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

ULM 3.0 http://www.snv.jussieu.fr/Bio/ulm/ulm.html; download the autoulm.exe file from this link or the following http://www.biologie.ens.fr/~legendre/ulm/ulm.html

R 3.0.2 http://cran.r-project.org/index.html

We have designed the exercises such that you can choose to use ULM or R to conduct the exercises. If you do not have a background using R, and you tend to be more comfortable using Graphical User Interface (GUI) software packages, you will want to use ULM (Unified Life Models) for conducting the workshop exercises. 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 build and examine 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 ULM and 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 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.

CONTENTS

Exercise 1: 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

For ULM users

1) Draw the life cycle of this species, making fledglings appear explicitly in your diagram.
2) Write the corresponding matrices for the pre birth-pulse and post birth-pulse models.
3) Use the text file "swallow.ulm" (i.e., *open* and then *compile* it using the 'lightbulb' button in ULM). Now *run* the file using the 'blue arrow' button, which will by default run the swallow matrix model for 50 time steps.
   a. Inspect the number of individuals in each age class in the pre birth-pulse model after 10 and 50 time steps as well as over all time steps using the default graphic.
   b. Use two different sets of initial values: N_1 = 10, N_2 = 0; then N_1 = 0, N_2 = 10. In the 'Interp' box use the command *changevar* as follows
      i. *changevar N1 0*
      ii. *changevar N2 10*
      iii. *run*
      iv. Use extensively *help* "*command name*" (e.g. *help run*)
4) Interpret the population growth rate provided by ULM. What happens when it is calculated over time periods of increasing length? (to change the time span for projecting the population dynamics keep re-using the commands *init* and *run* 5; *init* and *run* 10 etc.)

5) Obtain a graph of the logarithm of the total population size over time.
   a. First, use the command *newvar* and the function *ln0* to create this new variable and let us call it "lgN". For example, in the Interp box type
      i. *newvar* lgN *ln0*(N)
   b. Now graph this new variable using the following commands:
      i. *graph* t lgN
      ii. *xscale* 0 20
      iii. *yscale* 2 4
      iv. *init*
      v. *run* 20
   c. Superpose the graphs for the two different sets of initial values using the following commands and steps
      i. *addgraph*
      ii. change to the alternative initial values of N1 and N2 as you did above
      iii. *xscale* 0 20
      iv. *yscale* 2 4
      v. *run*
6) In similar fashion, obtain superimposed graphs of the "phase planes" (N1 on the x-axis and N2 on the y-axis). The phase plane is another way to examine convergence of the population's age structure to the stable age structure.
7) Write an ULM file for the post birth-pulse model (this is best done by modifying a copy of swallow.ulm) and do similar calculations. Examine the similarities and differences between the pre and post birth-pulse models.
8) Write a list of the ULM commands you used. Check with *help* their syntax and the various ways you can use them.

For R users

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 "Exercise1.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 2: 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
$s_0 = 0.482$ = 1st 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.

For ULM users

1) Examine the matrix model in the stork.ulm file and draw the corresponding life cycle. Now compile and run the stork.ulm model. Calculate the population growth rate from the dominant eigenvalue of the matrix by clicking the 'Matrix' menu at the top of the ULM page and selecting 'Properties'; to three decimals **write down the growth rate** on paper or in a spreadsheet. In addition to the long-term (asymptotic) population growth rate, note that the normalized reproductive values and stable age distribution are also provided, as are a number of other quantities that we will talk about later.

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 (look back to Exercise 1 if you forgot how to use the *changevar* command). Examine the population growth rate by again clicking the 'Matrix' menu at the top of the ULM page and selecting 'Properties'. 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:

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

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.

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*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 clicking the 'Matrix' menu at the top of the ULM page and selecting 'Sensitivities', then typing the name of the relevant demographic parameter in the 'Sensitivity of variable' box and hit enter (entrer). The total sensitivity and elasticity will appear in the boxes at the bottom of the screen.

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, compile and run the model for the short-lived barn swallows (using swallow.ulm), calculate the analytical sensitivities and elasticities for the analogous demographic parameters, and compare to the white stork.

For R users

1) Open the file "Exercise2.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*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:

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

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*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*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 3: 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 and ≥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 ≥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.

For ULM users

The information above is gathered in the matrix *A* in the ULM file bhgull1.ulm; the model for our first scenario, which assumes a slightly asymmetric juvenile dispersal.

1) Once you have compiled and run the model in bhgull1.ulm, click the Matrix tab and select Properties. Inspect the type of matrix that *A* is, and check that the population growth rate is close to stationary.
2) Use elasticity analysis to obtain T, the generation time, as described in the lecture.
3) Comment on the reproductive values at age 1 for the two locations.
4) Calculate the elasticity for adult survival $\partial \log \lambda / \partial \log s$, and use it to predict the change in λ 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 λ ≈ % change vital rate × elasticity, and $\lambda_{predict} = \lambda_{original} \times$ relative change in λ. Using the *changevar* command, induce this change and compare your predicted λ to the actual λ, and discuss how close your prediction was.
5) How is the ratio of breeding numbers (ratio) calculated in the ULM file?

6) Use the command *text ratio*, then run the model for 100 time steps to obtain the value of 'ratio' along the way. Explain why, like the population growth rate, the 'ratio' stabilizes over time.

Close the bhgull1.ulm file, then open the bhgull2.ulm file for the second scenario and compile it. In addition to juvenile dispersal, we will now consider adult dispersal probabilities of gb (Good to Bad) and bg (Bad to Good). The file is written with these probabilities set to 0. Check the matrix properties to make sure the long-term population growth rate is initially the same as in scenario 1.

7) Recent counts indicate a shift in numbers among the colonies with $N_{good} \approx 5000$ breeding pairs and $N_{bad} \approx 1200$ 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 using the *changevar* command, and 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 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.

For R users

The information above is gathered in the matrix **A** in the Exercise 3.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 λ 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 λ ≈ % change vital rate × elasticity, and $\lambda_{predict} = \lambda_{original} \times$ relative change in λ. Induce this change in the code and find the new dominant

eigenvalue of **A**. Compare your predicted λ to the actual λ, 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_{good} ≈ 5000 breeding pairs and N_{bad} ≈ 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 4: 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.

For ULM users

The information above is gathered in the ULM file chamois1.ulm; a deterministic model for chamois in the Bauges Mountains under 'good conditions'.

1) Assuming a constant, deterministic environment and the provided 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 ⅔ and all other survival parameters to ½ their baseline value in good conditions. On average, such catastrophes occur every 15 years. The information is gathered in the ULM file chamois2.ulm 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. In ULM, click the Monte Carlo tab and change the specifications on the right-hand side of the box to these specifications (first 100 years then try 1000 years). Run each Monte Carlo simulation by clicking the Monte Carlo tab again and selecting the red box beside the words 'Monte Carlo' (the simulations may require a few seconds to run).

For R users

The information above is contained in the Exercise 4.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 ⅔ and all other survival parameters to ½ 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 5: 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 1st time	Age 2 reproducing for the 2nd time
Notation:	S	Sd	R_{11}	NR_1	R_{21}	R_{22}

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).
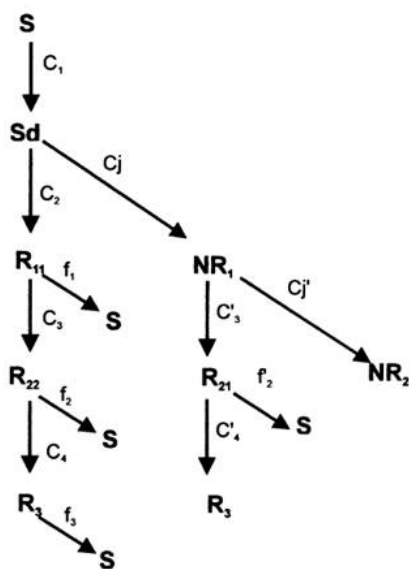
$$\begin{bmatrix} C_S & f_1C_2 & f_2C_3 & f_2{}'C_3{}' & f_3C_4 & f_3C_4{}' \\ C_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & C_2 & 0 & 0 & 0 & 0 \\ 0 & C_J & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & C_3{}' & 0 \\ 0 & 0 & 0 & C_3 & 0 & 0 \end{bmatrix}$$

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, *Cⱼ*, *C*₃, *C'*₃, *C'ⱼ*, *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_J	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 $C_2 + C_j$?

For ULM users

1) Poor and Good years happen at random in proportions P and 1-P. Using the ULM files grazed.ulm and ungrazed.ulm, 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. Use 500 Monte Carlo simulations over 1000 years. Change P by trial and error until you find the approximate answer.

