

# **Matrix Models for Population Management & Conservation**

## **Lab Exercises**

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## **Software**

Please download the following software to your laptop computer before coming to the matrix modeling workshop

R 3.2.3 <http://cran.r-project.org/index.html>

We have designed the exercises using R. If you do have some experience using R, however, you might find it useful to use R for carrying out the workshop exercises.

**Disclaimer:** Note that we WILL NOT be teaching attendees how to use R, as that is a topic for a workshop in and of itself.

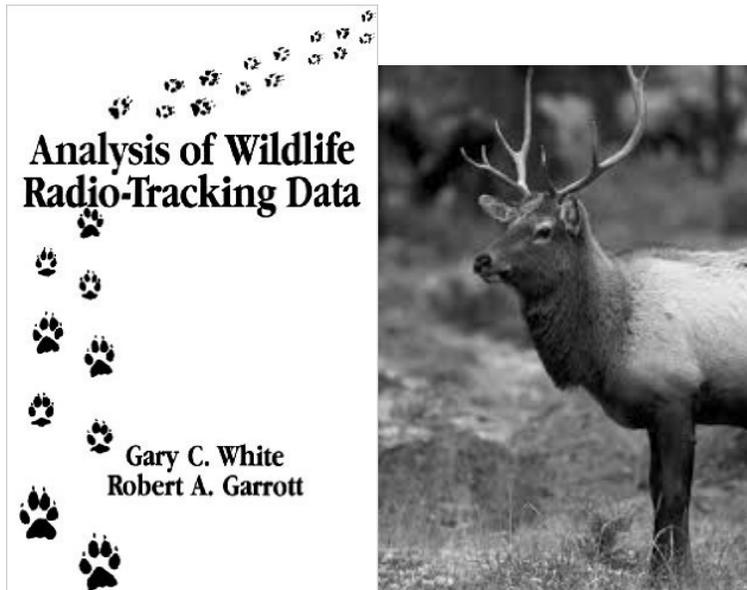
## **Approach to conducting the exercises**

We note that this is a workshop and our primary goal is to help you learn about the basics of modeling structured populations for conservation and management purposes. Additionally, we want to help you learn how to estimate demographic parameters and construct and analyze an array of useful matrix population models with computer software. There will not be an exam testing your memorization capabilities or anything like that.

Below are the exercises for this workshop and we are also providing you with (possible) solutions to the exercises in R to help you address difficulties and questions as the instructors frantically try to address questions in person during the workshop. However, we highly encourage you to conduct the exercises without referring to these solutions until absolutely needed to make progress. There are many potential solutions to some questions, each of which may be equally correct. You will learn more, and get more out of the workshop if you try to conduct the exercises on your own; only checking the solutions to make sure you are heading in a good direction. R users: after the first couple of exercises, we encourage you to try writing your own code to address the exercise problems before consulting the solutions.

## Exercise 1: The Known-Fate Model

This exercise closely follows the content of the 4th lecture and is mostly intended to show how to run program MARK to compute survival from 'known-fate' data.. We have prepared exercises for use in either MARK or RMark.



### Data input

Input data consists of summarized frequencies of encounter-histories. Encounter-history is distinguished here from capture-history by having two codes for each occasion - One for capture-status, and one for recapture-status. The possibilities here are: 11=captured and dead recovery, and 10=captured and not recovered as dead.

The example we'll use for this model contains 2 groups of animals: Treatment and Control. So, each encounter-history will have 2 frequencies following the encounter-history. The following is a sample MARK input file (knownfate.inp):

```
/* known fate example (pg 344) */  
10 19 21 /* 19 treatment-alive, 21 control-alive*/;  
11 38 38 /* 38 treatment-dead, 38 control-dead */;
```

Explanation: The '10 19 21' means that 19 animals from group 1 (treatment) and 21 animals from group 2 (control) were captured in time 1 and were not recovered as dead (ie. they survived). The '11 38 38' means that 38 animals from group 1 and 38 animals from group 2 were captured in time 1 and recovered as dead in time 2 (ie. they did not survive).

## Exercise

1. Open the file “Known\_Fate.r” in your preferred text editor for R (e.g., R Studio, Tinn-R, Notepad++). Note that the hash (#) symbol denotes comments in R and everything on the line after that symbol is ignored by R. The first non-comment lines in the file clear the R workspace (memory) and set the working directory(folder) to the folder where you have the exercises. You will need to modify the working directory. Execute these lines in R. (In R studio or Tinn-R, place the cursor on the first of these lines, then click the ‘Run’ button 3 times. In Notepad++, highlight those 3 lines, copy to clipboard, then paste into R window.)

```
rm(list=ls()) # clear workspace
setwd('h:/x/workshops/uf2016/exercises') # set working directory(folder)
library(RMark)
```

2. Assuming that you have already created a MARK input file, the first step in using RMark is to convert the input file into an RMark input “data-frame”. (You can think of a data-frame as a spreadsheet in R, where you can access the spreadsheet by rows and columns, or by variable(column) name. This conversion is done with the “convert.inp” function. The only required argument is the input filename (knownfate.inp), but since we have 2 groups in our input file, we also need to specify the group names to the convert.inp function. This is done with the group.df argument. The converted data-frame is saved with the R variable name, “mdeerinp”. Execute that line, then type the new variable name into the R window.

```
mdeerinp=
convert.inp('knownfate.inp',group.df=data.frame(trt=c('trt','cnt')))
mdeerinp
```

3. The 2<sup>nd</sup> step is to create a processed-data variable which contains other variables needed to setup and run the MARK models. The variable, “mdeerpr” is a “list” variable, or a variable which contains other variables. The RMark function to do this is “process.data” and requires the converted input from the previous step, the type of MARK models which will be run, and the group variable name (if applicable). Execute this line, then type ‘mdeerpr’ to see the contents of this variable.

```
mdeerpr = process.data(mdeerinp, model='Known', groups="trt")
mdeerpr
```

4. The 3<sup>rd</sup> step is to create design-matrix data variables, needed by MARK to build models. The RMARK function is “make.design.data” and the processed-data variable created in the previous step is needed as an argument to the function. Execute this line and type ‘mdeerdd’ to view the contents of this variable. This is a list-type variable and it contains a data-frame

variable (S) for the estimated parameter for the model-type (Known) we specified. The columns of S are the variables we can use in building MARK models.

```
mdeerdd = make.design.data(mdeerpr)
mdeerdd
```

*Modeling strategy is to develop 2 models. One represents the null hypothesis that there is no difference between the survival rates of the deer in the 2 treatments. The other model represents the alternative hypothesis that the treatment and control groups show different survival rates (control survival > treatment survival).*

5. Now we're ready to build our first MARK model. With only one survival interval in the data, we don't have a lot of choices in building models. We'll start with the most simple model (survival equal among treatment and control groups). To create a model, we call the 'make.mark.model' function with the processed-data variable created in step 3 (mdeerpr), the design-data variable created in step 4 (mdeerdd), title, and list of parameters as arguments. In this case, there is only 1 parameter (S) and we specify the model using an R formula. Here, formula=~1 means the parameter is a constant value. Execute these lines and type 'mod\_null' to examine what we've created. This variable is another list-variable which contains other variables to be used when we run the model.

```
Mod_null=make.mark.model(
  mdeerpr,mdeerdd,title='MuleDeerdata',
  parameters=list(
    S=list(formula=~1)
  )
)
mod_null
```

6. We can run the model by calling the 'run.mark.model' function with the model variable created in step 5 as the argument. Execute this line then type 'mod\_null\_out' to examine the contents. The output from MARK is stored in a text file and by typing 'mod\_null\_out', the text file is opened in notepad. This is the usual output you would get if you ran MARK interactively using its GUI. The output is also stored as an R list-variable. Type 'str(mod\_null\_out)' to display the structure of this list-variable. What is the survival rate estimate from this model? You can get it from the text output displayed in notepad, or by looking at the mod\_null\_out\$results\$real\$estimate variable.

```
mod_null_out=run.mark.model(mod_null)
str(mod_null_out)
print(mod_null_out)
```

```
print(mod_null_out$results$real)
```

- To run another model, we only need to repeat the last 2 steps: create.mark.model, and run.mark.model. With these data, the interest was in whether the treatment affected survival, so we'd like to try a model where survival is different for control and treatment groups. So, we make a new mark model, named mod\_trt, where survival is different among the 2 groups (`S=list(formula=~group)`). Execute these lines, as well as the line to run the model (`mod_trt_out=run.mark.model(...)`). What are the survival rate estimates for the 2 groups? Are they different? Are they significantly different?

```
mod_trt = make.mark.model(mdeerpr,mdeerdd,parameters=list(
  S=list(formula=~group)
))
mod_trt_out = run.mark.model(mod_trt)
print(mod_trt_out$results$real)
```

- We can create a table of model results by calling the 'model.table' function, with the names of the variables which contain the output of each model as an argument. Execute this line, and the next line to print the table. Assuming AIC was covered in the lecture, what does the table tell you about the effect of treatment on survival rates? Do a likelihood-ratio test between models. Does the likelihood-ratio test lead to the same conclusion as model selection?

```
# create AIC table of model results for model comparison
tbl=model.table(model.list=c("mod_null_out","mod_trt_out"),type="Known")
print(tbl)
```

Questions:

- Which model would you choose to best describe these data? Why?
- Does a "z-test" comparison of survival rates between the 2 groups agree with the AIC model selection table?
  - $Z = (S_{\text{cnt}} - S_{\text{trt}}) / (\text{var}(S_{\text{cnt}}) + \text{var}(S_{\text{trt}}))$
  - Need R function, pnorm
- Do the probability levels associated with the z-test and likelihood ratio test differ? If so, why?
  - $LR = \Pr(\text{Chi-sq}, k)$ , where  $\text{Chi-sq} = L_{\text{null}} - L_{\text{trt}}$  and  $k = \text{df}_{\text{null}} - \text{df}_{\text{trt}}$
  - Need R function, pchisq

## Exercise 2: The CJS Model

This exercise closely follows the content of the 5th lecture and is mostly intended to show how to run program MARK to compute survival and capture probabilities from 'capture-recapture' data.. We have prepared exercises for use in either MARK or RMark.



### Data input

#### Background

Data for this example came from the trapping of meadow voles, *Microtus pennsylvanicus*, at Patuxent Wildlife Research Center, Laurel, MD (Nichols *et al.*, 1984). Data were collected on a 10 x 10 grid of trapping stations spaced at 7.6m intervals in old field habitat. A single modified Fitch live trap (Rose, 1973) was placed at each station. Hay and dried grass were placed in the traps and whole corn was used as bait. Sampling occurred for five consecutive days each month, from June 1981 through December 1981. During each 5day trapping session, traps were opened in the evening of the first day, checked the following morning, locked open during the day, and reset in the evening, with the sequence repeated each day until 5 days had elapsed. A racoon, *Procyon lotor* (later captured), visited the traps on the final two nights of the second trapping session, essentially leaving only 3 days of trapping for this session. At each capture, animals were examined for a tag, sexed, weighed, and examined for external reproductive characteristics. Tagged animals were ear-tagged with numbered fingerling tags, and tag numbers of marked animals were recorded at each capture.

We used 'adult' (>22g) and 'young' (<=22g) animals and collapsed the 5 days of sampling each month into a single assessment of presence or absence, leaving six monthly sampling occasions.

