alpha t}N(t) \tag{3}$$

with $N(0) = N_0$, has been used to model the growth of cancerous tumors. Here, N is the number of cancer cells in a tumor, r is the initial growth rate of the tumor and α is a damping term that determines how the growth rate slows over time. (See https://www.nature.com/bjc/journal/v18/n3/pdf/bjc196455a.pdf for more details.)

(a) Solve the Gompertz equation for $N(t)$. (This is a nonautonomous equation, meaning t appears explicitly in the right hand side, but it is separable.)

(b) You should find that $N(t)$ approaches an asymptote as $t \to \infty$. That is, $\lim_{t\to\infty} N(t) = K$. Find K explicitly. (It may depend on the parameters r, α and N_0.)

(c) Show that equation (3) can be rewritten as

$$\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha \ln\left(\frac{K}{N}\right). \tag{4}$$

Problem 3 (10 points)

Suppose that we have the differential equation

$$\dot{x} = f(x). \tag{5}$$

Remember that an equilibrium x^* of this equation is a point such that $f(x^*) = 0$. We said that x^* was stable if solutions of (5) with initial conditions sufficiently close to x^* continued to approach x^*. That is, if $x'(t) = f(x)$ and $x^* - x(0) \ll 1$, then $\lim_{t\to\infty} x(t) = x^*$. Similarly, an equilibrium is unstable if solutions starting near x^* move away from x^*. (Technically, we should call this *asymptotic stability.*)

(a) Show that the differential equation $\dot{x} = x^3$ has an equilibrium at $x = 0$, and that $f'(x) = 0$. Draw a phase line (i.e., a plot of x vs $\dot{x}$) and use it to determine the stability of $x^* = 0$. Solve the differential equation with initial condition $x(0) = x_0 \neq 0$ and use the solution to confirm your stability conclusion.

(b) Repeat part (a) with the differential equation $\dot{x} = -x^3$.

(c) Repeat part (a) with the differential equation $\dot{x} = 0$.

Problem 4 (10 points)

The spruce budworm is an insect that periodically devastates populations of balsam fir trees in eastern Canada. In this problem, we will follow a model proposed by Ludwig, Jones and Holling in 1978 (http://www.math.ku.dk/ moller/e04/bio/ludwig78.pdf) to describe the populations of this pest. Our goal will be to reproduce figure 2 of that paper.

Ludwig et al. proposed that budworms would grow logistically in the absence of predators, and that predation (mostly by birds) was very small when budworm population was low, but rapidly reached a maximum level b once the population passed some threshold a. In particular, if we let $N(t)$ represent the number of budworms at time t and let R be a parameter representing the growth rate, let K be a parameter representing the carrying capacity of the environment, let b be a parameter representing the maximum predation rate and let a be a parameter representing a threshold population level where predation would increase, then we obtain the differential equation

$$\frac{\mathrm{d}N}{\mathrm{d}t} = RN\left(1 - \frac{N}{K}\right) - \frac{bN^2}{a^2 + N^2}. \tag{6}$$

(You can assume that all four parameters are positive.)

(a) Show that if we make the substitutions $x = N/a$, $\tau = bt/a$, $r = Ra/b$ and $k = K/a$, then (6) becomes

$$\frac{\mathrm{d}x}{\mathrm{d}\tau} = rx\left(1 - \frac{x}{k}\right) - \frac{x^2}{1 + x^2}. \tag{7}$$

(b) Show that $x^* = 0$ is an equilibrium of (7) and that it is always unstable.

(c) We can find the other fixed points of (7) by setting

$$r\left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2}. \tag{8}$$

After some simplification, this equation becomes a cubic, so we could solve it exactly and find 1, 2 or 3 more fixed points. However, solving a general cubic equation is unpleasant, so we will find these fixed points graphically. To do so, plot both $y_1 = r(1 - x/k)$ and $y_2 = x/(1 + x^2)$ for various values of r and k. Choose values of r and k so that y_1 and y_2 intersect in 1, 2 and 3 places. Figure 1 of the paper shows the case where y_1 and y_2 intersect in 3 places; you need to plot the other two possibilities. Use a graphical argument to determine the stability of each fixed point.

(d) We will now calculate the values of r and k such that (7) has exactly two equilbria. This can only happen if the line $r(1 - x/k)$ intersects the curve $x/(1 + x^2)$ tangentially. That is, we need both

$$r\left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2}, \tag{9}$$

and

$$\frac{\mathrm{d}}{\mathrm{d}x}\left[r\left(1-\frac{x}{k}\right)\right]=\frac{\mathrm{d}}{\mathrm{d}x}\left[\frac{x}{1+x^2}\right]. \tag{10}$$

Use these two equations to show that

$$r=\frac{2x^3}{(1+x^2)^2} \text{ and } k=\frac{2x^3}{x^2-1}. \tag{11}$$

Use these two equations to reproduce figure 2 of the paper.