Lab: Systems of Continuous Models

1 A Few Basic Concepts

For our last lab, we will be looking at the basics of simulating and analyzing continuous models. We have already laid the foundations for this lab through both the discrete labs and other continuous labs. In this lab we will demonstrate a bit more about the simulation of continuous models, but the analysis is quite similar to what you have been working with. Let's begin!

2 Models of Continuous Systems

One of the most classic systems of continuous equations is the Lotka-Volterra model, more commonly known as a predator-prey model. An excellent reference for this model can be found in chapter 6 of *Mathematical Models in Biology* by Leah Edelstein-Keshet. In general, this model tracks two populations, one which is the prey population and the other is a population of predators. In the classic example the prey species is the hare and the lynx is the predator species, but this model has since been adapted to include a wide range of species. In the practice assignment, we will even simulate a tri-trophic food chain with three species!

The hare species, H, can survive without the predator population and has a carrying capacity of K. When the predator population is excluded the prey population becomes a traditional logistic growth model. The predators, L, can not survive without prey and therefor will die off if the prey population goes extinct. The model is given by

$$\begin{aligned}\frac{dH}{dt} &= r(1-\frac{H}{K})H - pHL\\ \frac{dL}{dt} &= bHL - cL\end{aligned}$$

where r is the growth rate for the hare population, K is the carrying capacity for the hare population and p is the predation rate of the hares by the lynx population. In the lynx equation, b is the growth rate of the lynx population which is dependent on the hare population and c is the natural death rate of the lynx population. As you may have guessed we have some interesting dynamics going on besides the regular steady state dynamics. Let us begin by looking at a simulation. The code is very similar to the previous program. Be sure to save this MATLAB file as"lotkavolterra1.m".

```
% Your Name
% Today's Day
% Course Number
% Lotka-Volterra Model 1: From lecture notes
```

```
function[] = lotkavolterra1()

clc

% Number of time iterations (in hours)
n = 100;

% Parameter and Initial Conditions
global r; %birth rate for hares
global K; %carrying capcity for hares
global p; %predation rate for the hares
global b; %birth rate for the lynx population
global c; %natural death rate for the lynx population
r = 2;
K = 100;
p = 0.3;
b = 0.1;
c = 0.5;
intH = 50; % Initial hare population
intL = 10; % Initial lync population

%Solution Populations
Hare = zeros(1,n+1);
Lynx = zeros(1,n+1);

%Set initial conditions and place in the proper form
intcond = [intH intL];

% Simulation
% Note: this is the built in MATLAB function known as ode45
[time, Ans] = ode45(@systemlv, 0:n, intcond);
%Pulling out the solutions from the MATLAB function
for i=1:(n+1)
    Hare(i) = Ans(i,1);
    Lynx(i) = Ans(i,2);
end

% Plot
figure(1)
clf
hold on
set(gca,'fontsize',20)
plot(time, Hare,'b-','linewidth',3)
plot(time, Lynx,'r-','linewidth',3)
xlabel('Time (hours)')
```

```
ylabel('Populations')
legend('Hare','Lynx')
title('Predator-Prey Model')
hold off

%%%Differential Equation (Model)

function dy = systemlv(t,y)
%Parameters
global r;
global K;
global p;
global b;
global c;

%Note: The model is entered as a matrix using y(1) in place of H and y(2) in place of L.

dy = [r*(1-(y(1)/K))*y(1)-p*y(1)*y(2);
      b*y(1)*y(2)-c*y(2)];

% Model
% dH/dt = r(1-H/k)H-pHL
% dL/dt = bHL-cL
```

2.1 Fixed Point(s) of Discrete Systems

Through a nice little thought experiment we can actually find the general characterizations of the steady states. Let us start with the trivial state. Should we have a steady state when there are no hare and lynx populations? Yes. Now what would happen to the hare population if only the lynx population went extinct? Well, the hare population would be fine and settle down at its carrying capacity. On the other hand what would happen to the lynx population if all the hares went extinct? In our model the lynx population is dependent on the hare population for survival. If there are no hares, the lynx population would not be able to survive. This means that there should not be a steady state where the hares are extinct but the lynx population is not!