### Exercise

1. Open the file “ex2\_cjs2age.r” in your preferred text editor for. Note that the hash (#) symbol denotes comments in R and everything on the line after that symbol is ignored by

R. The first non-comment lines in the file clear the R workspace (memory) and set the working directory(folder) to the folder where you have the exercises. **You will need to modify the working directory.** Execute these lines in R.

```
rm(list=ls())           # clear workspace
setwd('h:/x/workshops/uf2016/exercises') # set working directory(folder)
library(RMark)
```

2. Assuming that you have already created a MARK input file, the first step in using RMark is to convert the input file into an RMark input “data-frame”. (You can think of a data-frame as a spreadsheet in R, where you can access the spreadsheet by rows and columns, or by variable(column) name. This conversion is done with the “convert.inp” function. The only required argument is the input filename (mp2age.inp), but since we have 4 groups in our input file, we also need to specify the group names to the convert.inp function. This is done with the group.df argument. The converted data-frame is saved with the name, “mpinp”. Execute that line, then type the new variable name into the R window.

```
mpinp=convert.inp('mp2age.inp',
  group.df=data.frame(agegrp=c('a','a','y','y'),sex=c('F','M','F','M'))
)
Mpinp
```

*Notice that I didn't name the age-group variable, “age”. This is intentional and due to the fact that RMark has a pre-defined variable named “age”. The RMark variable, “age” can be used for certain things, but not in this case where we want to classify animals into two groups: young at first capture and adult at first capture. We'll use the “age” variable to make models where animals can be “young” in the 1<sup>st</sup> occasion, then adult after.*

3. The 2<sup>nd</sup> step is to create a processed-data variable which contains other variables needed to setup and run the MARK models. The variable, “mppr” is a “list” variable, or a variable which contains other variables. The RMark function to do this is “process.data” and requires the converted input from the previous step, the type of MARK models which will be run, and the group variable name (if applicable). Execute this line, then type ‘mppr’ to see the contents of this variable.

```
mppr = process.data(mpinp, model='CJS', groups=c("agegrp","sex"))
```

- The 3<sup>rd</sup> step is to create design-matrix data variables, needed by MARK to build models. The RMARK function is “make.design.data” and the processed-data variable created in the previous step is needed as an argument to the function. Execute this line and type ‘mpdd’ to view the contents of this variable. This is a list-type variable and it contains a data-frame variables, Phi (for apparent survival) and p (capture probability) for the estimated parameters for the model-type (CJS) we specified. The columns of Phi and p are the variables we can use in building MARK models.

```
mpdd = make.design.data(mppr)
mpdd$Phi
```

- In order to build models where animals can be “young” for 1 capture occasion and “adult” for other occasions, we need to add a variable to our design-data variable. We’d like to create a new variable for Phi which takes on two values:

0 if animal is in group, “young” AND months-since-orig-capture <= 0

1 otherwise

```
mpdd$Phi$agecl=1 # create new variable, agecl
# next, get row numbers where group="y" and age=0
i=((substr(mpdd$Phi$group,1,1)=="y") & (mpdd$Phi$Age==0))
mpdd$Phi$agecl[i]=0 # set new variable to zero for those rows
print(mpdd$Phi) # look at new Phi data-frame
```

*Modeling strategy is to develop models corresponding to our hypotheses of how survival and/or capture probabilities are affected by age, sex and time.*

- Now we’re ready to build our first MARK model. We’ll start with the most simple model (survival constant over time and equal among age/sex groups). To create a model, we call the ‘make.mark.model’ function with the processed-data variable created in step 3 (mppr), the design-data variable created in step 4 (mpdd), title, and list of parameters as arguments. Here, formula=~1 means the parameter is a constant value. Execute these 3 lines and type ‘phi\_1\_p\_1’ to examine what we’ve created. This variable is another list-variable which contains other variables to be used when we run the model.

```
phi_1_p_1 = make.mark.model(mppr,mpdd,title='Patuxent Mp data',parameters=list(
  Phi=list(formula=~1),
  p=list(formula=~1)
))
```

7. We can run the model by calling the 'run.mark.model' function with the model variable created in step 6 as the argument. Execute this line then type 'phi\_1\_p\_1\_out' to examine the contents. The output from MARK is stored in a text file and by typing 'phi\_1\_p\_1\_out', the text file is opened in notepad. This is the usual output you would get if you ran MARK interactively using its GUI. The output is also stored as an R list-variable. Type 'str(phi\_1\_p\_1\_out)' to display the structure of this list-variable. What is the survival rate estimate from this model? You can get it from the text output displayed in notepad, or by looking at the phi\_1\_p\_1\_out\$results\$real variable.

```
phi_1_p1_out=run.mark.model(phi_1_p_1)
Phi_1_p_1_out$results$real
```

8. To run other models, we only need to repeat the last 2 steps: create.mark.model, and run.mark.model. With these data, the interest was in whether survival and/or capture probabilities were different among age and sex classes, as well as time. So, we make new mark models, with different assumptions about survival and capture probabilities. Execute these lines, as well as the line to run the models.

```
#      make model with age-specific survival, phi(a)p(.)
phi_a_p_1 = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl),
  p=list(formula=~1)
))
phi_a_p_1_out = run.mark.model(phi_a_p_1)
```

```
#      make model with age and sex-specific survival, phi(a*s)p(.)
phi_axs_p_1 = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl*sex),
  p=list(formula=~1)
))
phi_axs_p_1_out = run.mark.model(phi_axs_p_1)
```

```
#      make model with age and sex-specific survival, sex-specific capt. probs, phi(a*s)p(s)
phi_axs_p_s = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl*sex),
  p=list(formula=~sex)
))
phi_axs_p_s_out = run.mark.model(phi_axs_p_s)
```

```

#           make model with age,sex,time-specific survival, sex-specific capt. probs,
phi(a*s*t)p(s)
phi_axsXt_p_s = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl*sex*time),
  p=list(formula=~sex)
))
phi_axsXt_p_s_out = run.mark.model(phi_axsXt_p_s)

#           make model with age,time-specific survival, sex-specific capt. probs, phi(a*t)p(s)
phi_aXt_p_s = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl*time),
  p=list(formula=~sex)
))
phi_aXt_p_s_out = run.mark.model(phi_aXt_p_s)

#           make model with age,time-specific survival, sex-specific capt. probs
#           with additive effect of age on survival
phi_aPt_p_s = make.mark.model(mppr,mpdd,parameters=list(
  Phi=list(formula=~agecl+time),
  p=list(formula=~sex)
))
phi_aPt_p_s_out = run.mark.model(phi_aPt_p_s)

```

9. We can create a table of model results by calling the 'model.table' function, with the names of the variables which contain the output of each model as an argument. Execute this line, and the next line to print the table.

```

tbl=model.table(model.list=ls(pattern="phi.+out"),adjust=T,use.lnl=T)
print(tbl)

```

Shortcut: Instead of listing all of the models by name in the model list, I used the R function, "ls", which lists all variables in the workspace which start with "phi" and end with "out".

Questions:

1. The models with interaction between age and time and additive time + age effects were both competitive. In the interactive model, adult survival is higher in some months and young survival in others. Can this happen as well in the additive model? Why or why not?

2. In many species of vertebrates, young are predicted to have lower apparent survival than adults. Was this true in the example? What biological stories might explain the direction of the estimated average difference between young and adult survival?
3. The a priori hypothesis was that males would have higher capture probabilities than females. Was this true? What biology might underlie this prediction and difference?
4. Some population models (such as stochastic projection matrices) require estimates of true temporal variance of vital rates such as survival. But what other source of variation is present in the monthly variation among survival estimates? How can the true temporal variance be separately estimated?
5. The CJS model permits inference about capture and apparent survival probabilities, as shown. But under the JS model, we can also estimate abundance of adults. How do we do this?
6. Why can't we estimate the number of young in the same manner as for adults? What piece of information are we missing?

### Exercise 3: The Multistrata Model

This exercise closely follows the content of the 6th lecture and is mostly intended to show how to run program MARK to compute survival, transition and capture probabilities from 'capture-recapture' data.. We have prepared exercises for use in either MARK or RMark.



#### Data input

##### Background

Data for this example came from the trapping of meadow voles, *Microtus pennsylvanicus*, at Patuxent Wildlife Research Center, Laurel, MD (Nichols *et al.*, 1984). Data were collected on a 10 x 10 grid of trapping stations spaced at 7.6m intervals in old field habitat. A single modified Fitch live trap (Rose, 1973) was placed at each station. Hay and dried grass were placed in the traps and whole corn was used as bait. Sampling occurred for five consecutive days each month, from June 1981 through December 1981. During each 5-day trapping session, traps were opened in the evening of the first day, checked the following morning, locked open during the day, and reset in the evening, with the sequence repeated each day until 5 days had elapsed. A racoon, *Procyon lotor* (later captured), visited the traps on the final two nights of the second trapping session, essentially leaving only 3 days of trapping for this session. At each capture, animals were examined for a tag, sexed, weighed, and examined for external reproductive characteristics. Tagged animals were eartagged with numbered fingerling tags, and tag numbers of marked animals were recorded at each capture.

We used 'adult' (>22g) animals and collapsed the 5 days of sampling each month into a single assessment of presence or absence, leaving 11 monthly sampling occasions. For each capture, the location of capture was recorded. Individuals captured in locations with X-coordinate in the range 1-5, were assigned capture-code '1'. Those captured in locations with X-coordinate in the range 6-10 were assigned capture-code '2'.

### Exercise

1. Open the file “ex3\_multistrata.r” in your preferred text editor for R. **You will need to modify the working directory.** Execute the lines to clear the workspace, set the working directory and load the RMark library.

```
rm(list=ls()); setwd('h:/x/workshops/uf2016/exercises/ex3_multistrata_mp')  
library(RMark)
```

2. The first step is to convert the input file into an RMark input “data-frame. This conversion is done with the “convert.inp” function. The only required argument is the input filename (mp2age.inp), but since we have 2 groups in our input file, we also need to specify the group names to the convert.inp function. This is done with the group.df argument. The converted data-frame is saved with the name, “mpinp”. Execute that line, then type the new variable name into the R window.

```
mpinp = convert.inp('multistrata.inp',group.df=data.frame(sex=c('F','M')))
```

3. The 2<sup>nd</sup> step is to create a processed-data variable which contains other variables needed to setup and run the MARK models. The RMark function to do this is “process.data” and requires the converted input from the previous step, the type of MARK models which will be run, and the group variable name (if applicable). Execute this line, then type ‘mppr’ to see the contents of this variable.

```
mppr = process.data(mpinp, model='Multistrata', groups="sex")
```

4. The 3<sup>rd</sup> step is to create design-matrix data variables, needed by MARK to build models. The RMARK function is “make.design.data” and the processed-data variable created in the previous step is needed as an argument to the function. Execute this line.

```
mpdd = make.design.data(mppr)
```

*Modeling strategy is to develop models corresponding to our hypotheses of how survival, transition and/or capture probabilities are affected by sex and time. One of the primary objectives of the study was to determine the effects of habitat fragmentation. Just after the 4<sup>th</sup> month, a strip was mowed down the middle of the area. The hypothesis was that the mowing of the strip would cause movement of animals between the two grid halves to decrease after the 4<sup>th</sup> month.*

- Now we're ready to build our first MARK model. We'll start with the most simple model (survival transition and capture probabilities constant over time). To create a model, we call the 'make.mark.model' function with the processed-data variable created in step 3 (mppr), the design-data variable created in step 4 (mpdd), title, and list of parameters as arguments. As a reminder, the formula, "~1" means that the parameter is constant over all values of time and group (sex).

```
s_1_psi_1_p_1 = make.mark.model(mppr,mpdd,title='Patuxent MP data',parameters=list(
  S=list(formula=~1),
  Psi=list(formula=~1),
  p=list(formula=~1)
))
```

- We can run the model by calling the 'run.mark.model' function with the model variable created in step 5 as the argument. Execute this line then type 's\_1\_psi\_1\_p\_1\_out' to examine the contents. The output from MARK is stored in a text file and by typing 's\_1\_psi\_1\_p\_1\_out', the text file is opened in notepad. This is the usual output you would get if you ran MARK interactively using its GUI. The output is also stored as an R list-variable. Type 'str(s\_1\_psi\_1\_p\_1\_out)' to display the structure of this list-variable.

```
s_1_psi_1_p_1_out=run.mark.model(s_1_psi_1_p_1)
```

- To run other models, we only need to repeat the last 2 steps for each model. Run the next model by executing the appropriate lines in the file.

```
s_t_psi_t_p_t = make.mark.model(mppr,mpdd,parameters=list(
  S=list(formula=~time),
  Psi=list(formula=~time),
  p=list(formula=~time)
))
s_t_psi_t_p_t_out = run.mark.model(s_t_psi_t_p_t)
```

- To make a model where transition rates were one value before the mowing of the strip, and another value after the mowing, we'll need to create a new design-data variable. We'll call it "twoper" and set it to zero for the 1<sup>st</sup> 4 months and one for the last 6 months.

```
mpdd$Psi$twoper=0
mpdd$Psi$twoper[mpdd$Psi$Time>3]=1
```

9. We can now build and run our model where transition rates are one value for the 1<sup>st</sup> 4 months and another value after.

```
s_t_psi_2per_p_t = make.mark.model(mppr,mpdd,parameters=list(
  S=list(formula=~time),
  Psi=list(formula=~twoper),
  p=list(formula=~time)
))
s_t_psi_2per_p_t_out = run.mark.model(s_t_psi_2per_p_t) #      run model
```

10. We can create a table of model results by calling the 'model.table' function, with the names of the variables which contain the output of each model as an argument. Execute this line, and the next line to print the table.

```
tbl=model.table(model.list=ls(pattern="s_.+out"),type="Known")
print(tbl)
```

#### Questions:

- (1) This grid was part of an experiment designed to test hypotheses about effects of fragmentation on meadow vole population dynamics. If the fragmentation created by the strips of bare ground really affected movement, what predictions would we make about effects of fragmentation on the 3 sets of model parameters (survival, capture and movement probabilities)?
- (2) Based on AIC, which model appears to be best supported by the data? What conclusions can you draw from this experiment based on the AIC table? Are the parameter estimates themselves relevant to conclusions or does AIC provide all of the information that you need?
- (3) Have a look at the estimates of movement probabilities from the 2 time periods, before and after fragmentation. Are they consistent with your predictions?
- (4) Do the results from this grid provide strong inferences about effects of fragmentation? If not, what other information would be useful in strengthening the inferences?
- (5) In (1) did you make any predictions about changes in survival probability associated with fragmentation? If so, what was your rationale? The top model provided time-specific estimates of survival, so we could compute and compare means for the periods before and after fragmentation. Another way to obtain inference about this contrast is to look at estimates arising from the 3<sup>rd</sup> model, in which survival is computed for 2 time periods (before and after fragmentation). What do these look like? Are they consistent with predictions?

