BIOLOGY 309A: FINAL EXAM, 1994

Friday December 9, 1994, 14:00

Professor: Daniel Kaplan

Problem A

This problem is based (loosely) on experimental and theoretical work done in Michael Guevara's lab, here at McGill. You don't need to know anything about cardiac electrophysiology to do this problem.

Isolated ventricular cells, when given a small stimulus, produce an action potential, as shown in Figure 1 which shows transmembrane voltage v versus time t. If a constant bias current of a certain amplitude is given, then the cell never recovers after the action potential, and stays at a depolarized level of voltage, as shown in Figure 2.

A simple model for the voltage across the ventricular cell membrane is

$$\frac{dv}{dt} = -(0.3 + 0.03v + 0.002v^2 + 0.000025v^3) + I$$

where $v(t)$ is the transmembrane voltage measured in millivolts, and I is the injected bias current. A graph is shown in Figure 3 for $I = 0$. After a stimulation, the membrane voltage is set to +10 millivolts, and then recovers according to this differential equation.

(a) Using the graph, estimate what membrane voltage will the cell asymptotically approach when the bias current $I = 0$. Make a (rough) sketch of voltage versus time when $v(0) = +10$.

(b) Using the graph, estimate how big the the bias current I has to be so that after a stimulation, the membrane voltage goes to a resting value near 0 millivolts. Sketch (roughly) the resulting curve of dv/dt versus v, and mark the stable and unstable steady states.

(c) Is there any value for the bias current at which only a steady state with $v > 0$ is stable? Using the graph, estimate the range of values for I for which this steady state is the only stable one.

(d) In real cells, an action potential can be produced by a stimulus that makes the membrane voltage more negative, say $v(0) = -80$ mv. Does the model shown in Figure 3 reproduce this behavior?

Figure 1

Figure 2

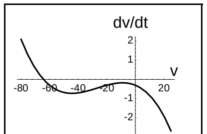

Figure 3

Problem B

The spruce budworm is a caterpillar that infests the spruce and fir forests of eastern Canada and the northeastern US. The budworm will stay at a low population level for many years and then will dramatically increase in population when the trees in the forest have reached a certain maturity. This explosion of the caterpillar population can be devastating to the forest.

A simple differential equation describing the growth of the budworm is given by

$$\frac{dx}{dt} = R(1 - x/Q) - \frac{x}{1 - x^2} \qquad (1)$$

where $x(t)$ is the number of budworms at any time, and Q is a parameter that stays fixed. R is a parameter that changes in time, and represents the food resources available to the budworm. As the forest grows and more food becomes available, R increases.

One way to think of Eq. 1 is as a balance between growth and death. We re-write Eq. 1 as

$$\frac{dx}{dt} = f(x) - g(x). \qquad (2)$$

The term

$$f(x) = R(1 - x/Q)$$

is positive for small x, and reflects the birth of new budworms. As the forest grows, R increases and $f(x)$ changes accordingly. The term

$$g(x) = \frac{x}{1 - x^2}$$

reflects death, and does not change with R.

Figure 1 shows $f(x)$ and $g(x)$ for $R = 0.3$ and $Q = 8$.

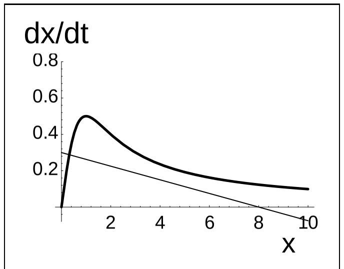

Figure 1

(a) Using Figure 1, find any steady states of x and say whether they are stable or unstable. (You can give an approximate numerical value for x at the steady state.)

(b) Find the x- and y-intercepts of $f(x)$ in terms of R and Q. In the parts (c) and (d), keep in mind that $f(x)$ is a line drawn between these two points

(c) Graphically, find a value for R at which there are 3 steady states. Give approximate numerical values for the positions of these steady states, and say which ones are stable and which ones are unstable.

(d) Graphically, find the smallest value for R at which there is only one steady state with a value of $x > 3$. Is this steady state stable or not?

(e) Imagine that the forest is immature, so that $R = 0.3$. The forest grows with time, so that R increases steadily. After 10 years, R reaches the value you found in part (d). Make a rough sketch of the budworm population versus time in years. (You can assume that the budworm reproduces with a short generation time, so that the population never takes more than a few weeks to reach its steady state value for any R.) Continue your graph, using the fact that if the budworm reaches $x = 3$, then the forest is wiped out, and R returns to 0.3 within a few months. Mark when the population explosion begins, and explain why it occurs.

