Solutions for Laboratory 5

Bio 535, Fall 2011

Introduction

The primary objective of this laboratory was to build your experience with implementing, running, and exploring single state variable models. In contrast to your last two laboratories, we solved a discrete time model here using a for-loop. We found chaotic behavior in the Ricker model, a discrete time analogue of the logistic model. In the course of this laboratory we developed our R programming skills and learned techniques for exploring the behavior of simulation models.

This was the first laboratory in which you were to write an R script from scratch. Now that you have some experience, we can discuss both the modeling results and provide some programming tips and tricks in R . To further facilitate your learning, I have included a copy of most of my R scripts in the Appendices.

Task 5.1: Parameter Sensitivity

In Task 5.1 we explored the behavior of the *Ricker model* that is a *discrete time* analogue of the logistic model. In this case, we did not require the numerical approximation techniques – we could use a more simple for-loop. Again we used sensitivity analysis to investigate the role of the parameters. In this case, we discovered that this simple yet completely deterministic model generated chaotic dynamics. Let's take a look at two different topics: programming tricks and dynamics.

Programming Tricks

For this task, I have placed three alternative programs into the appendices that build in complexity. Ricker-1.r is the simplest solution for the Ricker model that evaluates the model for single values of the maximum recruitment rate a and the cannibalism rate b. It is a perfectly adequate solution for the laboratory that will allow you to manually perform the required sensitivity analysis. Before examining the next two examples, make sure you understand this program.

The second example script, Ricker-2.r, uses the information from the first, but automates the sensitivity analysis of one parameter by placing the core of the program into a for loop. For this analysis, I have chosen to plot each run on a different graph. This allows us to quickly see the important differences between the runs.[1]

The final program, Ricker-3.r, builds on the second by adding the automation of a sensitivity analysis for the second parameter b. While it might be appropriate to put the different runs of b on the same six graphs we generated for a, I have chosen as a first step to simply generate three separate figures. To generate different plots I used a command called *quartz()* because it controls the plot windows on the Mac OS. On windows, you would use the *x11()*

[1] Often it is better to have different runs on the same graph, but here the dynamics quite different and lend themselves to separate plots.

Dynamics

What did you learn about the Ricker model from your sensitivity analysis? If we set the cannibalism rate b to 0, we can clearly see that changing the maximum number of viable recruits a alters the geometric rate of increase (decrease) of the population (Figure 1). However, if we add a small amount of cannibalism ($b = 0.001$) to the equation, we can generate a logistic type curve when a is around 2, where the population achieves a static, steady state solution at about 700 individuals (Figure 2). As a increases the qualitative nature of the dynamics change. When $a = 6$ the population overshoots the equilibrium point and then bounces around while slowly approaching it. This is termed a *damped oscillation*. Then, when $a = 10$ the population appears to have a two-state cycle, and an even greater value of a generates dynamics that look random or stochastic, but are technically *non-periodic*. Remember, this is a completely deterministic model. There are no random variables and if you re-run the simulation you will generate the exact same trajectory.

Task 5.2: Initial Conditions

Gurney and Nisbet (1998) describe **chaos** as the "combination of *non-periodic solutions* and *sensitive dependence on initial conditions*" (p. 29). Our work with the Ricker model so far has shown that it generates non-periodic solutions, but does it have the signature sensitivity to initial conditions? To test this, I ran the Ricker model with $a = 18$ and $b = 0.001$ and two very similar initial conditions: $N_0 = 100$ and $N_0 = 101$. The results drawn in Figure 4 show that the two solutions to the Ricker model do generate very different forecasts. These differences are large compared to the small change in initial conditions. Thus, we can conclude that the Ricker model is generating chaotic dynamics. See May (1974) or Otto and Day (2007, p.116–117) for more on this type of behavior.