### Exercise 4: The Barn Swallow Matrix Model

This exercise closely follows the content of the first lecture and is mostly intended as a first contact with matrix models. We have prepared exercises for use in either ULM or R. The R exercises are intended for those with experience using R [note that we will not have the time to introduce R to new users during this particular workshop]; otherwise use ULM.



Assume that the dynamics of a barn swallow *Hirundo rustica* population can be adequately represented by a model using two age classes (1st Year and After 1st Year, FY and AFY, with respective abundances denoted as  $N_1$  and  $N_2$ ), and the following vital parameters :

$f_1$ : number of females fledged per female aged 1

$f_2$ : number of females fledged per female aged 2 or more

$s_0$ : survival from fledging until the following spring

$s_1$  : annual probability of survival from age 1 to 2

$s_2$  : annual probability of survival for older birds

The estimated values of the demographic parameters are:  $f_1 = 1.5$  and  $f_2 = 3.0$  (assuming a balanced sex ratio at fledging time),  $s_0 = 0.2$ ,  $s_1 = 0.50$ , and  $s_2 = 0.65$

#### Exercise

1. Draw the barn swallow life cycle, making fledglings appear explicitly in your diagram.
2. Write the corresponding matrices in the pre birth-pulse and post birth-pulse models.
3. Open the file “Ex4Swallow.r” in your preferred text editor for R (e.g., Notepad++, TINN-R, R Studio). For the moment, we will not use R packages for population dynamics, but will instead use raw code to gain a thorough understanding of age-structured population dynamics. Later, we will introduce R packages that you might find useful. Inspect the first piece of code to see if you can interpret what it does; then run the code and inspect the output to see if you understand the code correctly. What happens to population growth rate over time?
4. The next piece of code allows you to loop through two different sets of initial values:  $n_1 = 10$ ,  $n_2 = 0$ ; then  $n_1 = 0$ ,  $n_2 = 10$ . The graph code provides comparisons of the age-specific abundances, total abundances, and population growth rates for the different initial conditions. What happens to the population growth rates and total abundances over time? You can change the time span of projection by changing the “tspan” variable, and

you can also view the numerical output by simply typing the name of the variable you want to inspect in R.

5. Now see if you can develop a graph that plots the abundance of one age class against the other ( $n_1, n_2$ ) for each of the initial conditions. This is called a “phase plane”, and is one way to view convergence of the population’s age structure to the stable age structure.
6. Now adjust the code to examine the population dynamics for the post birth-pulse model, and compare to dynamics of the pre birth-pulse model from above. You could just change a few lines of code, or you could ‘copy’, ‘paste’ and then adjust the code.



## Exercise 5: Perturbation Analysis of the White Stork Model

From the late 1950's to the mid-70's, the number of white storks (*Ciconia ciconia*) breeding in Alsace (eastern France) rapidly declined at a rate close to 15% per year. Here we examine the impact of various demographic parameters on the dynamics of this population. Let us consider the female life cycle (sex ratio = 1:1) with 4 age classes. The initial numbers of individuals in these age classes are assumed to be, respectively:  $N_1 = 80$ ,  $N_2 = 60$ ,  $N_3 = 40$ ,  $N_4 = 100$ .

The estimates of mean demographic parameters are:

$u = 0.45$  = proportion of breeders among 3 year old females (100% of females older than 3 breed)

$r = 0.818$  = proportion of breeders that are successful in fledging young

$b = 2.9$  = number of fledglings produced per 'successful pair' per year

$s_0 = 0.482$  = 1<sup>st</sup> year annual survival probability after fledging

$s_{1+} = 0.75$  = annual survival probability after the first year

A decline in survival was evident from analyses of ring recoveries of storks marked as chicks (1950-1970, A. Schierer data), but was difficult to precisely estimate because the small number of available recoveries prevented a robust time-dependent analysis. There was also evidence of a slight decline in reproductive output. Which type of change in demography is likely to have had a greater impact on stork population dynamics; changes in survival or changes in reproductive output? A perturbation analysis of a white stork matrix model can provide valuable insight into the effects 'changes' in demographic parameters have on population dynamics. This can provide insight into where conservation and management is needed, or where greater rigor in marking and statistical estimation is needed. The purpose of this exercise is to improve our understanding of how comparable changes in survival and reproductive success affect the white stork population growth rate relative to one another.

### Exercise

- 1) Open the file "Ex5Stork.r" in your preferred text editor. Examine the matrix model and draw the corresponding life cycle. Now run the first piece of code in R to calculate the long-term (asymptotic) population growth rate for white storks. This code uses the dominant eigenvalue

of the projection matrix, parameterized with the demographic parameters provided above, to perform this calculation. To three decimals **write down the growth rate** on paper or in a spreadsheet.

- 2) Emulating the decline in survival that was observed (but difficult to estimate precisely), decrease survival after the first year by 20% such that  $s_{1+} = 0.8 \cdot 0.75 = 0.6$  (just make this change in the code) and re-run the first piece of code. Calculate the change in population growth rate, relative to the change in survival, by performing the following numerical calculation, where ‘abs’ refers to the absolute value of a difference:

$$\frac{\text{abs}(\lambda_{\text{new}} - \lambda_{\text{original}})}{\lambda_{\text{original}}} \frac{\text{original demographic parameter}}{(\text{original demographic parameter} - \text{new demographic parameter})}$$

R can also be used as a calculator (or for doing advanced algebra and calculus), so you can perform this calculation in R and store or write down the result.

- 3) Change after-first-year survival back to the original value of 0.75. Now repeat the same exercise for first-year survival such that the new  $s_0 = 0.8 \cdot 0.482 = 0.3856$ . Add the calculated ‘change in population growth rate, relative to the change in survival’ to that from part 2 in order to quantify the total effect of change in survival.
- 4) Change first-year survival back to 0.482, and repeat the same exercise for the number of fledglings produced per successful pair per year, such that  $b = 0.8 \cdot 2.9 = 2.32$  (a much larger change in reproductive output than was actually observed). Note that you are changing fledgling production for adults of all ages simultaneously.
- 5) Although the changes made to the demographic parameters in steps 2, 3, and 4 were relatively large, do you think you were approximating the ‘sensitivities’ or the ‘elasticities’ of the population growth rate to change in the underlying demographic parameters? How would you go about numerically calculating the other perturbation metric?
- 6) Set all demographic parameters back to their original values. Compare your calculations from steps 2 – 4 to the exact analytical calculations by running the second piece of code. Note that the reproductive values and stable age distribution are also calculated because they are components of sensitivities and elasticities.
- 7) Discuss the relative effects of changes in survival vs. reproductive output on population growth rate of long-lived white storks.
- 8) If you have time, run the second piece of code for the short-lived barn swallows from Exercise 1 in order to calculate their sensitivities and elasticities for the analogous demographic parameters, then compare to the white stork.



## Exercise 6: Two-Site Matrix Models for Black-Headed Gulls

We use here data on a black-headed gull *Chroicocephalus ridibundus* population in central France. Approximately 3000 pairs breed in a large flourishing colony on a single pond; ~3000 pairs breed in ~20 other colonies at less favorable sites. Various results

indicate that many birds are forced to breed in less favorable sites by saturation of the largest colony. Matrix modeling could help us understand the functioning of this spatially structured population. For the sake of simplicity, we explore this issue using 2 sites: “Good” (G) and “Bad” (B).

The available information on demographic parameters can be summarized as follows. Resightings of birds marked as breeders in the largest colony up to 1985 were analyzed by capture-recapture methods to estimate the annual adult survival probability (0.82) and the age-specific proportion of breeders (approximately 0.3, 0.5, 0.7 and 1 for ages 2, 3, 4,  $\geq 5$ ) for the largest colony. Breeding appears to start at an earlier age in the small unfavorable colonies, and an educated guess for the age-specific proportion of breeders in the Bad site is 0.5, 0.8, 1 and 1 for ages 2, 3, 4, and  $\geq 5$ . The effective juvenile migration rates from each location to the other, and probabilities of survival from fledging to age 1, and age 1 to 2, can be viewed in the `bhgull1.ulm` file.

### Exercise

The information above is gathered in the matrix **A** in the `Ex6Gulls.r` file; the model for our first scenario, which assumes a slightly asymmetric juvenile dispersal.

- 1) View the matrix **A** in R by simply running the first piece of code defining **A**, and then typing `A` in R. You will see that it is a ‘mega-matrix’ with a matrix block in the upper left for the Good location, a matrix block in the lower right for the Bad location, and migration transitions in the upper-right and lower-left blocks. Find the long-term population growth rate using the `popbio` package, then by calculating the dominant eigenvalue of **A** in order to check that the population is close to stationary.
- 2) Run the following lines of code that calculate the stable age-by-location distribution and the reproductive values. Comment on the reproductive values at age 1 for the two sites.

- 3) Conduct an elasticity analysis for the lower-level parameters in order to obtain  $T$ , the generation time, as described in the lecture.
- 4) Using the lower-level elasticity for adult survival  $\partial \log \lambda / \partial \log s$ , predict the change in  $\lambda$  that would occur if adult survival ( $s$ ) were changed from 0.82 to 0.89, a change that seems plausible from data collected between 1985 and 1993. This can be done using the approximation: % change  $\lambda \approx$  % change vital rate  $\times$  elasticity, and  $\lambda_{\text{predict}} = \lambda_{\text{original}} \times$  relative change in  $\lambda$ . Induce this change in the code and find the new dominant eigenvalue of **A**. Compare your predicted  $\lambda$  to the actual  $\lambda$ , and discuss how close your prediction was.
- 5) In piece 2 of the code, how is the ratio of breeding numbers ('ratio') calculated?
- 6) Use the provided loop to calculate the 'ratio' over time and graph how it changes. Explain why, like the population growth rate, the 'ratio' stabilizes over time.

In addition to juvenile dispersal, we will now consider adult dispersal probabilities of  $gb$  (Good to Bad) and  $bg$  (Bad to Good). Piece 3 of the code has a re-parameterization of the matrix model to include this. Initially, the adult dispersal probabilities are set to 0 such that the demography is the same as above.

- 7) Recent counts indicate a shift in numbers among the colonies with  $N_{\text{good}} \approx 5000$  breeding pairs and  $N_{\text{bad}} \approx 1200$  pairs (ratio = 4.17). Can symmetrical dispersal ( $gb = bg > 0$ ) induce such a change in 'ratio'? Try dispersal probabilities of 0, 0.05, 0.1, 0.15, and 0.2 (by simply changing the parameter values at the top of the code in piece 3, and re-running the code in piece 3); remember to keep  $gb = bg$ .
- 8) Approximate, by successive change in  $bg$ , the level of adult dispersal from B to G ( $bg > 0$ ) that can lead to a ratio = 4.17 with no adult dispersal from G to B ( $gb=0$ ).
- 9) Interestingly, black-headed gull colonies move after reproductive failure. Comment on this trait in relation to the previous result.

## Exercise 7: Chamois in Random Environments



Deterministic model with constant parameters: A Capture-Mark-Recapture study was used to estimate survival in a population of chamois (*Rupicapra rupicapra*) in the Bauges Mountain Range (France). According to these analyses, four age classes were considered with the following annual survival probabilities:

from age 0 to 1:  $s_0 = 0.660$

from age 1 to age 2:  $s_1 = 0.897$

from age 2 to age 10:  $s_{2-10} = 0.962$

from age 11 onwards :  $s_{11+} = 0.733$

The proportion of breeding females at age 2 is  $m_2 = 0.66$ , and for older females it is  $m = 0.92$ . Each breeding female produces one young per year, with a balanced sex-ratio at birth. The initial population contains 1100 individuals.

