Project On Stochastic Differential Equations: Persistence Time Calculations For Biological Systems

In this project, persistence times or exit times for several biological problems are studied computationally. A computer code, written in MATLAB, is given that performs exit time calculations for two-species biological systems such as predator-prey and competition systems. In the MATLAB program, the Euler-Maruyama method is used to solve the stochastic differential equation (SDE) model for many sample paths. In the computations for each sample path, the population sizes start at specified initial levels. The calculations continue until either population size is less than unity or a specified maximum time is reached. Then, the exit time and the persisting species are recorded for that sample path. Described below are five different biological systems that are to be studied in this project. First, the MATLAB program is listed along with the output for a certain competition system.

MATLAB Program

The MATLAB program is called projsdeNIMBioS.m or projsdeNIMBioS.mat and is listed below. For many two-species biological systems, only nine statements may have to modified. These statements are indicated with a %***.

```
% A program for exit calculations for NIMBioS
% The Euler-Maruyama method is used for solving the SDEs
% nsamp sample paths are calculated
% The proportion exiting up to time t are calculated
% Exits occur when either population size is less than 1
% y1 and y2 are the two populations (different species)
% b1,d1,b2,d2 are the per capita birth and death rates
% y10 y20 are the initial population sizes
% Problem-dependent statements are marked with a %*** (9 statements)
% Accuracy generally increases as h decreases
% icase=1 corresponds to the deterministic problem and so nsamp=1
clf
clear
for icase=1:2
clear tt
clear yp1
clear yp2
nsamp=1000;                                    %***
tmax=100;                                       %***
nt=1000;                                         %***
y10=15;                                          %***
y20=15;                                          %***
if(icase==1) nsamp=1; end
h=tmax/nt;
hs=sqrt(h);
randn('state',2);  %initiates the random number generator
te1=zeros(nsamp,1);
te2=zeros(nsamp,1);
te3=zeros(nsamp,1);
```

```
jj1=0;
jj2=0;
jj3=0;
for jj=1:nsamp
    y1=y10;
    y2=y20;
    yp1(1)=y1;
    yp2(1)=y2;
    r=randn(nt+1,2);
    nchk1=0;
    nchk2=0;
    n=0;
    t=0;
    chk=0;
    tt(1)=0;
    while (chk==0)
    n=n+1;
    t=t+h;
    if(jj==nsamp) tt(n+1)=t; end
    b1=.84;                                           %***
    d1=.40+.01*y1+.022*y2;                            %***
    b2=.90;                                           %***
    d2=.75+.0067*y2+.005*y1;                          %***
    f1=b1*y1-d1*y1;
    f2=b2*y2-d2*y2;
    g1=sqrt(b1*y1+d1*y1);
    g2=sqrt(b2*y2+d2*y2);
    if(icase==1) g1=0; end
    if(icase==1) g2=0; end
    y1=y1+h*f1+hs*g1*r(n,1);
    y2=y2+h*f2+hs*g2*r(n,2);
    if(jj==nsamp) yp1(n+1)=y1; end
    if(jj==nsamp) yp2(n+1)=y2; end
% This is Euler's approximation to the SDE
if (y1 < 1)
      chk=1;
      jj1=jj1+1;
      te1(jj1)=t;
end
if (y2 < 1)
      chk=1;
      jj2=jj2+1;
      te2(jj2)=t;
end
if (t > tmax)
      chk=1;
      jj3=jj3+1;
      te3(jj3)=t;
      chk=1;
end
end % end of while (chk==0) loop
```

```
end % end of for jj=1:nsamp loop
tp=0; tp1=0; tp2=0; tp3=0;
if(jj1 ~= 0) tp1=sum(te1)/jj1; end
if(jj2 ~= 0) tp2=sum(te2)/jj2; end
if(jj3 ~=0)tp3=sum(te3)/jj3;end
if(jj1+jj2~=0)tp=(sum(te1)+sum(te2))/(jj1+jj2); end
p1=jj1/nsamp;
p2=jj2/nsamp;
p3=jj3/nsamp;
% tp1 and tp2 are mean exit times for populations 1 and 2
% tp3 is mean time for sample paths not exiting
% tp is mean exit time for paths that exit
% p1, p2 are proportions exiting for populations 1 and 2
% p3 is proportion not exiting in time tmax
disp('      ')
 if(icase==1) disp('    Deterministic Calculational Results'); end
 if(icase==2) disp('    Stochastic Calculation Results'); end
disp('         icase         nsamp            h            tmax')
disp((sprintf(' %12.0f %12.0f %12.5f %12.2f',icase,nsamp,h,tmax)));
disp('          tp1           p1')
disp((sprintf(' %12.6f %12.6f', tp1, p1)));
disp('          tp2           p2')
disp((sprintf(' %12.6f %12.6f', tp2, p2)));
disp('          tp3           p3')
disp((sprintf(' %12.6f %12.6f', tp3, p3)));
disp('          tp           p1+p2')
disp((sprintf(' %12.6f %12.6f', tp, p1+p2)));
  subplot(2,2,2*icase-1)
  set(gca,'fontsize',18,'linewidth',1.5);
  plot(yp1,yp2,'k-')
  xlabel('Pop. y1')
  ylabel('Pop. y2')
  if(icase==1) title('Deterministic'); end
  %if(icase==2) title('Stochastic'); end
  hold on
  subplot(2,2,2*icase)
  set(gca,'fontsize',18,'linewidth',1.5);
  plot(tt,yp1,'r-',tt,yp2,'k-')
  xlabel('Time t')
  ylabel('Pops. 1 and 2')
  if(icase==1) title('Deterministic'); end
  %if(icase==2) title('Stochastic'); end
  hold on
end % end of for icase=1:2 loop
hold off
```