We might also guess since we see both populations existing in real-life that there must also be a steady state where both populations are non-zero at the same time. This is true, but there is quite a bit more to this story than a steady state. First let us find the steady states mathematically and analyze their stability. Then we will talk about other situations where both populations are non-zero in the practice problems.

```
>> clear H L r K p b c Hfixed Lfixed
>> syms H L r K p b c Hfixed Lfixed
>> [Hfixed, Lfixed] = solve('r*(1-(H/K))*H-p*H*L', 'b*H*L-c*L', 'H,L')
```

MATLAB gives us all three states,

- the trivial steady state: $H = 0$ and $L = 0$
- the state with only the hares survive: $H = K$ and $L = 0$
- the state where both populations co-exist: $H = \frac{c}{b}$ and $L = \frac{r}{p}(1 - \frac{c}{bK})$

Notice that the third steady state is only biologically relevant (positive) when $1 - \frac{c}{bK} > 0$ or when $bK > c$. Biologically this means that the natural birth rate of the lynx population times the carrying capacity has to be larger than the death rate for the lynx population. Why might this need to be true?

Since we are working with specific parameter values, let's find our numerical values for the steady states.

```
>> clear H L Hfixed Lfixed
>> syms H L Hfixed Lfixed
>> [Hfixed, Lfixed] = solve('2*(1-(H/100))*H-0.3*H*L', '0.1*H*L-0.5*L', 'H,L')
```

or we could have just typed

```
>> subs(Hfixed, 'r,K,b,c,p', [2 100 0.1 0.5 0.3])
>> subs(Lfixed, 'r,K,b,c,p', [2 100 0.1 0.5 0.3])
```

Now that we have the numerical steady states we should find their stability.

3 Stability of Fixed Points

When we were working with discrete systems we found the stability by looking at the eigenvalues of the Jacobian evaluated at each separate steady state. We will need to do the same processes here. The difference will be how we evaluate the eigenvalues. In the previous lab we noticed that for discrete models the derivative evaluated at the steady state was stable if the absolute values were less than one. However with the continuous model we needed the derivative evaluated at the steady state to be negative. Now that we have many eigenvalues we will need to amend this slightly. For a continuous system's steady state to be:

- **Stable**, **All** of the eigenvalues must be NEGATIVE
- **Unstable**, **At least one** of the eigenvalues is POSITIVE
- **Undetermined**, **At least one** of the eigenvalues is ZERO

3.1 Review of the Jacobian and Eigenvalues

To review, we found the Jacobian by taking the derivatives of the right hand side of both equations with respect to a specific variable. Then we introduced the MATLAB command **jacobian** to do this for us. Remember, to use the **jacobian** command you need to enter in the right hand side equations from the model in order, separated by semicolons. For the predator-prey model we would need to enter the following commands:

```
>> clear H L r K p b c
>> syms H L r K p b c
>> jac = jacobian([r*(1-(H/K))*H-p*H*L; b*H*L-c*L],[H L])
```

Now that we have the jacobian let's put in our parameter values and then look at the stability for each of our three steady states by looking at the eigenvalues. Since we have three steady states we will have to do this three times!

```
>> Hf = subs(Hfixed, 'r,K,b,c,p', [2 100 0.1 0.5 0.3])
>> Lf = subs(Lfixed, 'r,K,b,c,p', [2 100 0.1 0.5 0.3])
>> jac1 = subs(jac, 'r,K,b,c,p,H,L', [2 100 0.1 0.5 0.3 Hf(1) Lf(1)])
>> eig(jac1)
>> jac2 = subs(jac, 'r,K,b,c,p,H,L', [2 100 0.1 0.5 0.3 Hf(2) Lf(2)])
>> eig(jac2)
>> jac3 = subs(jac, 'r,K,b,c,p,H,L', [2 100 0.1 0.5 0.3 Hf(3) Lf(3)])
>> eig(jac3)
```