2) Using the ungrazed.ulm file (compile it in ULM), examine the elasticities of the stochastic growth rate to 'simultaneous change in the mean & variance' of each demographic parameter. Do this by clicking the Matrix menu and selecting Stochastic sensitivities; in the 'Sensitivity to variable' box type the notation for one of the demographic parameters, use 100000 time steps and click run; repeat for all parameters in the matrix. 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.

For R users

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.

2) 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* 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 6: Exploitation in a Matrix Model with Two Sexes

We consider a matrix population model that could apply to red deer *Cervus elaphus* or similar ungulates, with plausible demographic mechanisms and parameter values for such species. The model considers the two sexes and is used to examine the effect of male harvest on the population dynamics.

The two sexes are assumed to be senescent after age 12. Post-reproductive age classes are not represented because they bear no influence on the population growth rate. Hence the matrix model has dimension 24 x 24. The model is said to be 'female dominant' as only females produce young of the two sexes. However, the probability that a female reproduces is modeled as dependent upon the ratio of reproductive males / reproductive females, and drops when there are too few males, as expected in a polygynous species. This is known as 'frequency dependence'; a special case of 'density dependence' that we will treat in greater detail in the next two exercises.

1) After carefully examining the respective files, deer.ulm or Exercise 6.r, describe the main demographic traits of this hypothetical red deer population that is based on the many studies of this charismatic species.

For ULM users

2) After compiling the file, use the 3 commands *init skip 100 run 1100* to find the asymptotic population growth rate of this sex-dependent model after discarding transient dynamics. Remembering to use the *changevar* command, do this for male harvest rates of 0, 0.1, 0.2, 0.3, and 0.4. Create a rough plot of the relationship between male harvest rate and asymptotic population growth rate. Denoting λ_0 as the asymptotic growth rate when h = 0, also calculate and plot $\lambda_0(1-h)$, which is the population growth rate assuming completely additive effects of the loss of males through harvest on the population growth rate. Comparing your two plots, what can you say about the degree of compensation in the harvest of male red deer at the population level?

For R users

2) Using the code in Exercise 6.r, use the two-sex matrix model for red deer and plot the relationship between male harvest rate and asymptotic population growth rate. Inspect the vector of harvest rates analyzed, and the resulting population growth rates, to find the harvest rate that lead to a stationary population. Denoting λ_0 as the asymptotic growth rate when h = 0, also calculate and plot $\lambda_0(1-h)$, which is the population growth rate assuming completely additive effects of the loss of males through harvest on the population growth rate. Comparing your two plots, what can you say about the degree of compensation in the harvest of male red deer at the population level?

Exercise 7: Management of Overabundant Cormorant

Since the early 1970's, an increase in the number of cormorants *Phalacrocorax carbo* breeding in Northern Europe resulted in an increase in the number of individuals wintering in France. This increase has induced many problems, in particular for fish breeding (aquaculture) in wetland areas of central France; ultimately leading to the establishment of a cormorant management plan. Very similar events have occurred with the double-crested cormorant in North America. The aim of this exercise is to evaluate, through matrix modeling, the effects of various strategies to limit cormorant numbers.
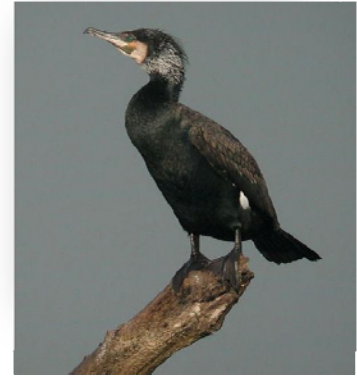
The number of cormorants wintering specifically in France has increased exponentially from the beginning of the 1970's to the 1990's at a rate of 15% per year. Similar increases have been observed in neighbouring countries (15.6% per year in Switzerland, 18% in U.K., 15.9 % in Italy from 1987 to 1994). Populations wintering in Central Europe have also exhibited high growth rates. In addition to parameters described in the ULM files, average demographic parameters for cormorants in Northern Europe are as follows:

Survival probability from age 0 to age 1: 0.64

Survival probability from age 1 to age 2: 0.86

Survival probability fom age 2 onwards: 0.89

Proportion of breeders at age 3: 0.10

Proportion of breeders at age 4: 0.60

Proportion of breeders from age 5 onwards: 1.00

For ULM users

1) Using the ULM file carbodi.ulm that provides a density-independent matrix model parameterized with the demographic parameters provided above as well as others described in the file, does a rate of growth of 15% per year seem plausible?

2) To limit the increase in numbers, a manager might be quite interested in knowing if it would be more efficient to remove eggs from nests or cull individuals capable of flight. By lowering the cs and cf variables in the ULM file, one at a time (e.g., from 1 to 0.9), which type of management action would lead to the largest reduction in population growth rate given equivalent percentage changes in clutch size vs. survival? What is the general rule explaining your findings?

3) The assumption of exponential growth is strong and will not be relevant in the long-term. There is no doubt that regulation through a density-dependent reduction of fertility or survival should eventually occur. Indeed, such a regulation may have already been present in Northern Europe after the year 2000. In order to model a density-dependent process, we can multiply nestling survival (commonly limited by per capita food availability) by a

function that decreases exponentially as a function of the number of breeding females. By adjusting the parameter B in the ULM file carbodd.ulm, determine a coefficient of density-dependence that would lead to an equilibrium number of breeding females (nbc) approximately equal to 20,000. The following ULM commands will be useful: *init, changevar, yscale 0 25000, graph t nbc, run 100, text nbc*.

4) In the density-dependent environment, estimate the percentage reduction in fecundity or survival required to decrease the equilibrium population size by approximately 20 % (use B = 12,900 and the associated equilibrium abundance from problem 3 above).

For R users

1) Using the density-independent matrix model for cormorants in the Exercise 7.r file that is parameterized with the demographic parameters described above (as well as others described in the file), does an annual rate of growth of 15% per year seem plausible?

2) To limit the increase in numbers, a manager might be quite interested in knowing if it would be more efficient to remove eggs from nests or cull individuals capable of flight. By lowering the cs and cf variables, one at a time (e.g., changing each one from 1 to 0.9), which type of management action would lead to the largest reduction in population growth rate given equivalent percentage changes in clutch size vs. survival? What is the general rule explaining your findings?

3) The assumption of exponential growth is strong and will not be relevant in the long-term. There is no doubt that regulation through a density-dependent reduction of fertility or survival should eventually occur. Indeed, such a regulation may have already been present in Northern Europe after the year 2000. In order to model a density-dependent process, we can multiply nestling survival (commonly limited by per capita food availability) by a function that decreases exponentially as a function of the number of breeding females. By looping through alternative values of the density-dependent coefficient for nestling survival B, use the second piece of code in Exercise 7.r to find the value of B that would lead to an equilibrium number of breeding females (nbc) equal to 20,000.

4) In the density-dependent environment, estimate the percentage reduction in fecundity or survival required to decrease the equilibrium population size by approximately 20 % (i.e., ~20,000×0.8; use the value of B that resulted in your answer for problem 3 above).

Exercise 8: 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 $N_* = K$.

For ULM users

1) Using the ULM file ricker.ulm and a low value of r (e.g., r = 0.25), explore the effect of changing K (the parameter for density dependence) on the dynamics of the population. Use plots as needed to interpret the effects of K.

2) Keeping K fixed at 100, what happens for $r > 2$? Explore progressively increasing values of r, starting from 1.7 and increasing by 0.2 for each new value of r examined (remember to use *changevar*, *init* and *run*).

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). 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. If you already have a graphics window open, click the 'clear' button. Then build a bifurcation diagram for the Ricker model and discuss it. To help, use the following sequence of commands:

addgraph
line
xscale 0 4
yscale 0 600
skip 100
parameter r 0.1 4 0.01
graph r N
run 800

4) Compile and run the file ddmp.ulm. This is 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) Obtain a bifurcation diagram for the sink population within the metapopulation, using the same commands as above but instead use *xscale 0 5*, *yscale 0 300, parameter r 0.1 5 0.01*, *graph r sink*.

For R users

1) Using the first part of the code in Exercise 8.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). 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.

Exercise 9: Demographic Stochasticity in the House Sparrow

Consider a short-lived species such as the house sparrow *Passer domesticus*, in which all individuals are assumed to breed at age 1.