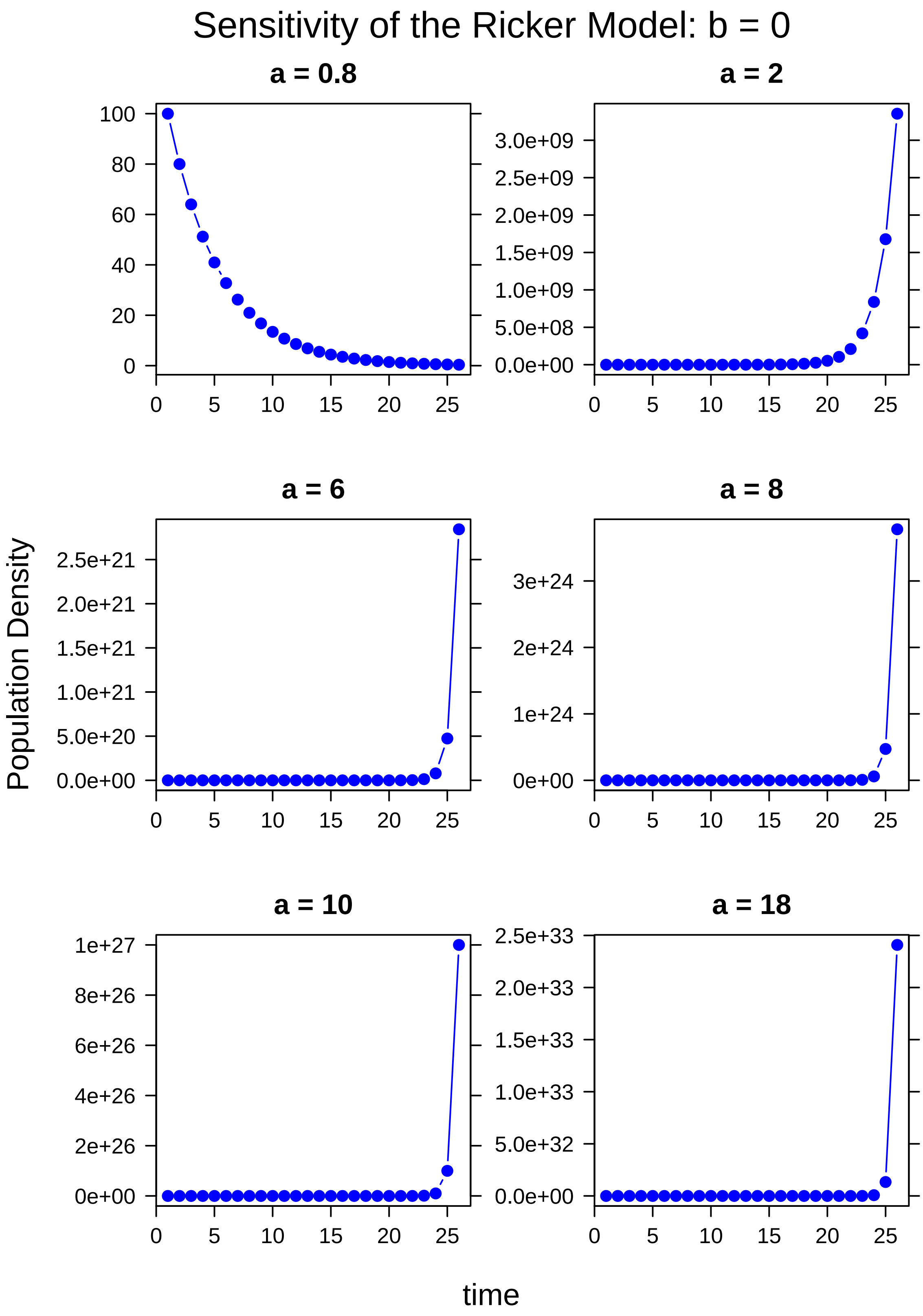

Figure 1: Ricker model sensitivity analysis with no cannibalism. These dynamics show geometric growth (exponential growth in discrete time).