Using the notation from above, "eig(jac1)" gives us the eigenvalues for the trivial state. The eigenvalues come out to be -0.5 and 2, but since we have one positive eigenvalue this state is **unstable**. Once again, this is good for our system. We do not want the species to go extinct! For the eigenvalues of the state where the hare population is at its carrying capacity and the lynx population is extinct (in our notation "eig(jac2)") we find that the eigenvalues are -2 and 9.5. Again, since one of the eigenvalues is positive this steady state is **unstable**. Finally, our last steady state where both populations coexist have the eigenvalues $-0.0500 + 0.9734i$ and $-0.0500 - 0.9734i$. How do we handle complex numbers? If you get complex numbers for your eigenvalues, then just concentrate on the real parts (i.e. -0.0500). Thus, this steady state is **stable** since all the *real parts* of the eigenvalues are negative. So then what does the imaginary part signify? If you get an imaginary number for your eigenvalues, then there will be *oscillatory* behaviour in the solution. You saw this in your simulations where the populations oscillated above and below the steady state as time increased.

You now know the basics about MATLAB and how to simulate and analyze mathematical models! Of course, there is always more to learn. These are, however, the beginning steps most mathematical biologists take when working with models.

4 General Notes on Discrete Systems

In our final summary please remember the following techniques for working with discrete and continuous systems:

Technique	Discrete	Continuous
Equilibrium States	(Fixed Points) To find: remove subscripts and solve the system	(Steady States) To find: set derivative equal to zero and solve the system
Stability	Take the jacobian of right hand side and evaluate it at the particular fixed point	Take the jacobian of right hand side and evaluate it at the particular steady state
(Stable)	If the absolute value of all the eigenvalues are LESS than 1	If all the eigenvalues are NEGATIVE
(Unstable)	If the absolute value of any eigenvalue is GREATER than 1	If any eigenvalue is POSITIVE

5 Practice Problems

1. Find the biologically relevant steady states of the following system:

$$\begin{aligned}\frac{dx}{dt} &= x(1-x)\\ \frac{dy}{dt} &= 2x + y(1-y)\end{aligned}$$

2. Using the model and steady states from the previous problem, find the stability of all the biologically relevant steady states.

3. Find the biologically relevant steady states of the following system:

$$\begin{aligned}\frac{dx}{dt} &= 2.5x - 0.1y - mx\\ \frac{dy}{dt} &= -0.2y + mx - 0.1y\end{aligned}$$

   with the parameter value $m = 3$ and again, this time with $m = 4$.

4. Using the model and the biologically relevant steady state from the previous problem, find the stability of this steady state for both parameters. Does your stability for the steady states hold when the values for m were changed?

5. In our predator-prey model, we alluded to another type of long-term behavior that was not as straight forward as a steady state. An example of this type of long-term behavior is a **limit-cycle**. In a period two limit cycle, the population oscillates between two different values every other year. For example, one year the population will be high and the next year the population will be low. Then the cycle will repeat. Using our predator-prey simulation, see if you can find values for the parameters r, p, b and c, so that the hare and lynx populations have regular oscillations, but never settle down to a steady state.

6. The following model is over a food chain with three species. The first species, x, gets eaten by the second species, y, which is preyed upon by species three, z.

$$\begin{aligned}\frac{dx}{dt} &= x(1-x) - \frac{5xy}{1+ax}\\ \frac{dy}{dt} &= \frac{5xy}{1+ax} - \frac{0.1yz}{1+2y} - 0.4y\\ \frac{dz}{dt} &= \frac{0.1yz}{1+2y} - 0.01z\end{aligned}$$

   This model was adapted from a 1991 model by Hastings and Powell in a manuscript titled "Chaos in a Three-Species Food Chain", in *Ecology* volume 72 pages 896-903. Simulate this model with three different parameter values for a:

(a) $a = 2$

(b) $a = 4$

(c) $a = 6$

with the initial populations of $x = 0.8$, $y = 0.2$, and $z = 10$. Be sure to change the notation in your MATLAB code so that $x = y(1)$, $y = y(2)$ and $z = y(3)$. What can you say about the longterm behavior of this system for each of the values of a? Do you think you would be able to analyze this system or is something else occurring?