The life cycle can be represented as follows:
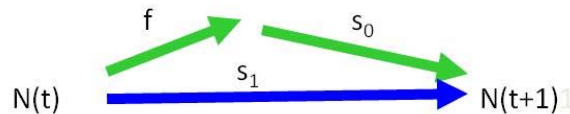
This leads to the deterministic model $N(t+1) = (f \times s_0 + s_1) N(t)$, which can be viewed as a scalar recurrence relationship or a 1 x 1 matrix model.

One can assume that the survival probabilities are affected by density dependence according to: $s_0 = s_{0,low} \, e^{-bN}$, and $s_1 = s_{1,low} \, e^{-bN}$ where e.g. $s_{0,low}$ represents the baseline survival probability from fledging to the first birthday when population density is low (we will start with $s_{0,low} = 0.2$ and $s_{1,low} = 0.5$). The number of young females fledged per female might logically be assumed to follow a Poisson distribution, here with a mean of $f = 3$.

The intensity of density-dependence (b) keeps the population small enough to make it sensitive to demographic stochasticity.

For ULM users

1) The model described above with parameter values is summarized in the ULM file sparrow.ulm. Using the Monte Carlo drop-down menu with 10,000 simulated trajectories and an extinction threshold of 1, fill in the table below to show that the population is rapidly doomed to extinction because of demographic stochasticity.

Time steps	Extinction Prob	Mean extinction time
100		
200		
300		
400		

2) The population size conditional on non-extinction (whose probability distribution is the "Quasi-Stationary Distribution") is given in ULM as "pop*(t)". Given this, estimate the equilibrium population size conditional on non-extinction ($\lim E(N_{t+1} / N_t > 0)$) over 100 time steps.

3) Obtain a formula for the deterministic equilibrium of the house sparrow model in the absence of demographic stochasticity, but in the presence of density dependence (N^*).

4) Using what you have learned above, complete the table below using f = 6/2 = 3 and b = 0.01.

$s_{0,low}$	$s_{1,low}$	λ_{max}	Deterministic equilibrium N^*	Cumulative Pr(extinction) over 1000 time steps	Stochastic equilib. $\lim E(N_{t+1} / N_t > 0)$
0.20	0.50				
0.25	0.50				
0.30	0.50				
0.30	0.60				

5) Given an infinite time horizon, what would be the overall probability of extinction in each scenario above? For the mathematically inclined: Why is the stochastic equilibrium smaller than the deterministic equilibrium?

6) Given the effect of λ_{max} on the risk of extinction over a finite time horizon, what do you think about the concept called the "extinction vortex"?

7) What happens when $s_{0,low}$ is additionally subject to random environmental variation? Keep $s_{1,low}$ at 0.5 and replace the numerical value for $s_{0,low}$ in the ULM file with "gaussf(0.25,0.05)", then recompile the file and run a Monte Carlo simulation as you did in problem 4.

For R users

1) The model described above with parameter values is summarized in the file Exercise 9.r. Examine the first piece of code to get a feel for how the scalar recurrence equation for house sparrow demography is implemented with demographic stochasticity. Run the first piece of code (including that for the plot) a few times to visualize the random impact of demographic stochasticity (coin flipping) on the dynamics of a small population.

2) Obtain a formula for the deterministic equilibrium of the house sparrow model in the absence of demographic stochasticity, but in the presence of density dependence (N*).

3) The population size conditional on non-extinction is distributed as the "Quasi-Stationary Distribution", and the stochastic equilibrium mean is denoted as lim E(Nt+1/ Nt >0). Part two of the code has lines of code to estimate moments (e.g., the mean) of the Quasi-Stationary Distribution, extinction probabilities, and extinction times (also conditional on E[N] > 0) across 10,000 simulations. Inspect and then run part two of the code to attain estimates of each of these 'population viability' parameters over 100, 200, 300, and 400 years.

4) Using what you have learned above, and the third piece of code, complete rows 1-4 in the table below by manually changing the vital rate values to those specified in the table. Each time you change a vital rate, re-run the entire third piece of code (it takes time to run).

$s_{0,low}$	$s_{1,low}$	λ_{max}	Deterministic equilibrium N^*	Cumulative Pr(extinction) over 1000 time steps	Stochastic equilib. $\lim E(N_{t+1} / N_t > 0)$
0.20	0.50				
0.25	0.50				
0.30	0.50				
0.30	0.60				
Beta(18.5,55.5)	0.50				

5) Given an infinite time horizon, what would be the overall probability of extinction in each scenario above? For the mathematically inclined: Why is the stochastic equilibrium smaller than the deterministic equilibrium?

6) Given the effect of λ_{max} on the risk of extinction over a finite time horizon, what do you think about the concept called the "extinction vortex"?

7) What happens when $s_{0,low}$ is additionally subject to random environmental variation? Keep $s_{1,low}$ at 0.5 and replace the numerical value for $s_{0,low}$ in the R code with "rbeta(1,18.5,55.5)", which specifies a Beta distribution for the environmental stochasticity in $s_{0,low}$ with a mean of 0.25 and variance of 0.0025. Then re-run part three of the code and complete row 5 of the table in problem 4 (note: you just need to un-comment a line of code within the time loop and comment out the original line for $s_{0,low}$).

Matrix Models for
Population Management & Conservation

Exercise Solutions for ULM

24-28 March 2014
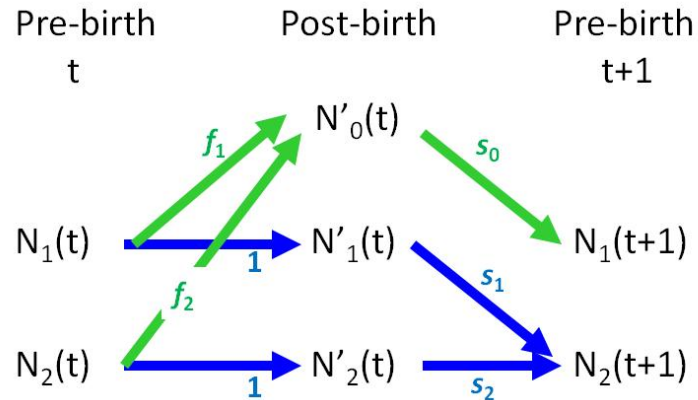**CNRS – CEFE**
Montpellier, France

Jean-Dominique Lebreton
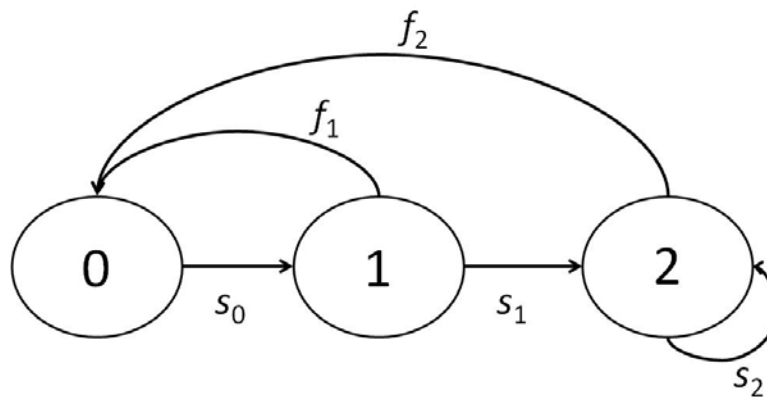**Olivier Gimenez**
Dave Koons

Solutions to Exercise 1: 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
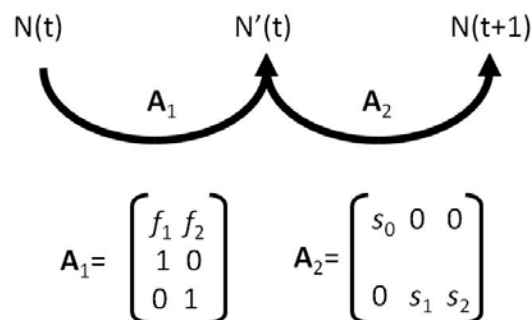

or you might have drawn something like this

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 birh-pulse models (alternatively, one could draw separate bubble-arrow diagrams). From the seasonal life-cycle one gets seasonal matrix projection models:

$$A_1 = \begin{bmatrix} f_1 & f_2 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} \qquad A_2 = \begin{bmatrix} s_0 & 0 & 0 \\ & & \\ 0 & s_1 & s_2 \end{bmatrix}$$

In turn, these can be used to construct the 2 x 2 annual pre birth-pulse matrix model: $\mathbf{A}_2$ x $\mathbf{A}_1$ =

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

or the 3 x 3 annual post birth-pulse matrix model: $\mathbf{A}_1$ x $\mathbf{A}_2$ =

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

The order of the matrices in a matrix product is from right to left, the order of time (e.g., pre birth pulse, first $\mathbf{A}_1$, then $\mathbf{A}_2$, hence product $\mathbf{A}_2$ x $\mathbf{A}_1$).