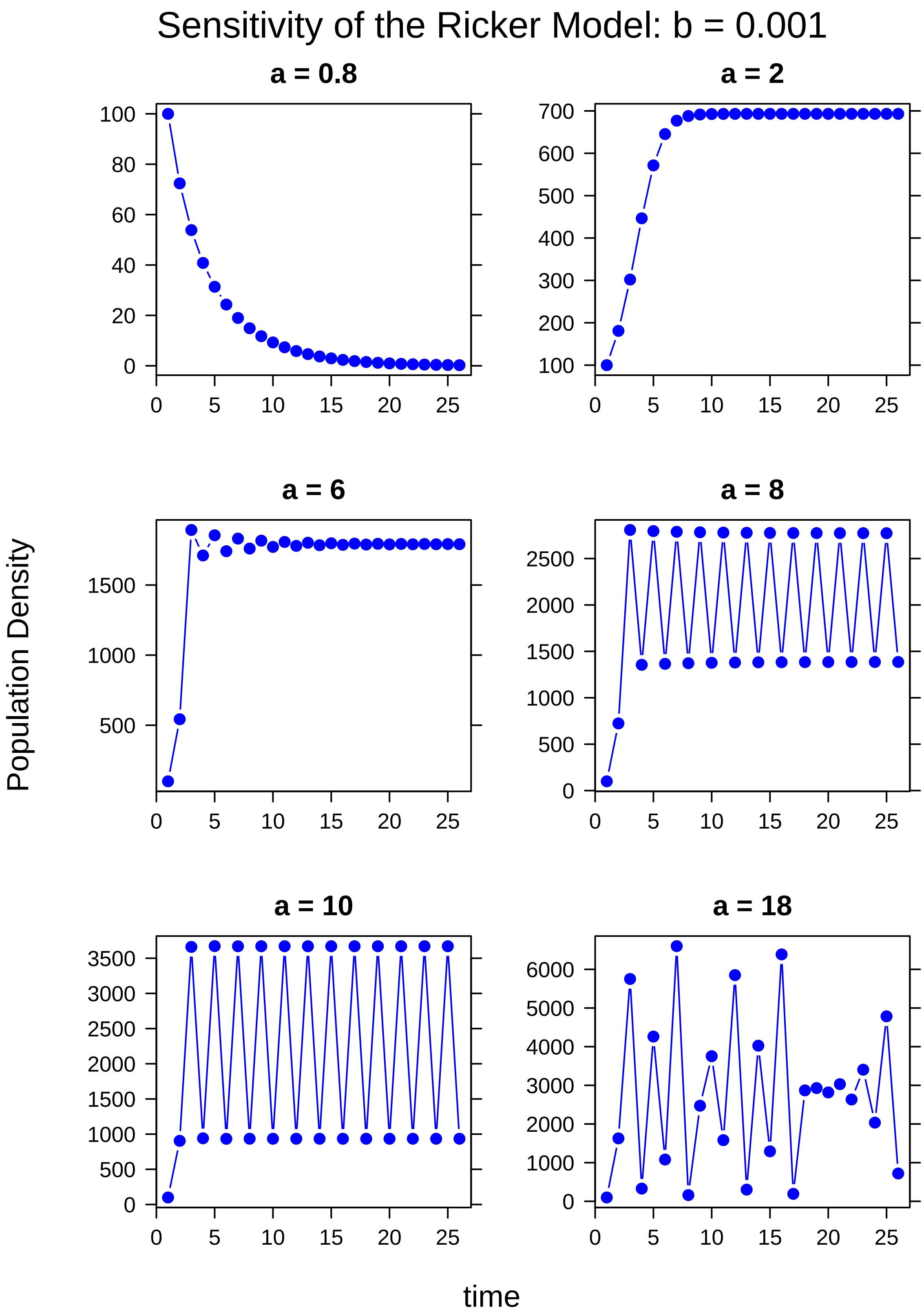

Figure 2: Ricker model sensitivity analysis with a small amount of cannibalism. Notice that as a gets large the solution becomes periodic and eventually exhibits chaotic dynamics.