The biological system studied in the above MATLAB program is a two-species competition model with per capita birth and death rates given by:

$$b_1 = .84, \ d_1 = .40 + .01y_1(t) + .022y_2(t), \ b_2 = .90, \ d_2 = .75 + .0067y_2(t) + .005y_1(t).$$

The resulting deterministic model is:

$$\frac{dy_1(t)}{dt} = (b_1(t) - d_1(t))y_1(t) = .44y_1(t) - .01y_1^2(t) - .022y_1(t)y_2(t)$$

$$\frac{dy_2(t)}{dt} = (b_2(t) - d_2(t))y_2(t) = .15y_2(t) - .0067y_2^2(t) - .005y_1(t)y_2(t)$$

with $y_1(0) = y_2(0) = 15$. The corresponding SDE model is:

$$\frac{dy_1(t)}{dt} = (b_1(t) - d_1(t))y_1(t) + \sqrt{(b_1(t) + d_1(t))y_1(t)}\,\frac{dW_1(t)}{dt}$$

$$\frac{dy_2(t)}{dt} = (b_2(t) - d_2(t))y_2(t) + \sqrt{(b_2(t) + d_2(t))y_2(t)}\,\frac{dW_2(t)}{dt}$$

with $y_1(0) = y_2(0) = 15$ and $W_1(t)$ and $W_2(t)$ are two independent Wiener processes. The SDE model is solved numerically using the Euler-Maruyama method:

$$y_{1,k+1} = (b_{1,k} - d_{1,k})y_{1,k}h + \sqrt{(b_{1,k} + d_{1,k})y_{1,k}h}\,\eta_{1,k}$$

$$y_{2,k+1} = (b_{2,k} - d_{2,k})y_{2,k}h + \sqrt{(b_{2,k} + d_{2,k})y_{2,k}h}\,\eta_{2,k}$$

for $k = 0, 1, 2, \ldots$ until either $y_{1,k+1}$ or $y_{2,k+1}$ is less than unity or time tmax is exceeded. This is performed for nsamp sample paths. The parameter h=tmax/nt is the time step in the method. The output of this program is listed below.

```
Deterministic Calculational Results
        icase           nsamp           h           tmax
          1               1         0.10000        100.00
      tp1            p1
   0.000000        0.000000
      tp2            p2
  87.100000        1.000000
      tp3            p3
   0.000000        0.000000
      tp             p1+p2
  87.100000        1.000000


    Stochastic Calculation Results
        icase           nsamp           h           tmax
          2              1000       0.10000        100.00
      tp1            p1
  11.346606        0.442000
      tp2            p2
  13.081541        0.558000
      tp3            p3
   0.000000        0.000000
      tp             p1+p2
  12.314700        1.000000
```