We prepared the swallow.ulm file for you using a text editor (e.g., Wordpad, Notepad, etc.). You can do this on your own using a text editor, saving, and then changing the name of the file extension (e.g., in the My Computer console on a Windows platform).

The directions for conducting steps 3-5 in ULM are provided in the Exercises document. Using the *help* command you will have found that *init* re-initializes the variables to their last value.

4. Interpret the population growth rate provided by ULM. What happens when it is calculated over time periods of increasing length?

The average per time step geometric growth rate is (final pop size/initial pop size)^(1/number of time steps). The larger the number of time steps, the smaller the effect of initial values. By increasing the number of time steps, and/or skipping the first ones (with command *skip*) you can check here that the growth rate converges to 1.05 regardless of the initial conditions (e.g. run 1000 with the original initial values leads to 1.049783, and run 10000 to 1.049974). This property of population growth in a deterministic enironment for a structured population is formalized in the strong ergodic theorem.

The directions for conducting steps 6 in ULM are provided in the Exercises document

6. In similar fashion, obtain superimposed graphs of the "phase planes" (N1 on the x-axis and N2 on the y-axis).

Clear the graph by clicking the *clear* button in the graphics box
Then use the following commands in the Interp dialog box (you should not need to use *addgraph* because it should already be "ON"):

```
xscale 0 100
yscale 0 100
graph n1 n2
run 50
init
changevar n1 0
changevar n2 10
run 50
```

You could use different scales for the axes if running over a different number of time steps.

7. Write an ULM file for the post birth-pulse model (this is best done by modifying a copy of swallow.ulm) and do similar calculations. Examine the similarities and differences between the pre and post birth-pulse models.

Here is ULM text for the post birth-pulse model, with blank lines removed for compactness

```
{ Swallow post- breeding
defmod swallow(3)
mat: a
vec: w
{ population vector
defvec w(3)
N0, N1, N2

{ population matrix
defmat a(3)
s0*f1, s1*f2, s2*f2
s0,    0,    0
0,    s1,    s2
{ initial number of fledglings
defvar N0= 40
{ initial number of FY
defvar N1 = 10
{ initial number of AFY
defvar N2 = 0
{ total post birth population size
defvar N = N0 + N1 + N2
{ juvenile survival rate
defvar s0 = 0.2
{ subadult survival rate
defvar s1 = 0.5
{ adult survival rate
defvar s2 = 0.65
{ FY female fecundity
defvar f1 = 1.5
{ AFY female fecundity
defvar f2 = 3
```

The long-term population growth rates are the same, but the stable structures do differ, and the effects of initial values differ too. The theoretical reasons for this will be examined later and can be addressed using in ULM the command *property* "matrix name"

8. Write a list of the ULM commands you used. Check with help their syntax and the various ways you can use them.
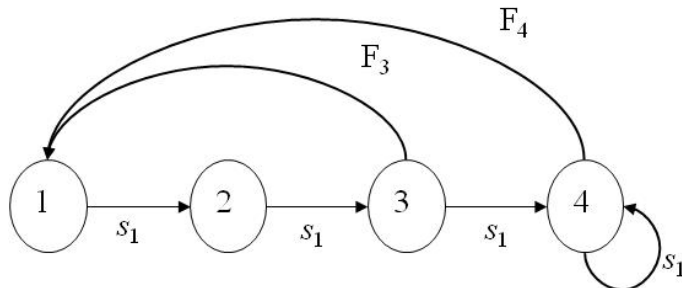
```
run
init
changevar
newvar
graph
```

```
addgraph
xscale
yscale
skip
```

Solutions to Exercise 2: Perturbation analysis of the white stork model

1. Examine the matrix model in the stork.ulm file and draw the corresponding life cycle. … write down the population growth rate on paper or in a spreadsheet.

λ = 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 $s_{1+} = 0.8*0.75 = 0.6$. Examine the population growth rate by again clicking the 'Matrix' menu at the top of the ULM page and selecting 'Properties'. 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:

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

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

	s_0	s_{1+}	b	λ	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.6	2.9	0.843	**0.851**

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	λ	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.3856	0.75	2.9	0.982	**0.167**

					1.018
Total rel. change					**1.018**

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*2.9 = 2.32.*

	s_0	s_{1+}	b	λ	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.75	2.32	0.982	**0.167**

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

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

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 you calculations from steps 2 – 4 to the exact analytical calculations by clicking the 'Matrix' menu at the top of the ULM page and selecting 'Sensitivities', then typing the name of the relevant demographic parameter in the 'Sensitivity of variable' box and hit enter (entrer).*

	Sensitivity	Elasticity	Approximation
s_0	0.335	0.159	0.167
s_{1+}	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.*

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 elasticitity 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, compile and run the model for the short-lived barn swallows (using swallow.ulm), calculate the analytical sensitivities and elasticities for the analogous demographic parameters, and compare to the white stork.*

	Sensitivity	Elasticity
s_0	1.826	0.3478
s_1	0.5217	0.2484
s_2	0.6522	0.4037
total	3	**1**
f_1	0.06957	0.09938
f_2	0.08696	0.2484
total	0.157	**0.348**

Although the elacticity 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 3: Two-site matrix models for black-headed gulls

1. Inspect the type of matrix that A is, and check that the population growth rate is close to stationary.

Among the various pieces of information, notice: "*Multisite -> YES [2 sites]*". Also, the population is close to stationary with λ = 0.997

2. Use elasticity analysis 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 elasticties to sg0 and sb0, i.e. 0.09756 + 0.03243 = 0.12999. Hence T = 1/0.12999 = 7.69 years.

3. Comment on the reproductive values at age 1 for the two locations.

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.

4. Calculate the elasticity for adult survival, and use it to predict the change in λ 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 × elasticity, and $\lambda_{predict} = \lambda_{original}$ × relative change in λ. Using the changevar command, induce this change and compare your predicted λ to the actual λ, 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 (using ULM). Thus, our predicted percentage and absolute changes in λ are 8.5% × 0.74 = 6.29% and λ = 0.997*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 s and λ.

5. How is the ratio of breeding numbers (ratio) calculated in the ULM file?

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. Using the command text ratio, then run the model for 100 time steps to obtain the value of 'ratio' along the way. 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 using the changevar command, and 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 on the chance of ending up in a better site.

Solutions to Exercise 4: 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 (λ = 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)?

Neglecting senescence (a common feature of ungulate populations) implies that we assume s11+ = 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 Δs = 0.229, leading thus to $\Delta\lambda/\Delta s$ = 0.08 and $\Delta\log(\lambda)/\Delta\log(s)$ = 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 λ 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 elasticity(m2)+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. In ULM, click the Monte Carlo tab and change the specifications on the right-hand side of the box to these specifications (first 100 years then try 1000 years). Run each Monte Carlo simulation by clicking the Monte Carlo tab again and selecting the red box beside the words 'Monte Carlo' (the simulations may require a few seconds to run).

The stochastic growth rate estimates over 100 and 1000 time steps (and 500 replicates) are approximately 1.104 and 1.105, respectively (answers may vary among people given these time horizons). The corresponding probabilities of pseudo-extinction were 0.002 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 5: 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 ULM files grazed.ulm and ungrazed.ulm, 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. Use 500 Monte Carlo simulations over 1000 years. Change P by trial and error until you find the approximate answer.

Using "*montecarlo 500 1000*" (with *init 1*, i.e. using the same random number generator seed), one obtains the following stochastic growth rates as a function of the expected proportion of Poor years, P:

P	Grazed	Ungrazed
1.00	0.838	0.629
0.87		0.981
0.865		0.995
0.86		1.010
0.81	0.996	
0.805	1.006	
0.80	1.018	

Unless all years are Poor, an Ungrazed kidney vetch population can sustain a higher probability of Poor years in a stochastic environment than a Grazed population.

2. ... examine the elasticities of the stochastic growth rate to 'simultaneous change in the mean & variance' of each demographic parameter.