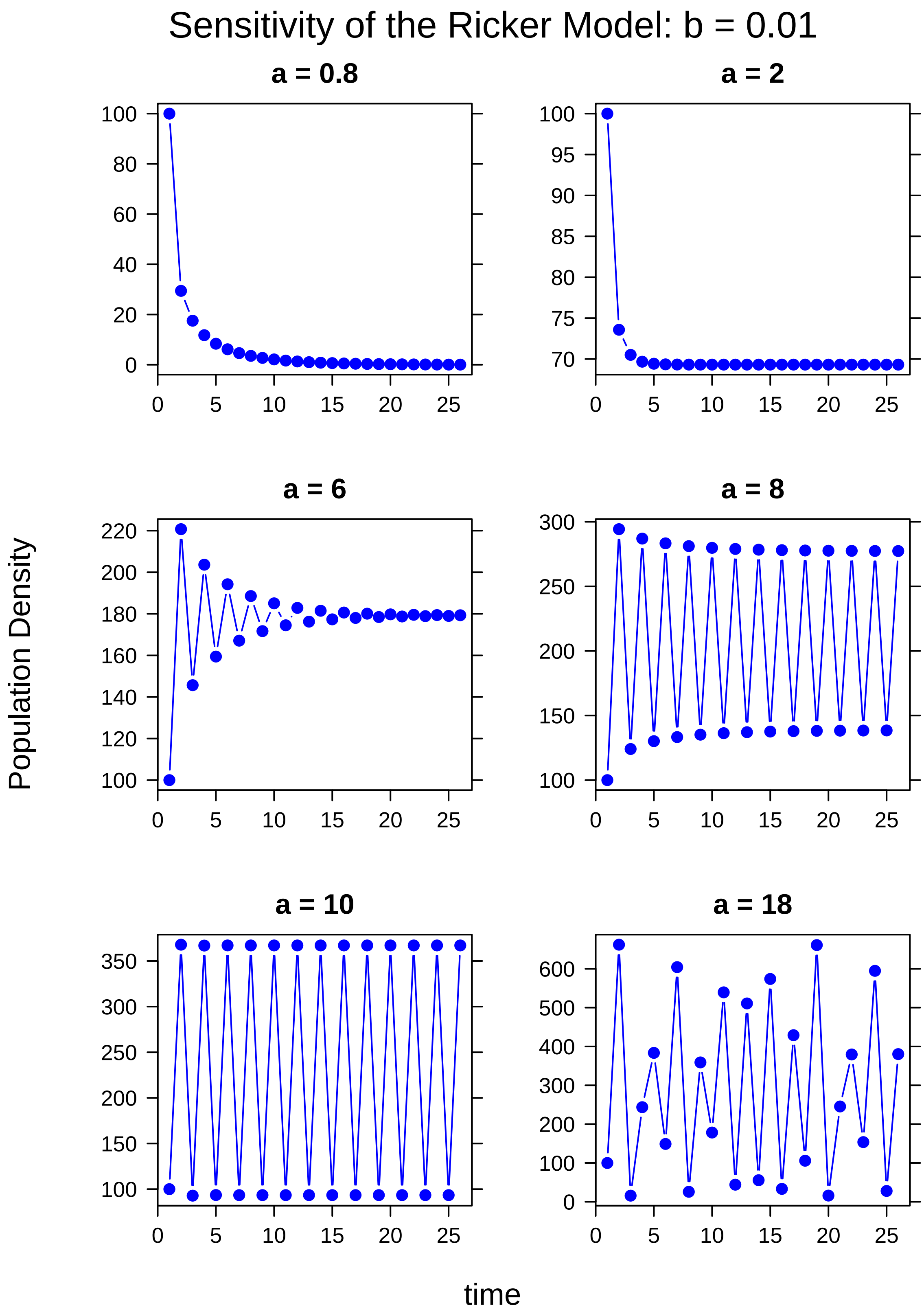

Figure 3: Ricker model sensitivity analysis with strong cannibalism. This shows that as the strength of cannibalism increases, the change in dynamics with a becomes stronger.