Problem C

Perhaps surprisingly, many technical and scientific applications make use of random numbers. Computer random number generators are widely used. It is important that computer random number generators not make numbers that are on a short cycle, or, worse, that approach a steady state.

One common type of computer random number generator is called a "linear congruential" generator. It consists of a finite-difference equation:

$$x_{t+1} = f(x_t),$$

where $f(x_t)$ is a piecewise linear function, as shown in Figure 1.

A plot of $x_{t+2} = f(f(x_t))$ is shown in Figure 2. It has $2^2 = 4$ linear segments. In general, a plot of x_{t+n} versus x_t will have 2^n linear segments.

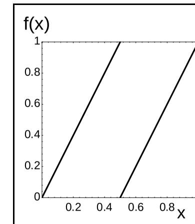

Figure 1

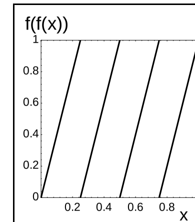

Figure 2

(a) Are there any fixed points in $f(x_t)$? Draw a copy of the figure in your answer notebook, and mark the fixed points, indicating whether they are stable.

(b) Are there any cycles of period 2 in the finite-difference equation? Draw a figure in your answer notebook, and mark them.

(c) How many cycles are there with a period less than n? Are any of them stable?

(d) Is this finite-difference equation chaotic? Justify your answer in terms of the definition of chaos.

(e) Real-world computers are implemented as boolean networks. Most computers use only 64 (or fewer) bits when doing numerical calculations. Given that the state has 64 boolean elements, how many possible states of the system are there? Is chaos possible in a boolean-network computer implementation of the finite-difference equation? How big does n have to be in (c), in order to have more cycles of period n than there are states of the computer boolean network?

[You're done with this problem now. The rest is just for your information.] In making real computer random number generators, many more than two linear segments are used in the function $f(x_t)$. One widely used random number generator has 16,807 linear segments. This number is carefully chosen so that none of the finite number of computer states lies on a cycle shorter that 2.1×10^9. Attempts to "fancy-up" the computer random number generator by making it more complicated than the linear congruential map, often end up introducing stable short cycles (or even stable fixed points!) and therefore make worse random number generators.

Problem D

You are attending the Convention of High-brow International Linear Dynamicists, which is devoted to proving that nonlinear dynamics is nonsense. You are surprised to hear one speaker using the Gompertz equation to model growth of bacteria in growth medium:

$$\frac{dx}{dt} = ke^{-\alpha t}x.$$

The speaker explains that this equation leads to limited growth, rather than exponential growth. You stand up to denounce the speaker as a nonlinear dynamicist in disguise.

(a) Show that the Gompertz equation actually is a linear differential equation.

After you apologize to the speaker, the speaker goes on to show that the Gompertz equation fits the data very well when the following experiment is done: A sterized growth medium is innoculated with a certain concentration of bacteria. The concentration of bacteria in the growth medium is measured continuously until the bacteria concentration stops increasing.

(b) Sketch a graph of bacterial concentration x versus time if the growth were really Gompertzian.

(c) Propose a simple experiment to test whether the growth is Gompertzian or Verhustian (that is: $dx/dt = kx - \beta x^2$).

Problem E

Consider a simple model of the economy, consisting of just 3 parts:

I total national income;

C total consumer spending; and

G government expenditure.

The differential equations are:

$$\frac{dI}{dt} = I - \alpha C$$
$$\frac{dC}{dt} = \beta(I - C - G)$$

where $1 < \alpha$ and $1 \leq \beta$.

Assume that government spending G is a constant.

1. Find the steady state in terms of G, α, and β. Draw the isoclines, and sketch the direction of flow in the phase plane.
2. Find the linear dynamics at the steady state. That is write the equations in the form of

$$\frac{dx}{dt} = Ax + By$$
$$\frac{dy}{dt} = Cx + Dy.$$

   What is the relationship between the variables x and y in the linearized equation, and the variables I and C?

3. Find the eigenvalues and classify the steady state as stable or unstable.
4. If $\beta = 1$, show that the economy oscillates.