Parameter	CS	C1	C2	CJ	C3	C3p	C4	C4p	f1	f2	f2p	f3
Stochastic Elasticity	0.41	0.19	0.12	0.06	0.15	0.04	~0	0.02	~0	0.15	0.04	0.02

Exercise 6: Exploitation in a Matrix Model with Two Sexes

*1. After carefully examining the respective files, deer.ulm or Exercise 6.r, describe the main demographic traits of this hypothetical red deer population that is based on the many studies of this charismatic species.*

- 2 yr old females have a lower fecundity than older females (parameter a2), likely because not all 2 yr olds breed.
- Prime age males (until age 8) have a natural survival probability (q) that is higher than that of older males (d).
- The model population has an uneven sex-ratio at birth (parameter sr, 60% of females at birth), further made more unbalanced in favor of females by the lower survival (+ harvesting) of males.
- The ratio reproductive males /reproductive females is based on males aged 4 or more and females aged 2 or more. Although sexually mature at an earlier age, it takes time for a bull to gain the stature needed to eventually compete for females.
- The probability of reproduction p is modeled as a logistic (monotonic) function of this ratio, with an arbitray parameter b that could be estimate from field data.

2. After compiling the file, use the 3 commands init skip 100 run 1100 to find the asymptotic population growth rate of this sex-dependent model after discarding transient dynamics. Remembering to use the changevar command, do this for male harvest rates of 0, 0.1, 0.2, and 0.3. Create a rough plot of the relationship between male harvest rate and asymptotic population growth rate. Denoting λ_0 as the asymptotic growth rate when h = 0, also calculate and plot $\lambda_0(1-h)$, which is the population growth rate assuming completely additive effects of the loss of males through harvest on the population growth rate. Comparing your two plots, what can you say about the degree of compensation in the harvest of male red deer at the population level?

One gets the following results: The growth rate λ decreases much less rapidly than $\lambda_0(1-h)$, as shown by the figure below, i.e; the harvest of males in such a polygynous species is highly compensatory at the population level. This would not be the case for harvest of females.

H	λ
0.00	1.011044
0.10	1.005112
0.20	1.000928
0.30	0.997971
0.40	0.995848
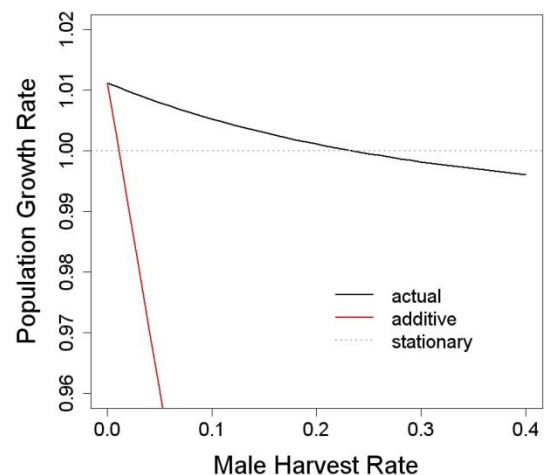
Exercise 7: Management of Overabundant Cormorant

1. Using the ULM file carbodi.ulm that provides a density-independent matrix model parameterized with the demographic parameters provided above as well as others described in the file, does a rate of growth of 15% per year seem plausible?

The demographic parameters and density-independent matrix model lead to a growth rate of 1.187, equal to 18.7 % growth per year, quite compatible with those estimated from winter surveys of abundance (15 %). This result confirms what are surprisingly high rates of population growth for such a large bird, but nevertheless possible given the combination of high survival and high fecundity. The high fecundity is thought to be associated to the fish diet that makes it possible to raise a large brood of large chicks that survive well.

2. To limit the increase in numbers, a manager might be quite interested in knowing if it would be more efficient to remove eggs from nests or cull individuals capable of flight. By lowering the cs and cf variables in the ULM file, one at a time (e.g., from 1 to 0.9), which type of management action would lead to the largest reduction in population growth rate given equivalent percentage changes in clutch size vs. survival? What is the general rule explaining your findings?

Taking the baseline scenario as a starting point, removing 10 % of the eggs (cf = 0.9) leads to an annual growth rate of 1.1705. The decrease in λ is 1.43 % (from 1.187 to 1.170). The ratio of the relative change in growth rate to the relative change in fecundity is thus only 0.14. In a similar fashion, removing 10% of individuals capable of flight (changing cf back to 1 and then cs to 0.9 for example) changes the annual growth rate from 1.187 to 1.069, a relative change in λ exactly equal to 10%.

As discussed before, we know this result is linked to generation time T, equal to 7.17 years in the baseline scenario. Its inverse, 0.14 is the elasticity of λ to a change in fecundity, while the elasticity to a change in survival (of all age classes) is 1; thus the 1:1 relationship between a percentage change in survival and the percentage response in λ.

It is not surprising that similar results were obtained by Bédard et al. (Colonial Waterbirds, 1995) in Canada for the double-crested cormorant *Phalacrocorax auritus*.

The intuitive explanation is that removing an egg or chick is not equivalent to removing an adult because few 'eggs' actually result in breeding adults. By removing flighted birds, including breeding adults, one removes their 'remaining lifetime production of offspring'. The effect of culling is thus stronger than egg removal.

3. The assumption of exponential growth is strong and will not be relevant in the long-term. There is no doubt that regulation through a density-dependent reduction of fertility or survival should eventually occur. Indeed, such a regulation may have already been present in Northern Europe after the year 2000. In order to model a density-dependent process, we can multiply nestling survival (commonly limited by per capita food availability) by a function that decreases exponentially as a function of the number of breeding females. By adjusting the parameter B in the ULM file carbodd.ulm, determine a coefficient of density-dependence that would lead to an

equilibrium number of breeding females (nbc) approximately equal to 20,000. The following ULM commands will be useful: init, changevar, yscale 0 25000, graph t nbc, run 100, text nbc.

Successive attempts lead to (for instance) the following values of nbc, the number of breeders in ULM file carbodd.ulm:

B	10,000	12,000	13,000	12,900
nbc	15,478	18,574	20,122	19,968

4. In the density-dependent environment, estimate the percentage reduction in fecundity or survival required to decrease the equilibrium population size by approximately 20 % (use B = 12,900 and the associated equilibrium abundance from problem 3 above).

The higher elasticity to the cull of flighted indivudals is again confirmed in the density-dependent environment. A drop of survival by only 2.5 % (cs=0.975) is sufficient to bring the equilibrium number of breeders to 16,200, close to a 20 % decrease (which would be an equilibrium abundance of 15,974), while it takes the removal of 25% of the eggs (cf = 0.75) to reach a similar level (16,197).

This density-dependent model is a bit arbitrary. Models with density-dependence in survival should show a stronger compensation of the management actions than does this one, precisely because of the higher elasticity to survival.

Exercise 8: The Ricker Model of Density Dependence

1. Using the ULM file ricker.ulm and a low value of r (e.g., r = 0.25), explore the effect of changing K (the parameter for density dependence) on the dynamics of the population. Use plots as needed to interpret the effects of K.
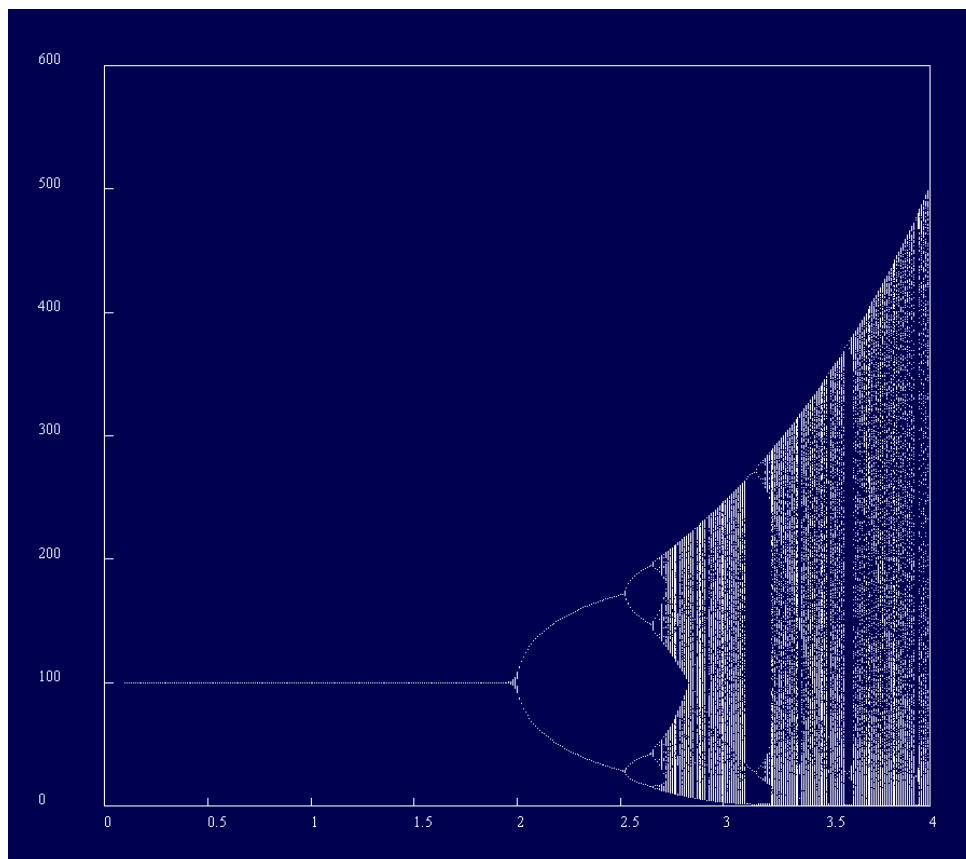
K is often called the carrying capacity for a population. For low to moderate values of *r*, K determines the equilibrium value of abundance where birth and death rates balance each other. By changing *K*, the equilibrium abundance changes.