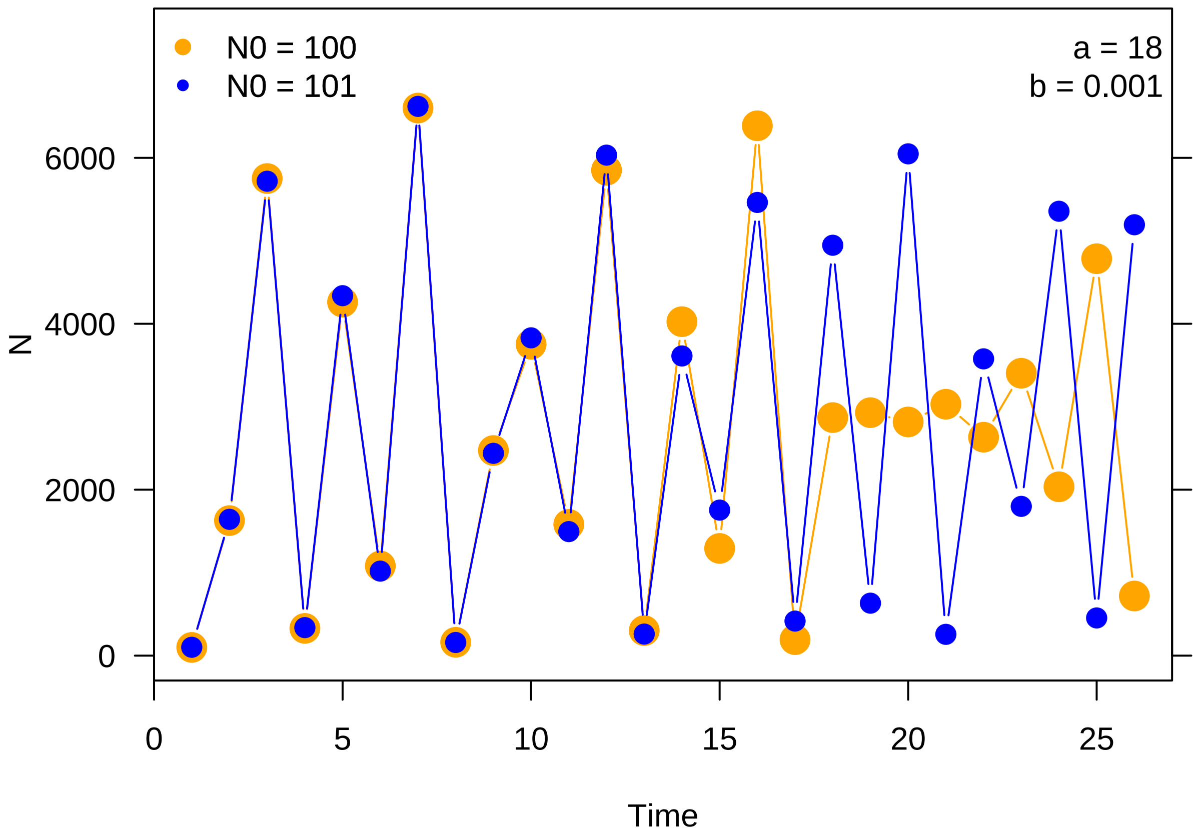

Figure 4: Small changes in the initial starting population density $N_0 = \{100, 101\}$ generate quite different forecasts of future population densities. In these simulations the model parameter are constant at $a = 18$ and $b = 0.001$. This illustrates the Ricker model's *sensitive dependence on initial conditions*, which is a key component of chaotic dynamics.

References

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological dynamics. Oxford University Press, New York.

May, R. 1974. Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. Science **186**:645–647.

Otto, S. P., and T. Day. 2007. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution. Princeton University Press, Princeton, NJ.