### Exercise

The information above is contained in the Ex7Chamois.r file in the section with comments entitled 'Chamois Models'.

- 1) Assuming a constant, deterministic environment and using the provided code with estimates of the demographic parameters, is this population viable?
- 2) What happens when senescence is ignored (i.e., when survival from age 11 onwards is assumed to be the same as the previous age class)?
- 3) Using  $s_{11+} = 0.733$ , which demographic parameters have the strongest impact on the deterministic population growth rate?

Model with environmental stochasticity: We will now consider the reality that chamois in the Bauges experience environmental variability. In some years 'catastrophic events' occur, strongly reducing all survival parameters. Given the timing of these events, fecundity is not affected. Juvenile survival is reduced to  $\frac{2}{3}$  and all other survival parameters to  $\frac{1}{2}$  their baseline value in good conditions. On average, such catastrophes occur every 15 years. The code for this is summarized in part 2 of the Exercise 4.r file where a Bernoulli distribution is used to implement the frequency of catastrophes and catastrophic levels of survival.

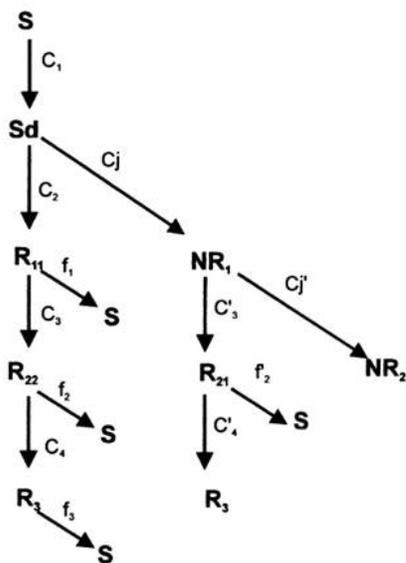
- 4) Qualitatively, what do you think this form of environmental stochasticity will do to the chamois population, and which estimator should you use for measuring the population growth rate in a variable environment?
- 5) Using a pseudo-extinction threshold of 100 individuals (when demographic stochasticity can begin to have important effects on population dynamics as we will discuss later), discuss the viability and rate of population growth of the chamois population based on 500 simulations over 100 years, and then over 1000 years.

### Exercise 8: Herbivory and Environmental Variation in the Common Kidney Vetch

The purpose of this exercise is to examine how variation between poor and good years can interact with sheep grazing and affect the population dynamics of a common legume, the common kidney vetch *Anthyllis vulneraria*. As many perennial flowering plants, its life cycle is best represented according to developmental and biological stages rather than according to only age *per se*. Each individual can only be in one of the following stages:

Stage:	Seed	Seedling	Age 1 Reproducer	Age 1 Non-reproducer	Age 2 reproducing for the 1 <sup>st</sup> time	Age 2 reproducing for the 2 <sup>nd</sup> time
Notation:	S	Sd	R <sub>11</sub>	NR <sub>1</sub>	R <sub>21</sub>	R <sub>22</sub>

The population dynamics is described by a stage-based model with the following complex life cycle and matrix model from Bastrenta et al. (1995), where *C* denote stage transition probabilities and *f* denote fecundities (there is no notion of a limiting sex because these plants can self-fertilize).



$$\begin{bmatrix} C_S & f_1 C_2 & f_2 C_3 & f_2' C_3' & f_3 C_4 & f_3 C_4' \\ C_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & C_2 & 0 & 0 & 0 & 0 \\ 0 & C_j & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & C_3' & 0 \\ 0 & 0 & 0 & C_3 & 0 & 0 \end{bmatrix}$$

**Fig. 1** Schematic life cycle of *Anthyllis vulneraria*. S = the seed stage, Sd = seedlings,  $R_{11}$  = individuals which reproduce for the first time when one year old,  $R_{22}$  = individuals which reproduce a second time after two years,  $R_{21}$  = individuals which reproduce for the first time after two years,  $NR_1$  = individuals which do not reproduce in their first year and  $NR_2$  = individuals which do not reproduce in their second year.  $C_1, C_2, C_j, C_3, C_3', C_4$  and  $C_4'$  are the survival probabilities from one life stage to another and  $f_1, f_2,$  and  $f_3$  signify age-specific fecundities. The survival probability of individuals having reached stage  $NR_2$  or  $R_3$  is zero.



Parameter estimates are as follows:

Regime Parameter	Good year Ungrazed	Poor year Ungrazed	Good year Grazed	Poor year Grazed
$f_1$	72	0	54	0
$f_2'$	246	1.0	82	0.4
$f_2 = f_3$	370	1.6	130	0.7
$C_s$	0.43		0.27	
$C_1$	0.11		0.46	
$C_2$	0.50		0.40	
$C_I$	0.17		0.10	
$C_3$	0.74		0.84	
$C_3'$	0.47		0.84	
$C_4$	0.48		0.50	
$C_4'$	0.32		0.50	

Here are some life cycle properties to think about before getting started with the stochastic matrix modeling: The  $C_4$  and  $C_4'$  parameters appear only in the top row of the matrix model and not in the lower right sector of the model. What does this imply about the kidney vetch life cycle? Given the way the top row in the matrix model is written, do you think it was built with a pre-breeding or post-breeding birth pulse parameterization? How would you interpret the value of  $C_2 + C_j$ ?

### Exercise

- 1) Poor and Good years happen at random in proportions  $P$  and  $1-P$ . Using the Ex8KidneyVetch.r file, determine the proportion  $P$  of Poor years that is sustainable under each of the two regimes, Grazed and Ungrazed. That is, the value of  $P$  below which the stochastic growth rate drops below 1.
- 2) Examine the last bit of code in the Ex8KidneyVetch.r file that takes you through the calculation of reproductive value, stable stage distribution, and matrix-entry elasticities in a stochastic environment. Once you have some experience applying these elasticities of the stochastic growth rate to 'simultaneous change in the mean & variance' of demographic parameters, you will be equipped to examine the more modern elasticities to changes in 'only the mean' or 'only the variance' of demographic parameters in stochastic environments (*sensu* papers by Tuljapurkar, Haridas, and colleagues since 2005). These elasticities could be used to, e.g., guide the management of the demographic parameters that most enhance the rate of population growth in variable Poor and Good conditions.

## Exercise 9: The Ricker Model of Density Dependence



To study the consequences of so-called “overcompensatory density-dependence”, that can lead to stable, cyclic, and even “chaotic” dynamics in the absence of environmental variability, we use the well known Ricker model, based on the recurrence equation:

$$N_{t+1} = N_t e^{r(1-N_t/K)}$$

William Ricker developed this model in his famous studies of stock-recruitment relationships in fisheries. The equilibrium population size in the Ricker model ( $N_*$ ), when it exists, is the

root of  $N_* = N_* e^{r(1-N_*/K)}$ , i.e. of  $1 - N_*/K = 0$ , which is  $N_* = K$ .

### Exercise

- 1) Using the first part of the code in Ex9Ricker.r, manually change the value of  $K$  (the parameter for density dependence) to explore its effect on the resulting population dynamics. Each time you change  $K$ , re-run the modeling code as well as that for the plot.
- 2) Keeping  $K$  fixed at 100, now explore the effects of progressively increasing values of  $r$ . Start from  $r = 1.7$  and increase it by 0.2 each time you re-run the code. What happens when  $r > 2$ ?
- 3) A “bifurcation diagram” plots the asymptotic values of a state variable (which is abundance in our case) against a model parameter, such as alternative values of  $r$  in the Ricker model (for more info see [http://en.wikipedia.org/wiki/Bifurcation\\_diagram](http://en.wikipedia.org/wiki/Bifurcation_diagram)). As you noted in question 2, there is not a stable equilibrium for large values of  $r$  and the asymptotic values of abundance might bounce around cyclically or even “chaotically”; a bifurcation diagram nicely summarizes the pattern. Using the second part of the code, build a bifurcation diagram for the Ricker model and discuss it as  $r$  increases.
- 4) Part three of the code contains a metapopulation model with density dependence and spatial structure, but not stage structure (Hey that is cool, you can combine multiple types of reality into a single matrix model! One could additionally add stage structure and environmental stochasticity; Caswell 2001). Examine the metapopulation matrix model and see if you can interpret the meaning of each transition.
- 5) Using the provided code, obtain a bifurcation diagram for the sink population within the metapopulation. Do the same for the source population.

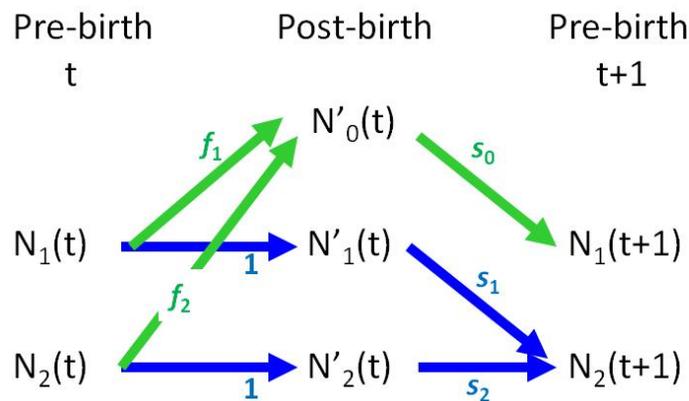
## Solutions:

Solutions to exercises 1-3 to be provided Sat.

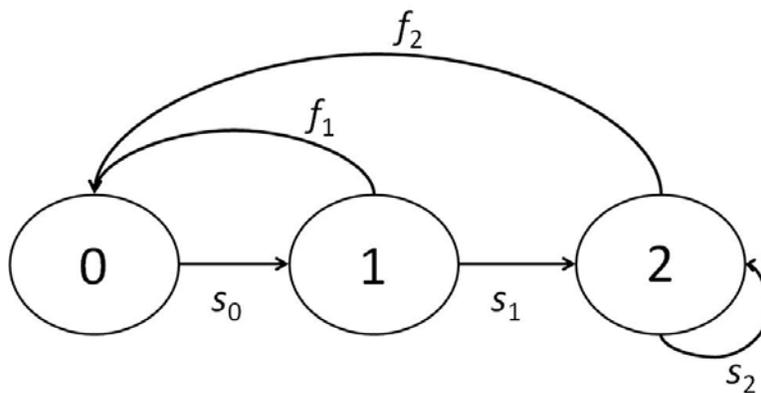
### Solutions to Exercise 4: The barn swallow matrix model

1. Draw the life cycle of this species, making fledglings appear explicitly in your diagram.

You might have drawn this as something like the following as shown in the lecture

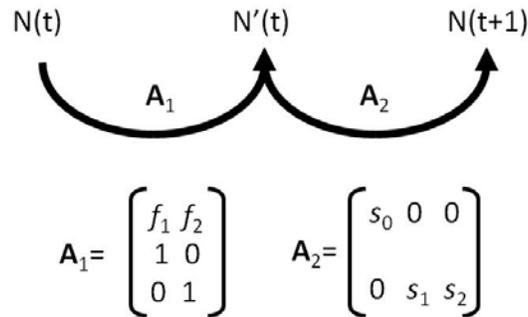


or you might have drawn something like this



2. Write the corresponding matrices for the pre birth-pulse and post birth-pulse models.

The seasonal life-cycle shown above is more useful in guiding construction of either the pre or post birth-pulse models (alternatively, one could draw separate bubble-arrow diagrams). From the seasonal life-cycle one gets seasonal matrix projection models:



In turn, these can be used to construct the 2 x 2 annual pre birth-pulse matrix model:  $A_2 \times A_1 =$

$$\begin{pmatrix} s_0 f_1 & s_0 f_2 \\ s_1 & s_2 \end{pmatrix}$$

or the 3 x 3 annual post birth-pulse matrix model:  $A_1 \times A_2 =$

$$\begin{pmatrix} f_1 s_0 & f_2 s_1 & f_2 s_2 \\ s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{pmatrix}$$

The order of the matrices in a matrix product is from right to left, the order of time (e.g., pre birth pulse, first  $A_1$ , then  $A_2$ , hence product  $A_2 \times A_1$ ).