2. Keeping K fixed at 100, what happens for r > 2? Explore progressively increasing values of r, starting from 1.7 and increasing by 0.2 for each new value of r examined (remember to use changevar, init and run).

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". For structured populations, chaotic dynamics can form beautiful "Fractals" (*sensu* Benoit Mandelbrot).

*3. … Then build a bifurcation diagram for the Ricker model and discuss it…*

The resulting bifurcation diagram below shows the transitions from stability to cycles to chaos as *r* increases (note the stability 'bifurcates'). Around *r* ≈ 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. The upper right contains a 0, indicating no dispersal from the sink to the source.

5. Obtain a bifurcation diagram for the sink population within the metapopulation, using the same commands as above but instead use xscale 0 5, yscale 0 300, parameter r 0.1 5 0.01, graph r sink.
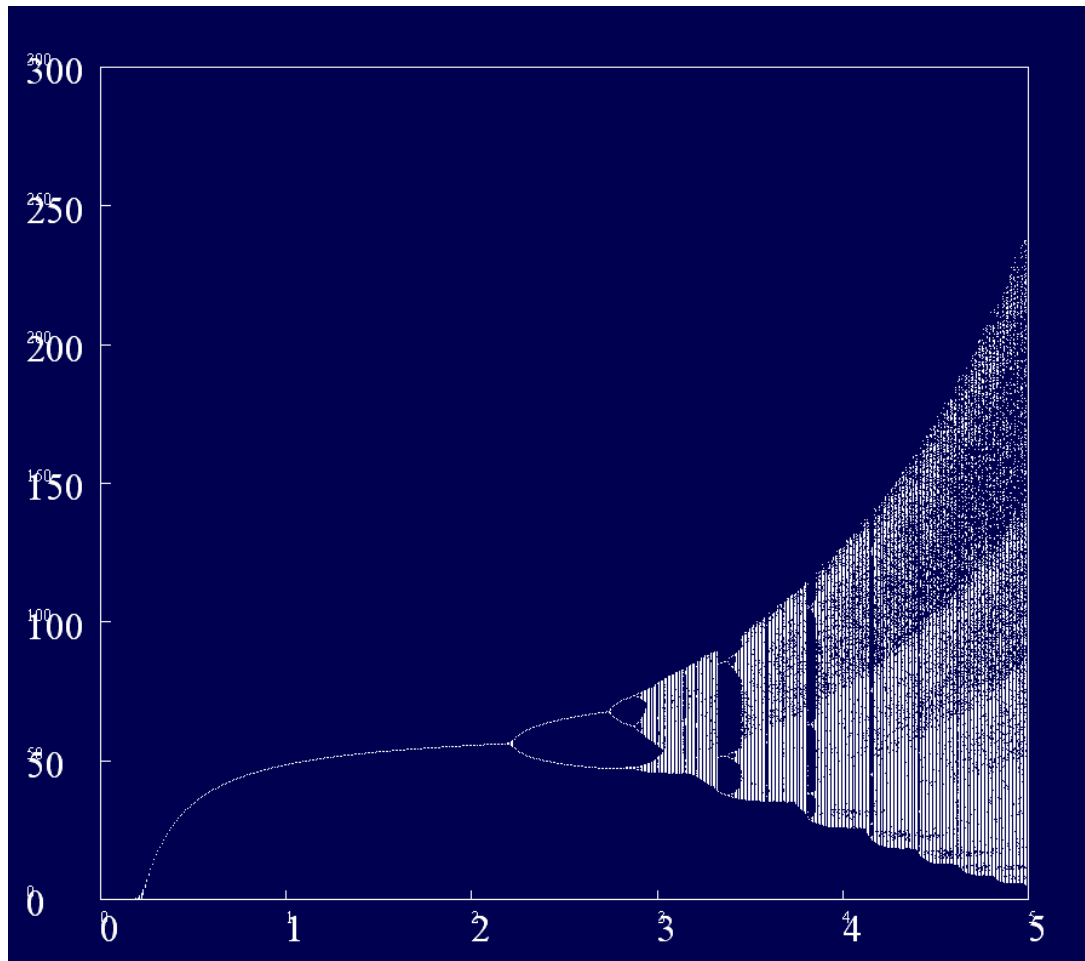
Exercise 9: Demographic Stochasticity in the House Sparrow

1. Using the Monte Carlo drop-down menu with 10,000 simulated trajectories and an extinction threshold of 1, fill in the table below to show that the population is rapidly doomed to extinction because of demographic stochasticity.

Time steps	Extinction Prob	Mean extinction time
100	0.8653	33.28
200	0.9866	49.58
300	0.9986	52.37
400	0.9998	52.78

2. The population size conditional on non-extinction (whose probability distribution is the "Quasi-Stationary Distribution") is given in ULM as "pop*(t)". Given this, estimate the equilibrium population size conditional on non-extinction (lim E(Nt+1 / Nt>0)) over 100 time steps.

For 100 time steps, lim E(Nt+1 / Nt>0) = 8.5 with a standard deviation of 5.2 and a range of 1-28. In this case, it would be difficult to calculate this over a longer time horizon because very few trajectories would remain extant (just a few in fact).

3. Obtain a formula for the deterministic equilibrium of the house sparrow model in the absence of demographic stochasticity, but in the presence of density dependence (N*).

To attain the solution we start with $N(t+1) = N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}$, then replace all values of N with N^*, the equilibrium abundance, $N^* = N^*(s_{0,low}f + s_{1,low})e^{-bN^*}$. We then solve for N^*

$N^* = \dfrac{1}{b}\log(s_{0,low}f + s_{1,low}) = \dfrac{\log(\lambda_{max})}{b}$. Note that $\lambda_{max} = s_{0,low}f + s_{1,low}$.

4. Using what you have learned above, complete the table below using f = 6/2 = 3 and b = 0.01.

$s_{0,low}$	$s_{1,low}$	λ_{max}	Deterministic equilibrium N^*	Cumulative Pr(extinction) over 1000 time steps	Stochastic equilib. lim $E(N_{t+1} / N_t>0)$
0.20	0.50	1.1	9.53	1	-
0.25	0.50	1.25	22.31	0.5146	20.0
0.30	0.50	1.4	33.65	0.003	32.2
0.30	0.60	1.5	40.55	0.0001	39.4
gaussf(0.25,0.05)	0.50	1.25	22.31	0.7763	19.2

5. Given an infinite time horizon, what would be the overall probability of extinction in each scenario above? For the mathematically inclined: Why is the stochastic equilibrium smaller than the deterministic equilibrium?

Given an infinite time horizon, the overall probability of extinction is always = 1; all populations will eventually go extinct. However, the probability of extinction over a finite time horizon does

vary markedly, as does its complement, the probability of reaching the quasi-stationary distribution.

For the math-stat fans, the stochastic equation is $E[N(t+1)] = N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}$, which implies $E[N(t+1)] = E[N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}]$. When $N(t)$ is distributed as the QSD and P is the probability of extinction in one time step, then $E[N(t+1)] = (1-P)E[N(t)]$; the population goes extinct with probability P or transitions to a new population size distributed according the QSD with probability $1-P$. By Jensen's inequality, the convexity of the model function $\lambda_{\max} x e^{-bx}$ in the domain considered is such that $E[N(t)](s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > E[N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}]$, and hence $E[N(t)](s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > (1-P)E[N(t)]$. This implies that $(s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > 1$ because the variance of the QSD makes the effect of the convexity much larger than that of P. Then $(s_{0,low}f + s_{1,low})e^{-bE[N(t)]} < 1 = (s_{0,low}f + s_{1,low})e^{-bN^*}$ which finally implies for the QSD mean taht $E[N(t)] < N^*$.