Appendices

A Ricker Model Programs

A.1 Simple Ricker Model Program

```
# Ricker Model
# From Gurney and Nisbit (1998)
# October 11, 2006 implemented by S.R. Borrett, revised Sept. 15 2007
#
# This is a discrete time model that Gurney and Nisbit (1998) use to
# model a fish stock.   "We work with a time increment (delta_t) of
# 1 year, and denote the stock of mature individuals at the census
# date in year t by Xt.  Juveniles mature the year after their birth.
# Adult fish spawn once before dying and produce a maximum of [a]
# viable recruits to hte followin year's stock.  Due to cannibalism on
# eggs by adults, the juvenile survivorship in a year when ther are Xt
# adults is exp(-b*Xt), where b is a parameter related to the
# intensity of cannibalism." (p. 27) For my implenetaiton I have
# chosen to use N instead of X as the state varaible  Ricker-2
# shows effects of increasing parameter a from 0.8 to 18.
# ------------------------------------------------------------------------------

# Script Purpose: Explore the sensitivity of the ricker model to
# variation in its parameters -- one parameter at at time

rm(list=ls())  # clear working memory
# -- PROGRAM INPUT --
# Model setup
ti = 1;  # initial time
tf = 25; # final time
tspan = ti:tf # vector of discrete time points (notice that our one
      # unit of time could represent any time length
      # such as 20 minutes)
No<-100;       # initial condition


# Parameters
a = 18  # maximum number of viable recruits
b = 0.001; # cannibalism intensity

N<-rep(0,length(tspan));# this initializes our population vector
N[1]<-No; # put our initial condition in the first place
                        # of our population vector

# -- PROGRAM ACTION --
for (i in tspan){    # it is better not to use t for time because it
```

```
                     # is reserved for a function
    N[i+1]<-a*N[i]*exp(-b*N[i]);    # update rule
  }


# -- PROGRAM OUTPUT --
# -- data visualiztion --
tspan = 1:(tf+1);
plot(tspan,N,type="b",  # type="b" plots both points and lines.
     col="blue", ylab="N",xlab="Time",
     main="Ricker Model",pch=20,cex=2)
```

A.2 Automating Sensitivity Analysis

```
# Ricker Model
# From Gurney and Nisbit (1998)
# October 11, 2006
# implemented by S.R. Borrett Oct. 11, 2006, revised Sept. 15 2007
#
# This is a discrete time model that Gurney and Nisbit (1998) use to
# model a fish stock.  "We work with a time increment (delta_t) of 1
# year, and denote the stock of mature individuals at the census date
# in year t by Xt.  Juveniles mature the year after their birth.
# Adult fish spawn once before dying and produce a maximum of [a]
# viable recruits to hte followin year's stock.  Due to cannibalism on
# eggs by adults, the juvenile survivorship in a year when ther are Xt
# adults is exp(-b*Xt), where b is a parameter related to the
# intensity of cannibalism." (p. 27) For my implenetaiton I have
# chosen to use N instead of X as the state varaible
#
# Ricker-2 shows effects of increasing parameter a from 0.8 to 18.
# ----------------------------------------------------------------------------

# Script Purpose: Explore the sensitivity of the ricker model to
# variation in its parameters -- one parameter at at time

# -- PROGRAM INPUT --
# model setup
ti = 1;  # initial time
tf = 25; # final time
No<-100;               # initial condition

# Parameters
a_val = c(0.8, 2,6,8,10,18);  # the parameter whose sensitivity we are
                              # investigating is now a vector
b = 0.001;

# pdf(file="ricker-sensitivity-a.pdf",width=8.5,height=6) # this sends
# the plot output to a PDF file

opar<-par(mfrow=c(2,3),oma=c(2,3,2,0), mar=c(4,4,3,1),las=1,
          cex.axis=1.2,cex.main=1.6,pty="s") # change default graphics
                                             # parameters


# -- PROGRAM ACTION --
for (a in a_val){ # this is our outer loop that changes steps
                        # through the parameter valeus

   # These model pararmeters need to be defined within this first loop.
```

```
   # Can you figure out why?
  tspan = ti:tf           # vector of discrete time points (notice
                          # that our one unit of time could represent
                          # any time length such as 20 minutes)
  N<-rep(0,length(tspan));# this initializes our population vector
  N[1]<-No;   # put our initial condition in the first
                          # place of our population vector

    for (i in tspan){    # it is better not to use t for time because
                         # it is reserved for a function
      N[i+1]<-a*N[i]*exp(-b*N[i]);    # update rule
    }

  # -- PROGRAM OUTPUT --
  # -- data visualiztion --
  tspan = ti:(tf+1);   # I need to add one more time step to tspan
                        # because I used i+1 to define N
  plot(tspan, N, type="b", pch=20, cex = 2,
   col="blue",main=paste("a = ",a,sep="") ,xlab="",ylab="")
  axis(4,labels=FALSE)
  rm(tspan, i, N)    # clean up workspace so that I can reuse
                         # these variables
}

# Now I am going to add some labels to the plots
mtext("time",side=1,line=0,outer=TRUE,cex=1.2)
mtext("Population Density",
      side=2,line=1,outer=TRUE,cex=1.2,las=0)
mtext("Sensitivity of the Ricker Model",
      side=3,line=0,outer=TRUE,cex=1.4)
rm(opar)

# dev.off() # this closes and completes the PDF file
```