*3. Inspect the first piece of code to see if you can interpret what it does; then run the code and inspect the output to see if you understand the code correctly. What happens to population growth rate over time?*

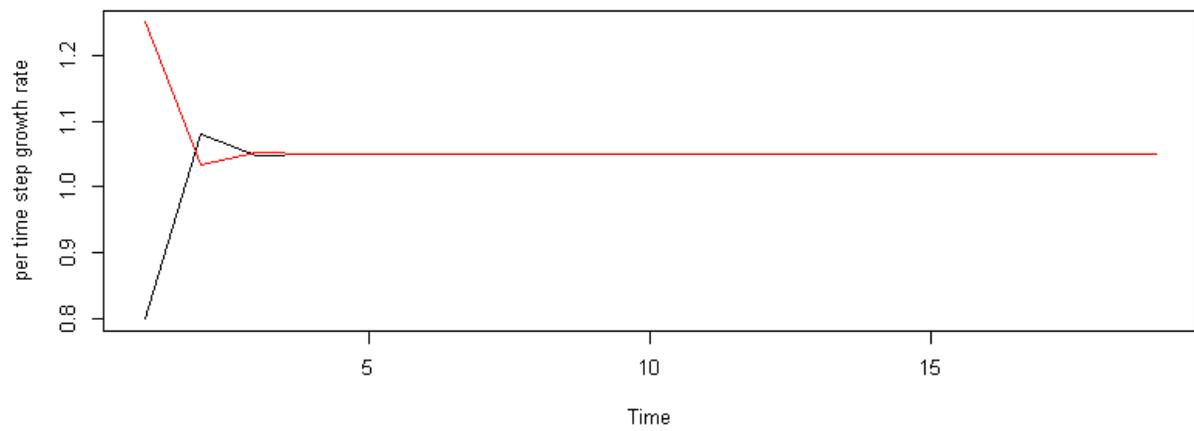
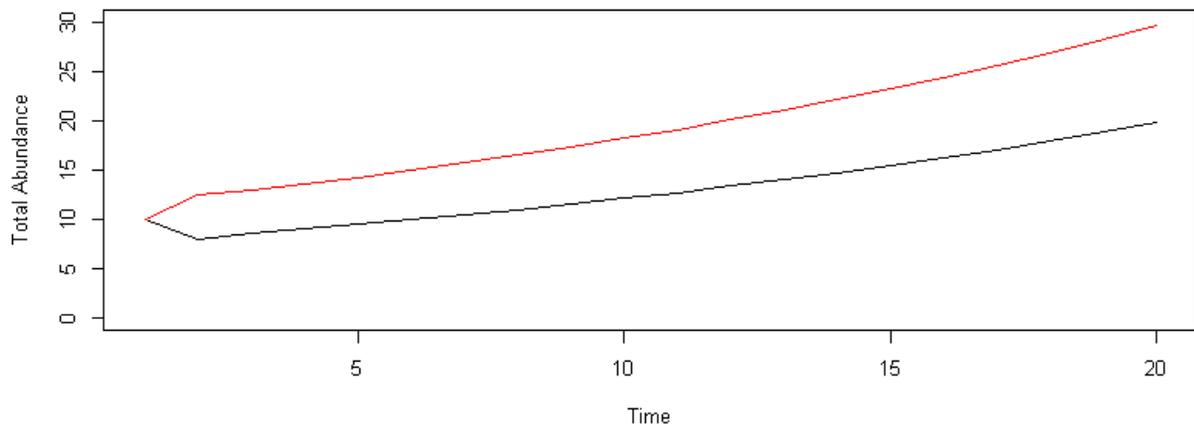
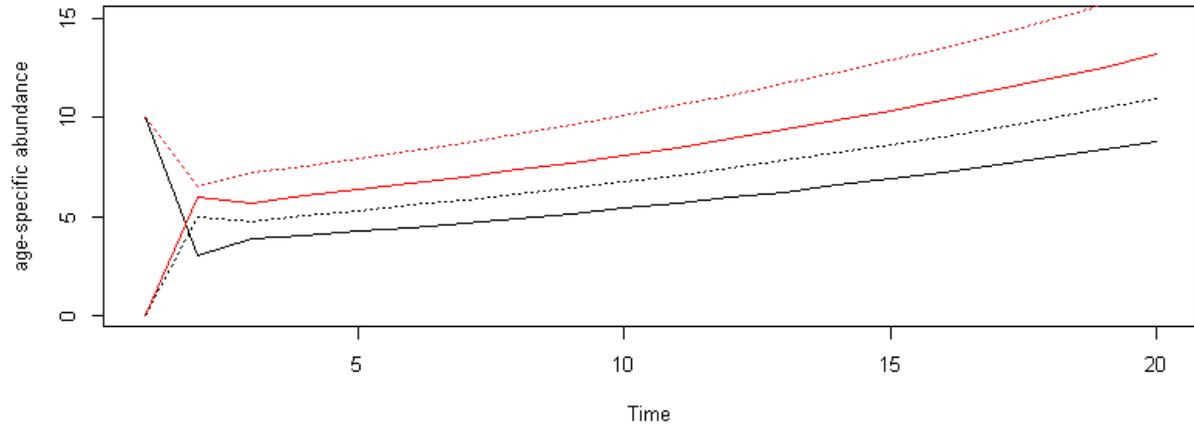
You find that the annual population growth rate (gr; pop size at time t/pop size at time t-1) converges to a value of 1.05 by the 6<sup>th</sup> time step and remains there. The property of independence of the long-term growth rate in a deterministic environment for structured populations is formalized in the strong ergodic theorem. This, and additional theory, will be addressed later.

*4. The next piece of code allows you to loop through two different sets of initial values:  $n_1 = 10, n_2 = 0$ ; then  $n_1 = 0, n_2 = 10$ . The code for the graphs provides comparisons of the age-specific abundances, total abundances, and population growth rates for the different initial conditions. What happens to the population growth rates and total abundances over time?*

In the graphical output provided by the code you ran (and can modify), we confirm what was observed in the first step: the population growth rate converges to 1.05 regardless of the initial conditions. However, the population abundances are affected by the initial conditions; they never converge to the same value. The two populations with different initial conditions eventually grow at the same rate but

that which starts with more AFY birds has a higher total abundance in the long run. Later, we will discuss the theoretical reasons for why this occurs.

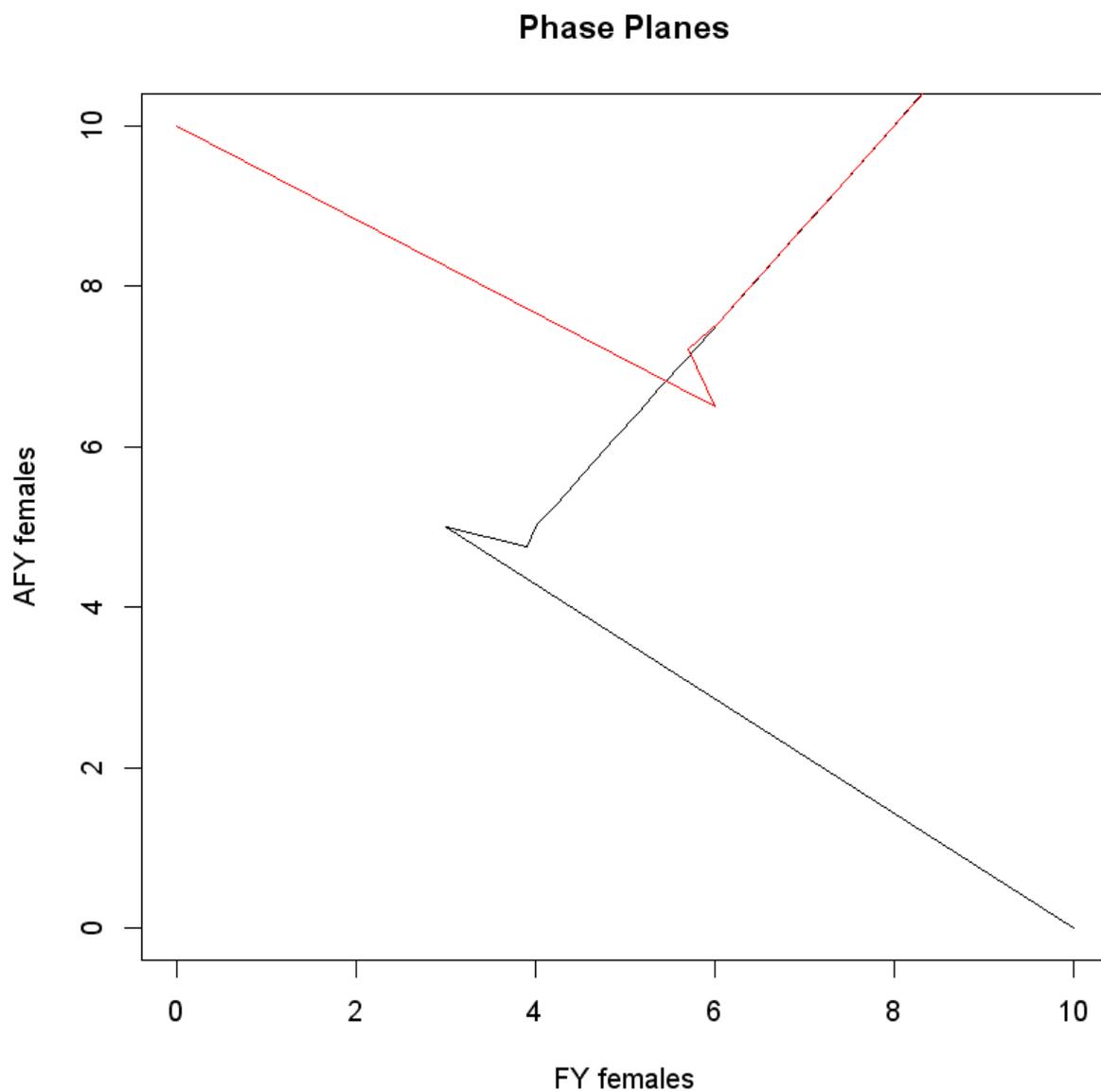
Population Modeling – UF2016



5. Now see if you can develop a graph that plots the abundance of one age class against the other ( $n_1$ ,  $n_2$ ) for each of the initial conditions. This is called a “phase plane”, and is one way to view convergence of the population’s age structure to the stable age structure.

Following step 4, all you need to add is the following code (which can be modified to adjust graphic properties)

```
# create phase-plane plot  
plot(n[1,],n[2,],type="l",xlab="FY females",ylab="AFY females",  
      main="Phase Planes",xlim=c(0,10),ylim=c(0,10))  
lines(n[3,],n[4,],col="red")
```



6. Now adjust the code to examine the population dynamics for the post birth-pulse model, and compare to dynamics of the pre birth-pulse model from above. You could just change a few lines of code, or you could ‘copy’, ‘paste’ and then adjust the code.

The following adjustments in the code would be needed for the post birth-pulse matrix model:

Note that we’re dealing at once with the two different initial conditions, but you can treat them separately to make the code simpler

```
# Create the post birth-pulse swallow matrix population model

A <- matrix(c(
  f1*s0, f2*s1, f2*s2,
  s0, 0, 0,
  0, s1, s2), nrow = 3, byrow = TRUE)

tspan <- 20 # time span for projections

rows <- dim(A)[1]
cols <- dim(A)[2]

# Build some matrices for storing eventual output

n <- matrix(0,rows*2,tspan) # storage of age-specific abundances
N <- matrix(0,tspan,2) # storage of total abundances
gr <- matrix(0,tspan-1,2) # storage of time-specific population growth rates

n[,1] <- c(0,10,0,0,0,10) # initial population abundances in each age class
# for two different initial conditions

# Project population forward for each initial condition and store output
for (j in 1:2) { # j is for the initial condition
  N[1,j] <- sum(n[(j*3-2):(j*3),1]) # treat the first time separately
  for (t in 1:(tspan-1)) { # t is for time
    n[(j*3-2):(j*3),t+1] <- A%*%n[(j*3-2):(j*3),t]
    N[t+1,j] <- sum(n[(j*3-2):(j*3),t+1])
  }
}
```

## Population Modeling – UF2016

```
    gr[t,j] <- sum(n[(j*3-2):(j*3),t+1])/sum(n[(j*3-2):(j*3),t])
  }
}

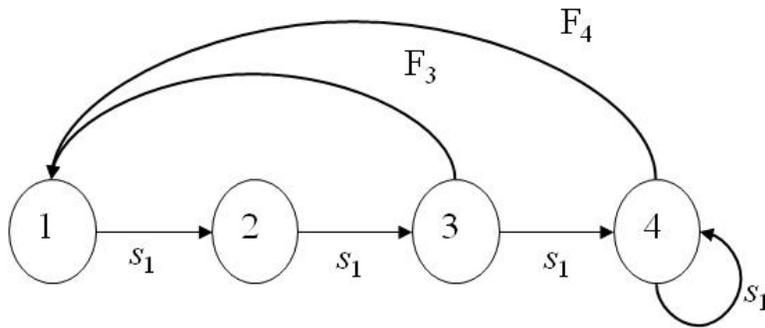
par(mfrow=c(3, 1))          # Set graphics window to 3 rows with 1 column
plot(1:tspan,n[1,],type="l",xlab="Time",ylab="age-specific abundance",
     ylim=c(0,40))
lines(1:tspan,n[2,],lty=3)
lines(1:tspan,n[3,],lty=4)
lines(1:tspan,n[4,],col="red")
lines(1:tspan,n[5,],lty=3,col="red")
lines(1:tspan,n[6,],lty=4,col="red")
plot(1:tspan,N[,1],type="l",xlab="Time",ylab="Total Abundance",ylim=c(0,50))
lines(1:tspan,N[,2],col="red")
plot(1:(tspan-1),gr[,1],type="l",xlab="Time",ylab="per time step growth rate",
     ylim=c(1,2.6))
lines(1:(tspan-1),gr[,2],col="red")

# create phase-plane plot
plot(n[2,],n[3,],type="l",xlab="FY females",ylab="AFY females",
     main="Phase Planes",xlim=c(0,10),ylim=c(0,10))
lines(n[5,],n[6,],col="red")
```

### Solutions to Exercise 5: Perturbation analysis of the white stork model

1. ...Examine the matrix model and draw the corresponding life cycle.... To three decimals write down the growth rate on paper or in a spreadsheet.