6. Given the effect of λ_{max} on the risk of extinction over a finite time horizon, what do you think about the concept called the "extinction vortex"?

From the table above, the shift in extinction probabilities over a finite time horizon is very sharp with the change in λ_{max}, and nearly creates a sharp borderline between populations rapidly doomed to extinction and those for which the probability of extinction is very small or even negligible, so the vortex may largely result from the fact that a population is on one side or the other of the borderline. This result does not imply that other factors contributing to accelerated extinciton in small populations (e.g., Allee effects) should be neglected.

7. What happens when $s_{0,low}$ is additionally subject to random environmental variation? Keep $s_{1,low}$ at 0.5 and replace the numerical value for $s_{0,low}$ in the ULM file with "gaussf(0.25,0.05)", then recompile the file and run a Monte Carlo simulation as you did in problem 4.

The population abundance varies quite a bit, and the risk of extinction over 1000 years increases notably (shown in the last line of the Table for problem 4 above). As a result of the larger variance of population size, the average number of individuals in the QSD is even smaller than in the absence of random environmental variation. The combined effects of environmental and demographic stochasticity on population viability can be biologically significant for small populations of conservation concern.

Matrix Models for
Population Management & Conservation

Exercise Solutions for R

24-28 March 2014
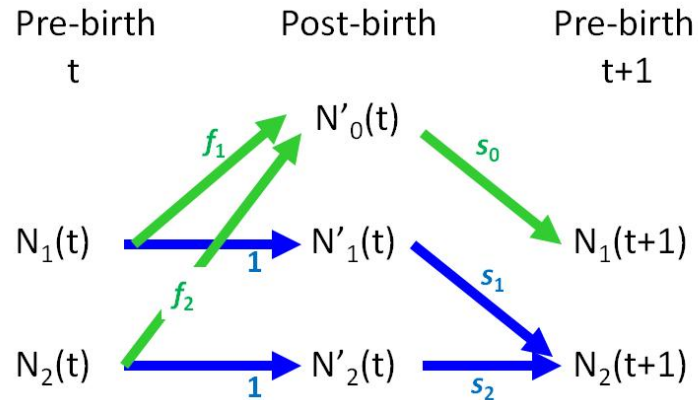**CNRS – CEFE**
Montpellier, France

Jean-Dominique Lebreton
Olivier Gimenez
Dave Koons

CENTRE D'ECOLOGIE FONCTIONNELLE ET EVOLUTIVE
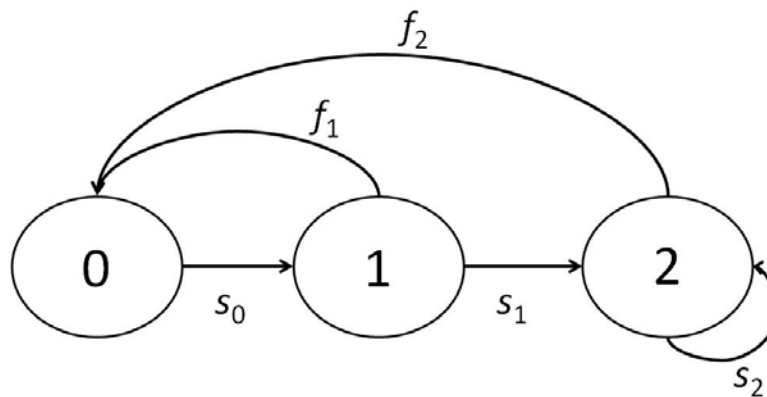**U.M.R 5175, 1919 Route de Mende, 34293 MONTPELLIER CEDEX 5, France**

Solutions to Exercise 1: 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 birh-pulse models (alternatively, one could draw separate bubble-arrow diagrams). From the seasonal life-cycle one gets seasonal matrix projection models:

$$A_1 = \begin{bmatrix} f_1 & f_2 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} \qquad A_2 = \begin{bmatrix} s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{bmatrix}$$
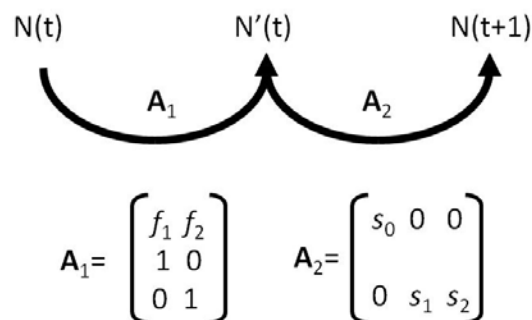
In turn, these can be used to construct the 2 x 2 annual pre birth-pulse matrix model: $A_2 \times A_1 =$

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

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 6th 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.
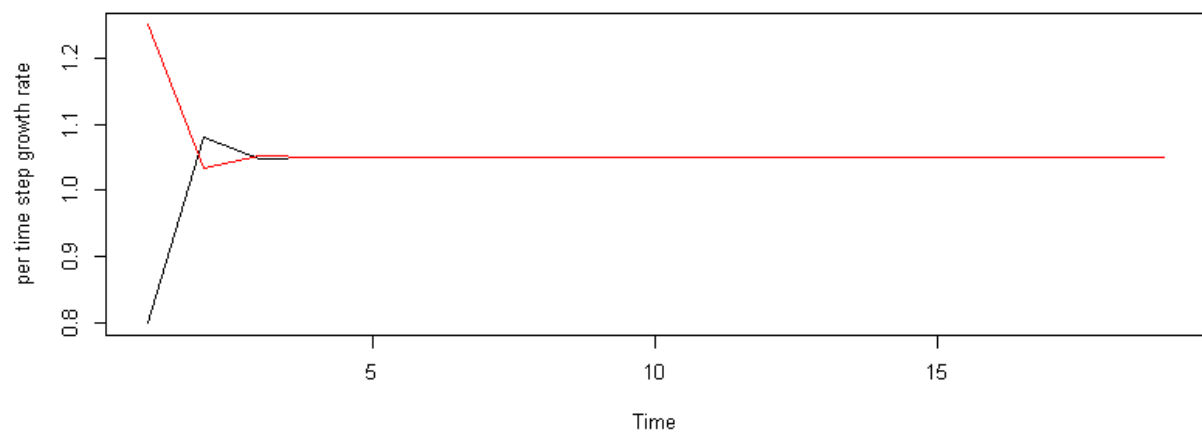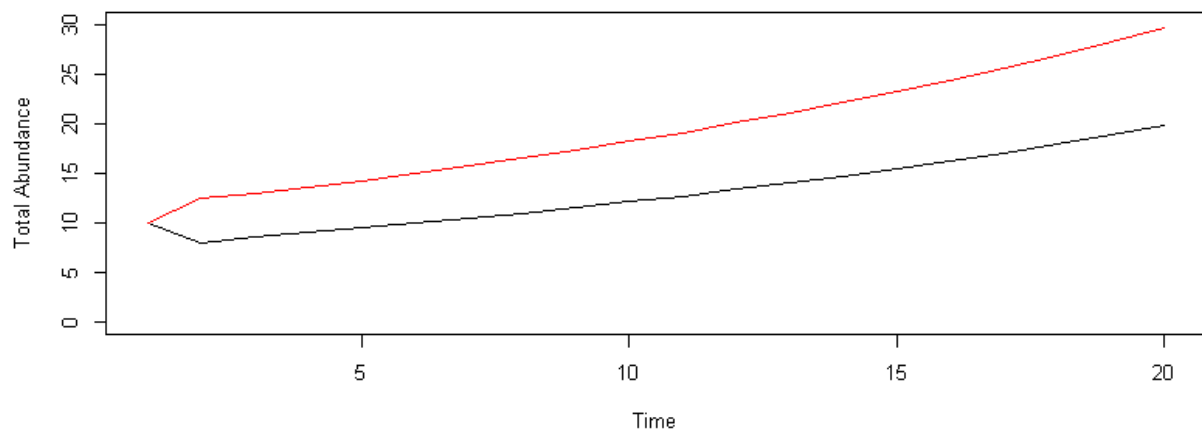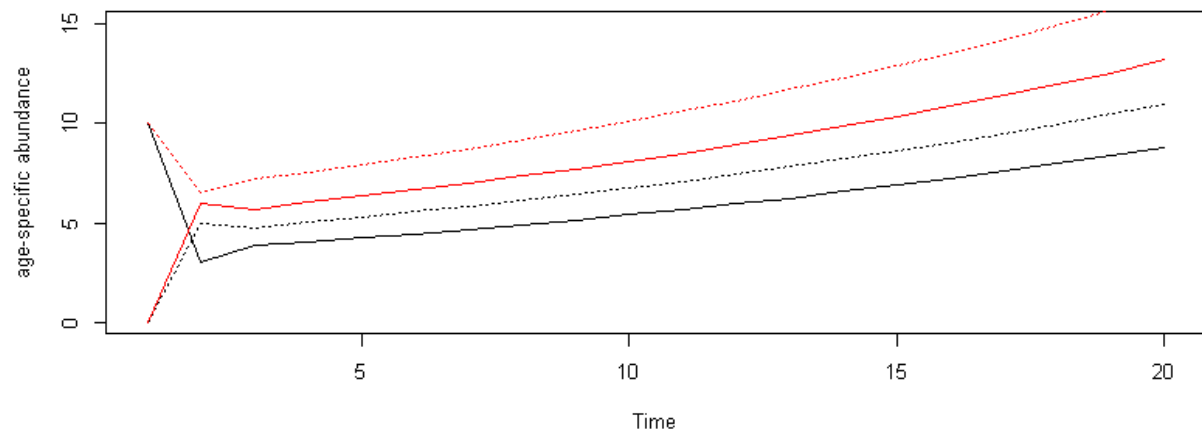
5. Now see if you can develop a graph that plots the abundance of one age class against the other (n_1, n_2) for each of the initial conditions. This is called a "phase plane", and is one way to view convergence of the population's age structure to the stable age structure.