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The calculational results indicate that for the deterministic model, the first species always out-competes the second species and the time it takes for the second species to have a population less than unity is 87.1. For the stochastic model, the second species out-competes the first species about 44% of the time. The average time to extinction for a species is 12.3. The figure shows the calculational results of the deterministic model and one sample path of the stochastic model.
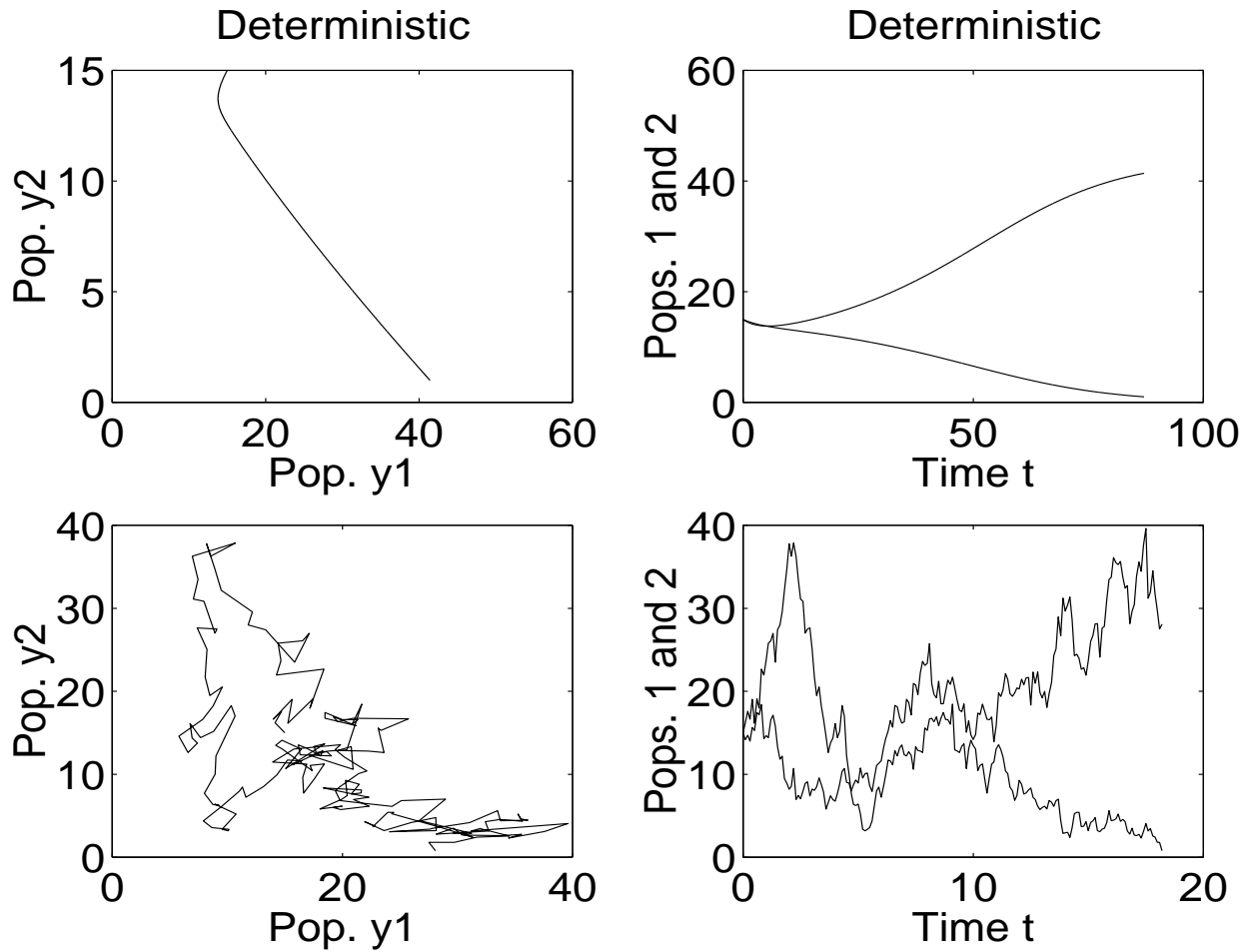

Figure 1: Calculational Results For The Deterministic And Stochastic Models For A Competition System

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Project Outline and Systems To Study

A. Introduction

(1) In this project, it is helpful to have some understanding of the MATLAB program. Please read through the program and get a feel for what the program is doing.

(2) There are nine statements that depend on the biological system and the problem. These statements are marked with a %***. You should locate these statements and understand the meanings of the different parameters.

B. Competition System 1

In this part, you study the system described in the above MATLAB program. The following questions should be answered. These questions will help you understand the program.

(Question 1) For the deterministic results, what does it mean if p1=1 or p2=1?

(Question 2) Consider the stochastic results. What does it mean if p1=.442 and p2=.558 for 1000 sample paths?

(Question 3) Suppose that p3 is not equal to 0? What does this mean? Try changing tmax to tmax=20 and run the program again. What happens?