$\lambda = 1.016$



Where  $F_3 = s_0 * u * r * b/2$   
and  $F_4 = s_0 * r * b/2$

2. Emulating the decline in survival that was observed (but difficult to estimate precisely), decrease survival after the first year by 20% such that  $s_{1+} = 0.8 * 0.75 = 0.6$  (just make this change in the code) and re-run the first piece of code. Calculate the change in population growth rate, relative to the change in survival, by performing the following numerical calculation where abs refers to the absolute value of a difference:

$$\frac{\text{abs}(\lambda_{\text{new}} - \lambda_{\text{original}})}{\lambda_{\text{original}}} \frac{\text{original demographic parameter}}{(\text{original demographic parameter} - \text{new demographic parameter})}$$

Parameters not shown in the following tables were never changed in parts 2, 3 and 4

	$s_0$	$s_{1+}$	$b$	$\lambda$	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.6	2.9	0.843	<b>0.851</b>

Relative change is calculated as  $(1.016 - 0.843) / 1.016 * 0.75 / (0.75 - 0.6) = 0.851$

3. Change after-first-year survival back to the original value of 0.75. Now repeat the same exercise for first-year survival such that the new  $s_0 = 0.8 * 0.482 = 0.3856$ . Add the calculated 'change in population growth rate, relative to the change in survival' to that from part 2 in order to quantify the total effect of change in survival.

	$s_0$	$s_{1+}$	$b$	$\lambda$	Relative Change

original	0.482	0.75	2.9	1.016	
new	0.3856	0.75	2.9	0.982	<b>0.167</b>
Total rel. change					<b>1.018</b>

4. Change first-year survival back to 0.482, and repeat the same exercise for the number of fledglings produced per successful pair per year such that  $b = 0.8 \cdot 2.9 = 2.32$ .

	$s_0$	$s_{T+}$	$b$	$\lambda$	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.75	2.32	0.982	<b>0.167</b>

5. Although the changes made to the demographic parameters in steps 2, 3, and 4 were relatively large, do you think you were approximating the sensitivities or the elasticities of the population growth rate to change in the underlying demographic parameters? How would you go about numerically calculating the other perturbation metric?

These were numerical approximations to the ‘elasticities’. We can infer this because we were comparing the ‘relative’ change in population growth rate to the ‘relative’ change in the demographic parameter. A more exact approach would be to induce small proportional changes in the demographic parameters. Or, just use calculus and calculate derivatives on the log scale to ‘measure the effects of small proportional changes’.

To numerically approximate the sensitivities, one would use an equation like the following

$$\frac{\text{abs}(\lambda_{\text{new}} - \lambda_{\text{original}})}{(\text{original demographic parameter} - \text{new demographic parameter})}$$

To calculate exact sensitivities, one would calculate the derivative of population growth rate with respect to a demographic parameter on the absolute scale.

6. Set all demographic parameters back to their original values. Compare your calculations from steps 2 – 4 to the exact analytical calculations by running the second piece of code. Note that the reproductive values and stable age distribution are also calculated because they are components of sensitivities and elasticities.

```
# attain total sensitivity and elasticity to change in overall survival
totalSsens <- sum(llsenselas[4:5,2])
totalSsens
totalSelas <- sum(llsenselas[4:5,3])
totalSelas
```

	Sensitivity	Elasticity	Approximation
$s_0$	0.335	0.159	0.167
$s_{I+}$	1.14	0.841	0.851
total	1.475	1	1.018
$b$	0.056	0.159	0.167

Wow, our numerical approximations to the elasticities were surprisingly close! This implies that the relationships between population growth rate and these demographic parameters are close to linear.

Note that the elasticity to (a simultaneous change in all) survival parameters is equal to 1; this will be discussed in the lecture portion of the workshop.

*7. Discuss the relative effects of changes in survival vs. reproductive output on population growth rate of long-lived white storks.*

```
# calculate how many times greater the elasticity to change in overall survival
```

```
# is relative to overall fledgling production
```

```
totalSelas/l1senselas[3,3]
```

The elasticity of white stork population growth rate to a proportional change in survival across all ages (1) is approximately 6 times greater than the elasticity for fledgling production across all ages. This implies that an ~ 60% change in fledgling production would be needed to achieve the same effect on population growth rate as a 10% change in survival.

*8. If you have time, run the second piece of code for the short-lived barn swallows from Exercise 1 in order to calculate their sensitivities and elasticities for the analogous demographic parameters, then compare to the white stork.*

```
# Barn Swallow application
```

```
swallow.vr <- list(f1=1.5,f2=3,s0=0.2,s1=0.5,s2=0.65)
```

```
swallow.A <- expression(s0*f1, s0*f2,
```

```
  s1, s2)
```

```
# then apply the following popbio function
```

```
l1senselas <- vitalsens(swallow.A,swallow.vr)
```

```
l1senselas
```

```
# total sensitivities and elasticities
```

```
totalSsens <- sum(l1senselas[3:5,2])
```

```
totalSsens
```

## Population Modeling – UF2016

```
totalSelas <- sum(llsenselas[3:5,3])
totalSelas
totalfsens <- sum(llsenselas[1:2,2])
totalfsens
totalfelas <- sum(llsenselas[1:2,3])
totalfelas
```

	Sensitivity	Elasticity
$s_0$	1.826	0.3478
$s_1$	0.5217	0.2484
$s_2$	0.6522	0.4037
total	3	<b>1</b>
$f_1$	0.06957	0.09938
$f_2$	0.08696	0.2484
total	0.157	<b>0.348</b>

Although the elasticity to (a simultaneous change in all) survival parameters is again equal to 1, the elasticity to changes in fledgling production in this short-lived species is more than twice as large as in the long-lived storks. An explanation for this difference will be explained in lecture.

### Solutions to Exercise 6: Two-site matrix models for black-headed gulls

1. Find the long-term population growth rate using the popbio package, then by calculating the dominant eigenvalue of  $\mathbf{A}$  in order to check that the population is close to stationary.

The population is close to stationary with  $\lambda = 0.997$

2. Run the following lines of code that calculate the stable age-by-location distribution and the reproductive values. Comment on the reproductive values at age 1 for the two sites.

```
rv[1]
rv[6]
```

The reproductive values at age 1 (since we are in a pre birth-pulse formulation), are 0.08 and 0.07, for Good and Bad locations, respectively. Although the connection by juvenile dispersal between the two sites make the numbers in the two sites grow at the same asymptotic rate, individuals born in the two sites differ in their contribution to growth, as measured by reproductive value. The dispersal is moderate, so an individual born in a Bad location will on average stay in that location and experience a lower average demographic performance than one born in the Good location, even if it has some chance to moving to Good. The juvenile dispersal does, however, make the reproductive values closer to one another than they would be in the absence of exchange among the colonies.

3. Conduct an elasticity analysis for the lower-level parameters in order to obtain  $T$ , the generation time, as described in the lecture.

The most straightforward way to calculate generation time as a function of elasticities, is to calculate the inverse of total elasticity to an “immature parameter” in the fertility component of the matrix model. Here the elasticity to an overall change in such a parameter can be obtained as the sum of the elasticities to  $sg_0$  and  $sb_0$ , i.e.  $0.09756 + 0.03243 = 0.12999$ . Hence  $T = 1/0.12999 = 7.69$  years.

```
T <- 1/(llsenselas$elasticity[1]+llsenselas$elasticity[9])
```

*4. Calculate the elasticity for adult survival, and use it to predict the change in  $\lambda$  that would occur if adult survival ( $s$ ) were changed from 0.82 to 0.89, a change that seems plausible from data collected between 1985 and 1993. This can be done using the approximation: % change  $\lambda \approx$  % change vital rate  $\times$  elasticity, and  $\lambda_{predict} = \lambda_{original} \times$  relative change in  $\lambda$ . Using the `changevar` command, induce this change and compare your predicted  $\lambda$  to the actual  $\lambda$ , and discuss how close your prediction was.*

The proposed change in survival represents an 8.5% change ( $0.89/0.82 = 1.085$ ). The elasticity of the population growth rate to a change in adult survival across all ages and locations is 0.74. Thus, our predicted percentage and absolute changes in  $\lambda$  are  $8.5\% \times 0.74 = 6.29\%$  and  $\lambda = 0.997 \times 1.0629 = 1.06$ . The actual result is 1.06 and any difference past the second decimal is due to slight nonlinearity in the relationship between the vital rate and  $\lambda$ .

```
predpercent <- ((0.89/0.82-1)*100)*llsenselas$elasticity[3]
```

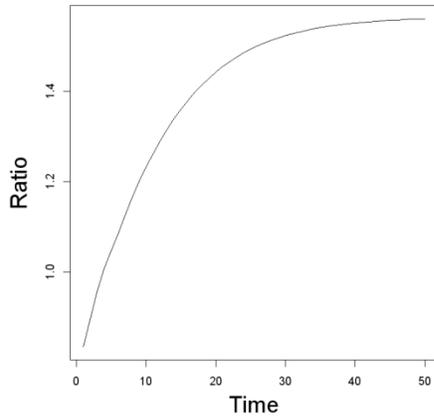
```
predLambda <- (predpercent/100+1)*Lambda
```

*5. In piece 2 of the code, how is the ratio of breeding numbers ('ratio') calculated?*

The numbers of breeders per location are calculated based on the age-specific abundance times the age-specific proportion of individuals that actually breed each year, summed across ages within a location. The 'ratio' is then calculated by taking this number for the Good location and dividing it by that for the Bad location.

*6. Use the provided loop to calculate the 'ratio' over time and graph how it changes. Explain why, like the population growth rate, the 'ratio' stabilizes over time.*

It stabilizes to 1.566 because the age-by-location structure stabilizes.



7. Can symmetrical dispersal ( $gb = bg > 0$ ) induce such a change in ‘ratio’? Try dispersal probabilities of 0, 0.05, 0.1, 0.15, and 0.2 (by simply changing the parameter values at the top of the code in piece 3, and re-running the code in piece 3); remember to keep  $gb = bg$ .

By changing progressively  $gb$  and  $bg$  to the same increasing value, the abundance in G relative to B actually decreases. Thus, it is clear that symmetrical adult dispersal cannot explain the currently large relative abundance of the Good colony.

$gb = bg$	0.00	0.05	0.10	0.15	0.20
ratio	1.56	1.18	1.06	1	0.96

8. Approximate, by successive change in  $bg$ , the level of adult dispersal from B to G ( $bg > 0$ ) that can lead to ratio = 4.17 with no adult dispersal from G to B ( $gb=0$ ).

Here are the results from a few changes in  $bg$ :

$bg$	0	0.1	0.13	0.14	0.135	0.134
ratio	1.56	3.50	4.09	4.29	4.19	4.176

9. Interestingly, black-headed gull colonies move after reproductive failure. Comment on this trait in relation to the previous result.