A.3 Varying Two Parameters

```
# Ricker Model
# From Gurney and Nisbit (1998)
# October 11, 2006
# implemented by S.R. Borrett Oct. 11, 2006, revised Sept. 15 2007
#
# This is a discrete time model that Gurney and Nisbit (1998) use to
# model a fish stock.  "We work with a time increment (delta_t) of 1
# year, and denote the stock of mature individuals at the census date
# in year t by Xt.  Juveniles mature the year after their birth.
# Adult fish spawn once before dying and produce a maximum of [a]
# viable recruits to the following year's stock.  Due to cannibalism
# on eggs by adults, the juvenile survivorship in a year when ther are
# Xt adults is exp(-b*Xt), where b is a parameter related to the
# intensity of cannibalism." (p. 27) For my implenetaiton I have
# chosen to use N instead of X as the state varaible
#
# Ricker-3 shows effects of increasing parameter a from 0.8 to 18 and
# b from 0.01 to 0.
# ----------------------------------------------------------------------------

# Script Purpose: Explore the sensitivity of the ricker model to
# variation in its parameters -- one parameter at at time

# -- PROGRAM INPUT --
# model setup
ti = 1;  # initial time
tf = 25; # final time
No<-100;       # initial condition


# Parameters
a_val = c(0.8, 2,6,8,10,18);  # the parameter whose sensitivity we are
                              # investigating is now a vector
b_val = c(0.01,0.001,0);      # param sens to b.  notice that b = 0
                              # turns off the cannabalism

##### MAIN PROGRAM #####
## LOOP #1
for (b in b_val){

  fn = paste("ricker-sensitivity-a-b-",b,".pdf",sep="")
  pdf(file=fn,width=6,height=8.5) # this sends the plot output to a PDF
                                  # file quartz(width=6,height=10)
  opar<-par(mfrow=c(3,2),oma=c(2,3,2,0),
          mar=c(4,5,3,1),las=1,cex.axis=1.2,
          cex.main=1.6) # change default graphics parameters
```

```
  ## LOOP #2
  for (a in a_val){    # this is our outer loop that changes steps
                     # through the parameter valeus

        # These model pararmeters need to be defined within this first
   # loop.  Can you figure out why?
    tspan = ti:tf # vector of discrete time points (notice that
                        # our one unit of time could represent any
                        # time length such as 20 minutes)
    N<-rep(0,length(tspan)); # this initializes our population vector
    N[1]<-No;  # put our initial condition in the
                                 # first place of our population
                                 # vector

    # -- MODEL LOOP -- #
    for (i in tspan){  # it is better not to use t for time because it
                     # is reserved for a function
      N[i+1]<-a*N[i]*exp(-b*N[i]);    # update rule
    }

     # -- PROGRAM OUTPUT --
     # -- data visualiztion --
    tspan = ti:(tf+1);   # I need to add one more time step to tspan
                                        # because I used i+1 to define N
    plot(tspan, N, type="b", pch=20, cex = 2,
         col="blue",main=paste("a = ",a,sep="") ,xlab="",ylab="")
    axis(4,labels=FALSE)
    rm(tspan, i, N)   # clean up workspace so that I can reuse these
                        # variables
  }

  # Now I am going to add some labels to the plots
  mtext("time",side=1,line=0,outer=TRUE,cex=1.2)
  mtext("Population Density",side=2,line=1,
        outer=TRUE,cex=1.2,las=0)
  mtext(paste("Sensitivity of the Ricker Model: b = ",b,sep=""),
        side=3,line=0,outer=TRUE,cex=1.4)  # builds a dynamic label
  rm(opar)

  dev.off() # this closes and completes the PDF file

}
```