(Question 4) Reset tmax=100 but try nt=20. Examine tp for the new case. Do you think that the results are more accurate when nt is made larger?

(Question 5) Set b1=.80 rather than b1=.84. (First reset nt to 1000 and tmax to 100.) What happens? Are the results different than when b1=.84? What does this tell us about the sensitivity of competition to the parameter values?

C. Competition System 2

The second system to study is another competition system where the per capita birth and death rates are:

$$b_1 = .45, \ d_1 = .4 + .02y_1(t) + .01y_2(t), \ b_2 = .6, \ d_2 = .5 + .01y_2(t) + .02y_1(t).$$

Several questions that should be answered about this system are:

(Question 1) For this biological system, can you write down the deterministic and stochastic systems? For example, if $\dfrac{dy_1}{dt} = a + by_1 + cy_2 + ry_1y_2 + sy_1^2 + uy_2^2 + v\dfrac{dW_1(t)}{dt} + z\dfrac{dW_2(t)}{dt}$, what are $a, b, c, r, s, u, v,$ and z?

(Question 2) For the deterministic model, which system persists? For the stochastic model, what proportions of populations 1 and 2 persist?

(Question 3) Change b2 to b2=.50. What happens? Are the results sensitive to the values of the parameters? What does this tell us about competition of species in a varying environment where the parameters depend on position?

D. Predator-Prey System

The third system to study is a predator-prey system where per capita birth and death rates are:
$$b_1 = .5, \ d_1 = .05y_2(t), \ b_2 = .2 + .01y_1(t), \ d_2 = .4.$$
The initial population sizes are: y10=40 and y20=5. Also, for this problem, set tmax=90 and nt=3000. Several questions that should be answered about this system are:

(Question 1) Write down the deterministic system of differential equations. By inspecting the equations, can you tell that the first population is the prey and second population is the predator? For the deterministic model, which system persists? For the stochastic model, what proportions of populations 1 and 2 persist?

(Question 2) Why are the results of the stochastic model so different from those of the deterministic model?

E. SIS Epidemic System

The fourth system models an epidemic consisting of susceptible and infected sub-populations where recovery and infection rates are, respectively,

$$\gamma y_2 \quad \text{and} \quad \alpha y_1 y_2$$

where $\gamma = .1$ and $\alpha = .001$. The initial population sizes are: y10=120 and y20=5. Set tmax=500, nt=5000, and nsamp=100. The susceptible population size is y_1 and the infected population size is y_2. As the sub-populations in this biological system are the same species, the stochastic model does not fit into the general model of two interacting species as assumed in the program. It can be shown that the stochastic SIS model has the form:

$$\frac{dy_1(t)}{dt} = (\gamma y_2(t) - \alpha y_1(t)y_2(t)) + \sqrt{\gamma y_2(t) + \alpha y_1(t)y_2(t)} \ \frac{dW_1(t)}{dt}$$

$$\frac{dy_2(t)}{dt} = (-\gamma y_2(t) + \alpha y_1(t)y_2(t)) - \sqrt{\gamma y_2(t) + \alpha y_1(t)y_2(t)} \ \frac{dW_1(t)}{dt}$$

with only one Wiener process $W_1(t)$ appearing in the system. (In the deterministic SIS model, the last term in each equation of the above system is not present.) To study this system using the computer program, the statement y2=y2+h*f2+hs*g2*r(n,2) needs to be modified to y2=y2+h*f2+hs*g2*r(n,1) where, of course, appropriate statements need to be included for f1, f2, g1, and g2. In particular,

$$f_1 = \gamma y_2 - \alpha y_1 y_2, \ g_1 = \sqrt{\gamma y_2 + \alpha y_1 y_2}, \ f_2 = -\gamma y_2 + \alpha y_1 y_2, \ g_2 = -\sqrt{\gamma y_2 + \alpha y_1 y_2}.$$

Several questions that should be answered about this system are:

(Question 1) Show, by examining the equations, that for this problem, $y_1(t) + y_2(t) = y_1(0) + y_2(0)$ for all $t > 0$ for either the deterministic or stochastic model. Determine for the deterministic model, what the populations $y_1(t)$ and $y_2(t)$ approach as $t \to \infty$.

(Question 2) What happens in the calculations? Why do the results of the stochastic model differ from those of the deterministic model? Try tmax=100 and nt= 1000. Explain what happens.

F. Choose a Population System

The final biological system is one of your choosing. Remember, though, the MATLAB program, as set up, assumes that the two species are different. Use the program to study persistence of your biological system.