As long as there are differences in reproductive values and limited dispersal costs (cf the “Ideal Free Distribution”), there will be selective pressures for individual behaviors that enhance their reproductive value. The key here is that a Bad location remains Bad, and a Good location remains Good. Given this condition, if an individual is in a Bad site, even moving at random is favored because of the chance of ending up in a better site.

### Solutions to Exercise 7: Chamois in Random Environments

1. Assuming a constant, deterministic environment and the provided estimates of the demographic parameters, is this population viable?

The asymptotic growth rate is high ( $\lambda = 1.16$ ) indicating the population is viable in a constant environment.

2. What happens when senescence is ignored (i.e., when survival from age 11 onwards is assumed to be the same as the previous age class)?

`s11 <- 0.962`

Neglecting senescence (a common feature of ungulate populations) implies that we assume  $s_{11+} = 0.962$ , which changes the asymptotic growth rate to 1.18. This is not a large change and at first seems like a contradiction to the important role survival play in the population dynamics of long-lived species.

For example, we only observed  $\Delta\lambda = 0.02$  for  $\Delta s = 0.229$ , leading thus to  $\frac{\Delta\lambda}{\Delta s} = 0.08$  and

$\frac{\Delta \log(\lambda)}{\Delta \log(s)} = 0.08 * 0.733 / 1.16 = 0.05$ . The paradox is simply that there are few females left in this age class (7.56 %) with a low reproductive value, so they contribute little to the population growth rate and have a small sensitivity. The exact sensitivity and elasticities are 0.0470 and 0.0296, respectively. They differ from the finite increment approximations because of the nonlinearity of  $\lambda$  wrt this parameter. The reproductive values in absence and presence of senescence show very different patterns. In the absence of senescence, the reproductive value remains constant with age, because the age of a female does not influence the number of future reproductions expected. When there is senescence, the reproductive value decreases when females approach senescence, i.e. before age at senescence.

3. Using  $s_{11+} = 0.733$ , which demographic parameters have the strongest impact on the deterministic population growth rate?

The full sensitivity results (obtained using *sensitivity 'parameter name'*) are:

Parameter	Sensitivity	Elasticity
m2	0.044	0.025
m	0.188	0.149
f	0.405	0.174
s0	0.307	0.174
s1	0.226	0.174
s210	0.752	0.622
s11	0.047	0.03

The three “immature” parameters, f, s0, s1 have the same elasticity, 0.174, which is also  $\text{elasticity}(m2) + \text{elasticity}(m)$ , and is equal to  $1/T = 1/5.746$ .

While the “impact” of parameters has to be judged according to what are plausible orders of magnitudes in their variation (as we will explain later), it is clear that the prime age survival s210 has a very high absolute and proportional sensitivity because it pertains to survival of age classes with high numbers and the highest reproductive values.

4. Qualitatively, what do you think this form of environmental stochasticity will do to the chamois population, and which estimator should you use for measuring the population growth rate in a variable environment?

The population growth rate is likely to be lower than the deterministic growth, to an extent that can be determined only by simulation or though approximation of the ‘stochastic growth rate’.

*5. Using a pseudo-extinction threshold of 100 individuals (when demographic stochasticity can begin to have important effects on population dynamics as we will discuss later), discuss the viability and rate of population growth of the chamois population based on 500 simulations over 100 years, and then over 1000 years.*

The stochastic growth rate estimates over 100 and 1000 time steps (and 500 replicates) are approximately 1.106 and 1.105, respectively (answers may vary among people given these time horizons). The corresponding probabilities of pseudo-extinction were 0 and 0.002. Despite their strong impact on survival, these infrequent catastrophic years do not threaten the long-term viability of the chamois population.

## **Solutions to Exercise 8: Herbivory and Environmental Variation in the Common Kidney Vetch**

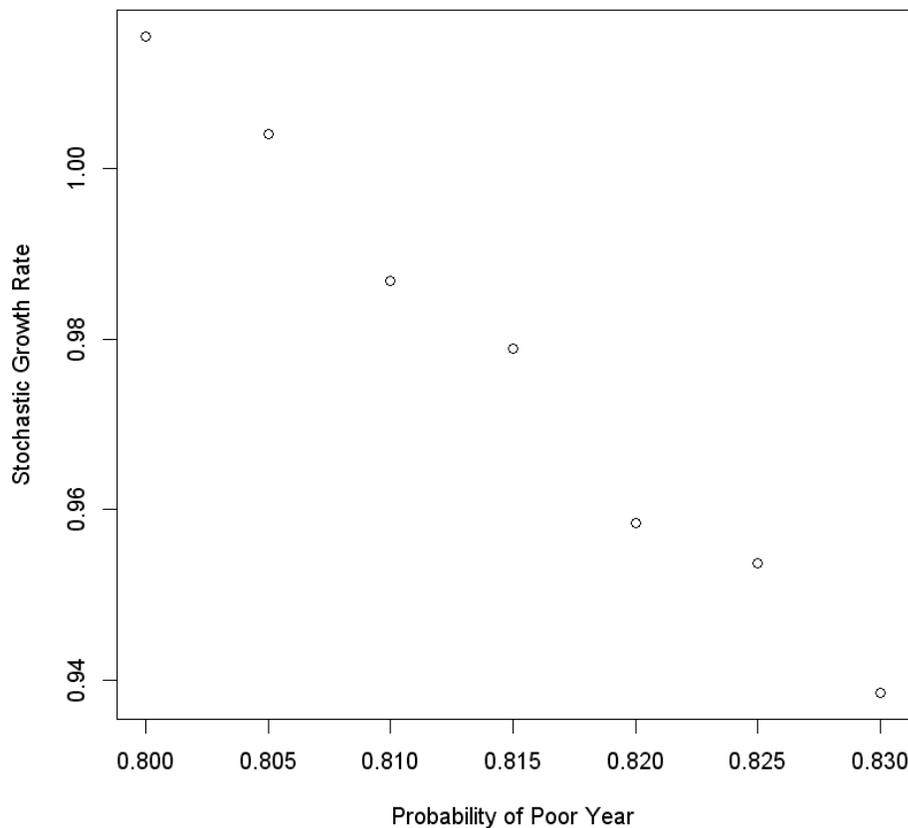
The  $C_4$  and  $C_4'$  parameters appear only in the top row of the matrix model and not in the lower right sector of the model. What does this imply about the kidney vetch life cycle? Given the way the top row in the matrix model is written, do you think it was built with a pre-breeding or post-breeding birth pulse parameterization? How would you interpret the value of  $C_2 + C_j$ ?

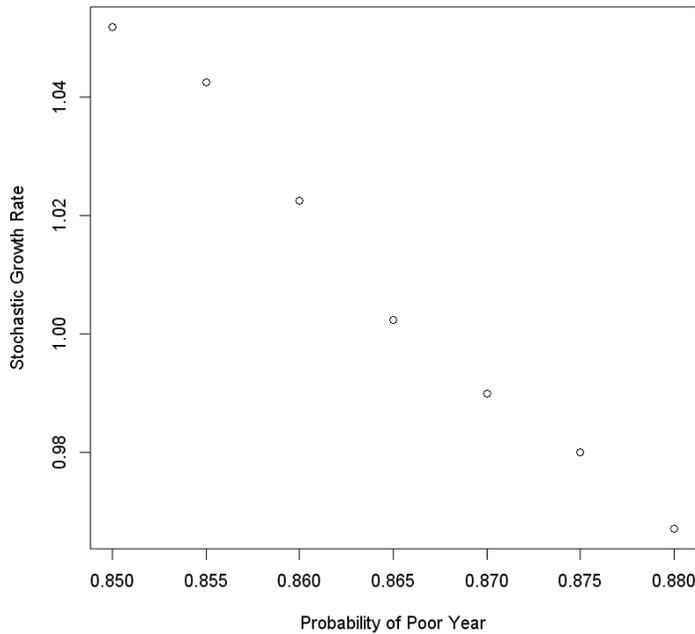
$C_4$  and  $C_4'$  do not appear as survival probabilities in the last row of the matrix because individuals in the last stage die after reproducing. The fecundities in the top row are multiplied by survival probabilities of the 'parent plant', and thus the model is a post-reproductive birth pulse model.

$C_2 + C_j$  is a survival probability, while  $C_2 / C_2 + C_j$  and  $C_j / C_2 + C_j$ , summing up to 1, could be interpreted as transition probabilities among the corresponding stages, 'conditional on survival' (sometime called 'growth' in the plant matrix model literature).

1. Poor and Good years happen at random in proportions  $P$  and  $1-P$ . Using the Exercise 5.r file, determine the proportion  $P$  of Poor years that is sustainable under each of the two regimes, Grazed and Ungrazed. That is, the value of  $P$  below which the stochastic growth rate drops below 1.

**Grazed:** (Note that it takes a while to conduct these simulations)





**Ungrazed**

Note that the Ungrazed sites can sustain a higher probability of Poor years and still stay viable (stochastic growth rate  $\geq 1$ )

2. If you have time, examine the last bit of code in the Exercise 5.r file that takes you through the calculation of reproductive value, stable stage distribution, and matrix-entry elasticities in a stochastic environment. Once you have some experience applying these elasticities of the stochastic growth rate to ‘simultaneous change in the mean & variance’ of demographic parameters, you will be equipped to examine the more modern elasticities to changes in ‘only the mean’ or ‘only the variance’ of demographic parameters in stochastic environments (sensu the papers by Tuljapurkar, Haridas, and colleagues since 2005). These elasticities could be used to, e.g., guide the management of the demographic parameters that most enhance the rate of population growth in variable Poor and Good conditions.

Note that the popbio package has a function ‘stoch.growth.rate’ for calculating the stochastic growth rate and a ‘stoch.projection’ function from which the stochastic stable stage distribution can be attained, but there is no built-in function for the stochastic elasticities; thus the involved code. Below are the elasticities of the stochastic growth rate to changes in each of the ‘matrix entries’.

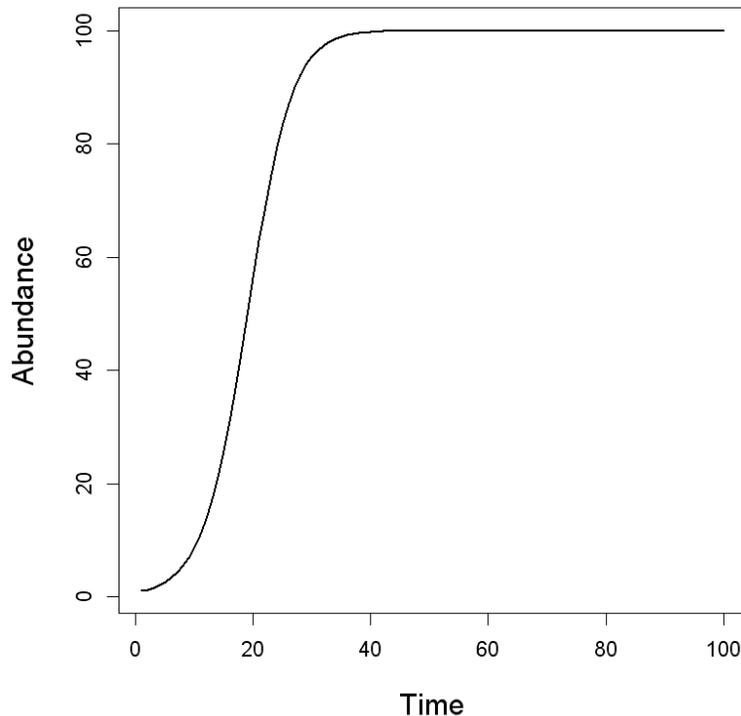
```
[,1] [,2] [,3] [,4] [,5] [,6]
[1,] 0.329 0.025 0.134 0.045 0 0.021
[2,] 0.225 0.000 0.000 0.000 0 0.000
[3,] 0.000 0.134 0.000 0.000 0 0.000
[4,] 0.000 0.066 0.000 0.000 0 0.000
[5,] 0.000 0.000 0.000 0.000 0 0.000
[6,] 0.000 0.000 0.000 0.021 0 0.000
```

It seems that managing conditions that help enhance seed survival and germination rate would most affect the stochastic growth rate in common kidney vetch in ungrazed environments.

## Exercise 9: The Ricker Model of Density Dependence

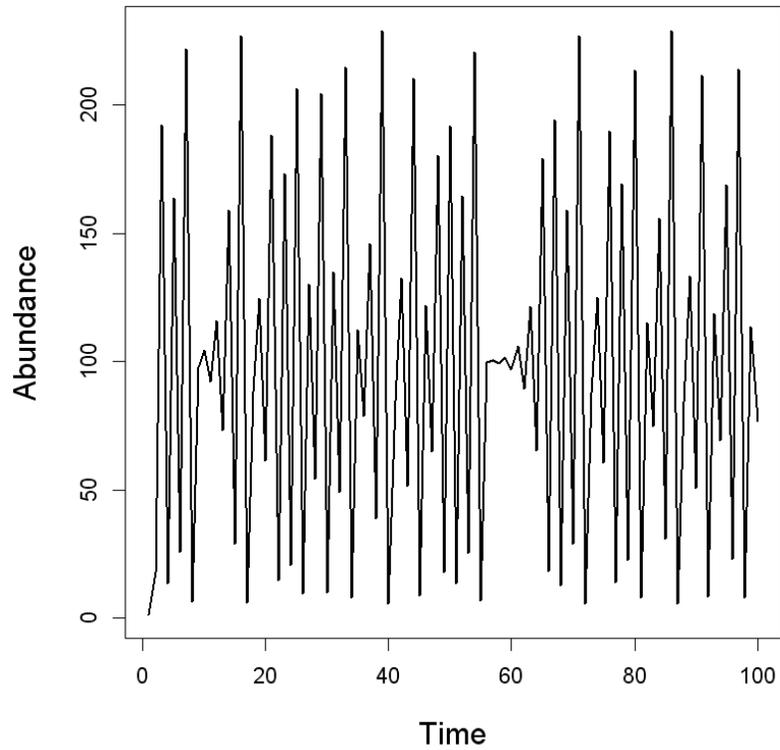
1. Using the first part of the code in *Ex9Ricker.r*, manually change the value of  $K$  (the parameter for density dependence) to explore its effect on the resulting population dynamics. Each time you change  $K$ , re-run the modeling code as well as that for the plot.

$K$  is often called the carrying capacity for a population. For low to moderate values of  $r$ ,  $K$  determines the equilibrium value of abundance where birth and death rates balance each other. By changing  $K$ , the equilibrium abundance changes as shown in the example plot below.



2. Keeping  $K$  fixed at 100, now explore the effects of progressively increasing values of  $r$ . Start from  $r = 1.7$  and increase it by 0.2 each time you re-run the code. What happens when  $r > 2$ ?

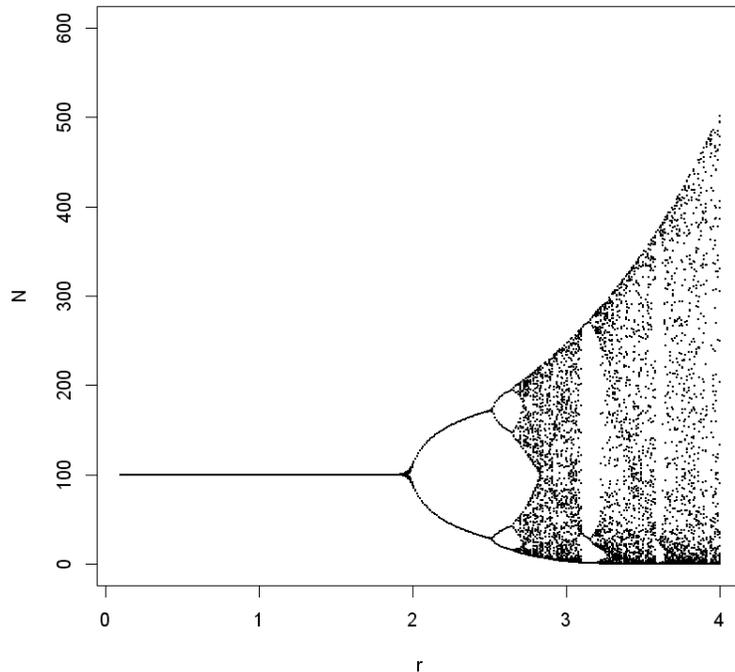
At first we observe damped cycles that stabilize, then perpetual cycles that do not disappear, then cycles with two different types of peaks and troughs (a 4-cycle), and eventually the cycles become erratic where the values of abundance at the peaks and troughs never repeat themselves, which is called “chaos” (shown below in the example plot). For structured populations, chaotic dynamics can form beautiful “Fractals” (*sensu* Benoit Mandelbrot).



Shown for  $r = 2.9$

3. ... Using the second part of the code, build a bifurcation diagram for the Ricker model and discuss it as  $r$  increases.

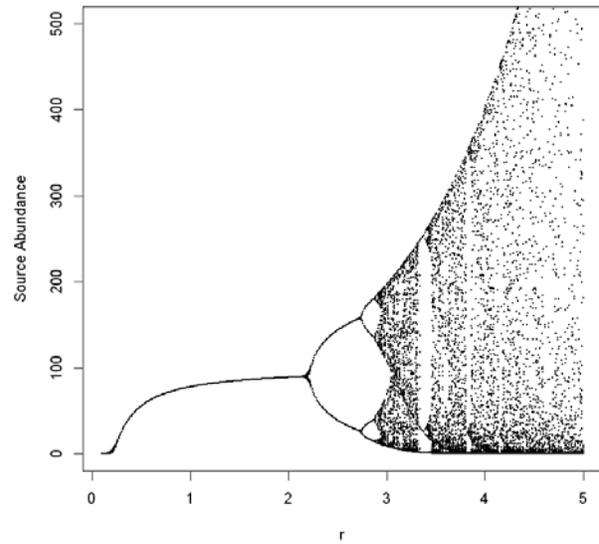
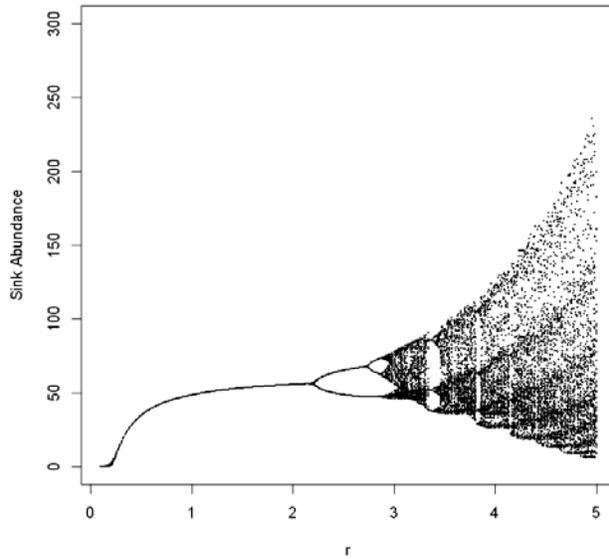
The resulting bifurcation diagram below shows the transitions from stability to cycles to chaos as  $r$  increases (note the stability 'bifurcates'). Around  $r \approx 2.78$ , chaos starts to occur.



4. ... Examine the metapopulation matrix model and see if you can interpret the meaning of each transition.

The density-dependent metapopulation model is a 2-by-2 matrix model. The (Ricker) density-dependent population dynamics of the source population is summarized in the upper left multiplied by the probability of individuals staying in the source location, the lower left represents the production of individuals in the source population multiplied by the probability they 'disperse' to the sink (some individuals must disperse because the source habitat fills up and reaches its carrying capacity). In the bottom right the demography in the sink population is summarized by a simple survival probability. There is no local production in the sink, it all comes from the source. A non-zero equilibrium abundance of individuals can nevertheless exist in the sink because of the continual flow of individuals from the source (as shown in the plot that can be produced with the provided code). The upper right of the matrix contains a 0, indicating no dispersal from the sink to the source.

5. Using the provided code, obtain a bifurcation diagram for the sink population within the metapopulation.



## References

The references from which the exercises were built are in *Italic*. The other references concern background theory, alternative presentations or further developments of the subject of each exercise.

### General

Caswell, H. (2001). *Matrix population models*. Sinauer, Sunderland Mass.  
<http://www.sinauer.com/detail.php?id=0965>

Lebreton, J.D. (2006). Dynamical and statistical models of Vertebrate population dynamics. *Comptes Rendus Biologies*, 329:804-812.

Legendre, S. & Clobert, J. (1995). ULM, a software for conservation and evolutionary biologists, *Journal of Applied Statistics*, 22: 817-834. DOI:10.1080/02664769524649

Stubben, C. & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, 22(11):1-23

#### **Exercise 4: Swallow**

Anonymous: [http://en.wikipedia.org/wiki/Matrix\\_population\\_models](http://en.wikipedia.org/wiki/Matrix_population_models)

Arnold, D. and Yokoyama, K.: The Leslie matrix.  
<http://online.redwoods.cc.ca.us/instruct/darnold/linalg/Leslie1/context-leslie1-s.pdf>

Caswell, H.(2001). *Matrix population models*. Sinauer, Sunderland Mass. Chapter 1.

#### **Exercise 5: White Stork**

Caswell, H.(2001). *Matrix population models*. Sinauer, Sunderland Mass. Chapter 9.

*Lebreton, J.D. (1978). Un modèle probabiliste de la dynamique des populations de Cigogne blanche C.c.ciconia en Europe occidentale. pp.277-343 in Legay, J.M. & Tomassone, R. (Eds) Biométrie et Ecologie. Société Française de Biométrie & INRA, Paris.*

#### **Exercise 6 : Black-headed Gull**

Caswell, H. (1982). Stable population structure and reproductive value for populations with complex life cycles. *Ecology* 63: 1223-1331

Caswell, H.(2001). *Matrix population models*. Sinauer, Sunderland Mass. Chapter 3 & 4.

*Lebreton, J.D. (1996). Demographic models for subdivided populations : the renewal equation approach. Theoretical Population Biology, 49, 3 : 291-313.*

Lebreton, J.D., Khaladi, M. & Grosbois, V. (2000). An explicit approach to evolutionarily stable strategies: no cost of dispersal. *Mathematical Biosciences*, 165: 163-176.

#### **Exercise 7: Chamois**

Caswell, H.(2001). *Matrix population models*. Sinauer, Sunderland Mass. Chapter 14.

Gaillard, J.-M., Loison, A. & Toïgo, C. (2003). Variation in life history traits and realistic population models for wildlife management: the case of ungulates. Pages 115-132 in Festa-Bianchet, M. & Appolonio, M. (eds). *Animal behavior and wildlife conservation*. Island press, Washington.

Loison, A. (1995). *Approches intra et inter spécifiques de la dynamique des populations: l'exemple du Chamois*. Ph.D. Thesis. Université Lyon I. 310 p.

### **Exercise 8 : Kidney vetch**

Bastrenta, B., Lebreton, J.D. & Thompson, J.D. (1995). Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. *Journal of Ecology* 83:603-611

Caswell, H.(2001). Matrix population models. Sinauer, Sunderland Mass. Chapter 3 & 4.

Caswell, H. & Werner, P.A. (1978). Transient Behavior and Life History Analysis of Teasel (*Dipsacus Sylvestris* Huds.) *Ecology* 59:53–66. <http://dx.doi.org/10.2307/1936631>

Haridas, C. & Tuljapurkar, S. (2005). Elasticities in variable environments: properties and implications. *American Naturalist*, 166:481-495.

Haridas, C. & Tuljapurkar, S. 2007. Time, transients and elasticity. *Ecology Letters*, 10:1143-1153.

Tuljapurkar, S., Horvitz, C.C. & Pascarella, J.B. (2003). The many growth rates and elasticities of populations in random environments. *American Naturalist*, 162:489-502.

### **Exercise 8: Ricker model**

Caswell, H.(2001). Matrix population models. Sinauer, Sunderland Mass. Chapter 16.

Lebreton, J.-D. & Gonzales-Davila, G. 1993. An introduction to models of subdivided populations. *Journal of Biological Systems*, 1: 389-423.

May, R.M. 1976. Simple mathematical models with very complicated dynamics. *Nature* 261 (5560): 459–67. [doi:10.1038/261459a0](https://doi.org/10.1038/261459a0)

Sharov, A. (1996). Chaos. <http://home.comcast.net/~sharov/PopEcol/lec9/chaos.html>

### **Exercise 9: Sparrow**

Caswell, H.(2001). Matrix population models. Sinauer, Sunderland Mass. Chapter 15.

Gosselin, F. & Lebreton, J.-D. 2000. The potential of branching processes as a modeling tool for conservation biology. In Ferson, S., Burgman, M. (Ed.) *Quantitative methods for conservation Biology*. Springer, ch.13.

Lebreton, J.D., Gosselin, F. & Niel, C. (2007). Extinction and viability of populations: paradigms and concepts of extinction models. *Ecoscience* 14: 472-481.