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")
```
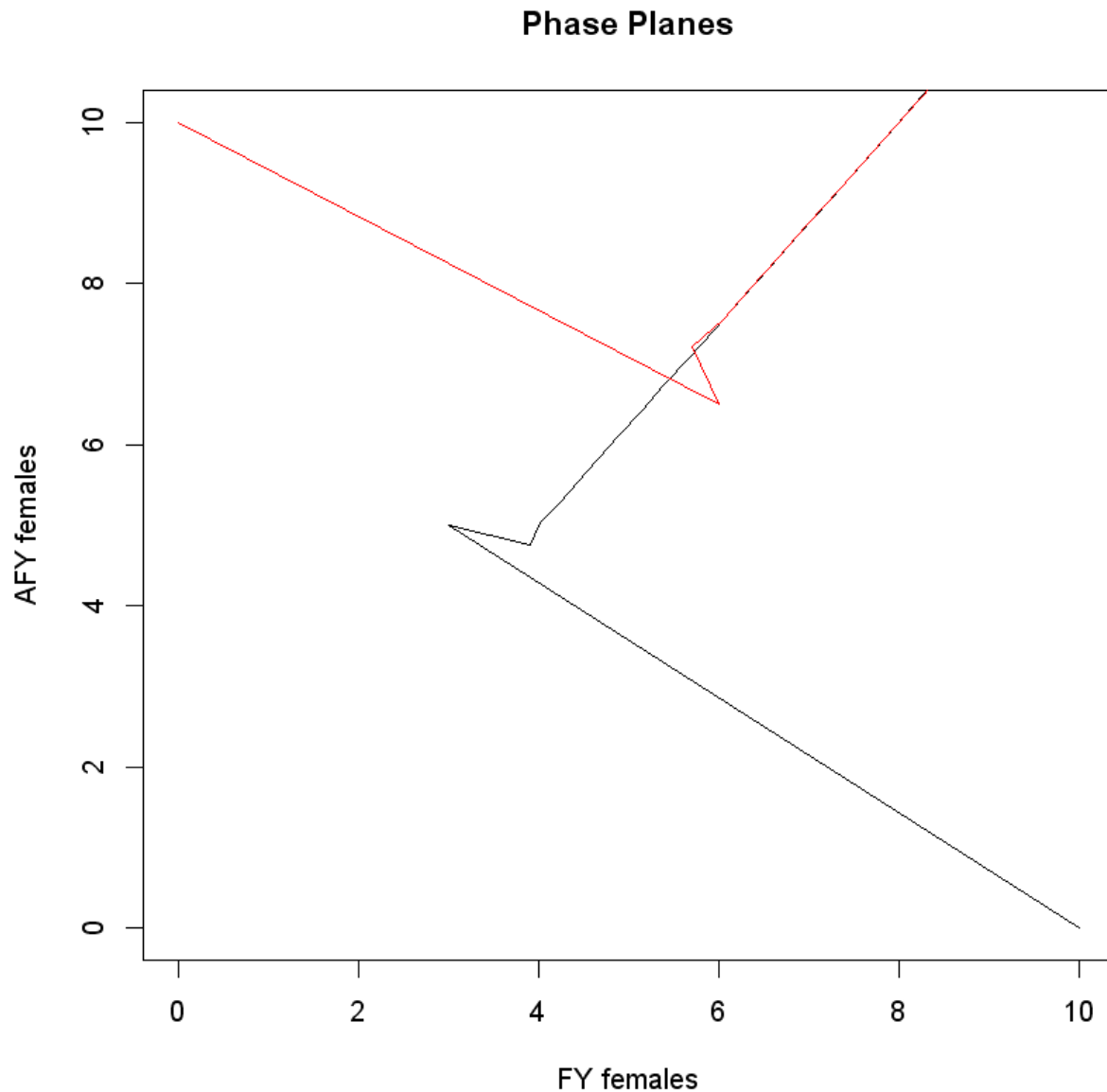

Phase Planes

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

```r
# 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])
    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")
```
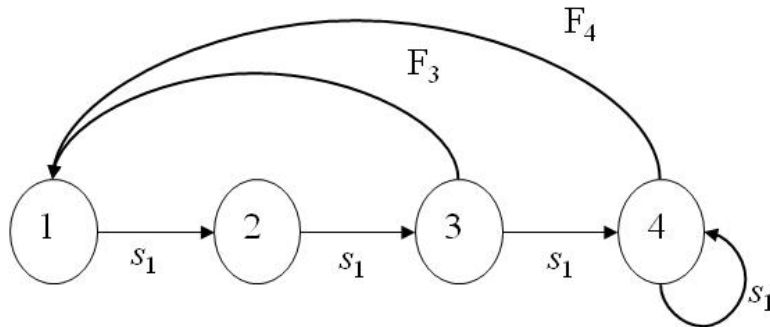
Solutions to Exercise 2: Perturbation analysis of the white stork model

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.

λ = 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:

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

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

	s_0	s_{1+}	b	λ	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.6	2.9	0.843	**0.851**

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	λ	Relative Change
original	0.482	0.75	2.9	1.016	

new	0.3856	0.75	2.9	0.982	**0.167**
Total rel. change					**1.018**

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*2.9 = 2.32.*

	s_0	s_{1+}	b	λ	Relative Change
original	0.482	0.75	2.9	1.016	
new	0.482	0.75	2.32	0.982	**0.167**

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

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

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_{1+}	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/llsenselas[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 elasticitiy 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
llsenselas <- vitalsens(swallow.A,swallow.vr)
llsenselas

# total sensitivities and elasticities
totalSsens <- sum(llsenselas[3:5,2])
totalSsens
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	**1**
f_1	0.06957	0.09938
f_2	0.08696	0.2484
total	0.157	**0.348**

Although the elacticity 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 3: 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 **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 sg0 and sb0, 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 λ 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 λ ≈ % change vital rate × elasticity, and $\lambda_{predict} = \lambda_{original}$ × relative change in λ. Using the changevar command, induce this change and compare your predicted λ to the actual λ, 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 λ are 8.5% × 0.74 = 6.29% and λ = 0.997*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 λ.
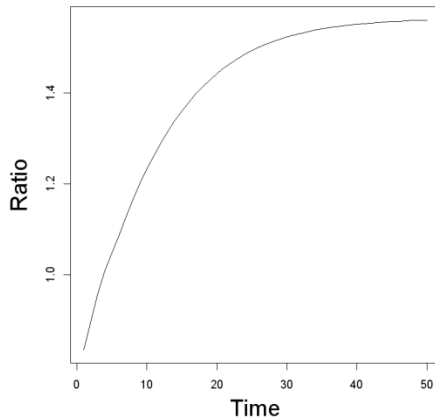
```
predpercent <- ((0.89/0.82-1)*100)*llsenselas$elasticity[3]
predLambda <- (predpercent/100+1)*Lambda
```

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 4: 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 (λ = 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 s11+ = 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 Δs = 0.229, leading thus to $\Delta\lambda / \Delta s$ = 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 λ 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 elasticity(m2)+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 5: 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)
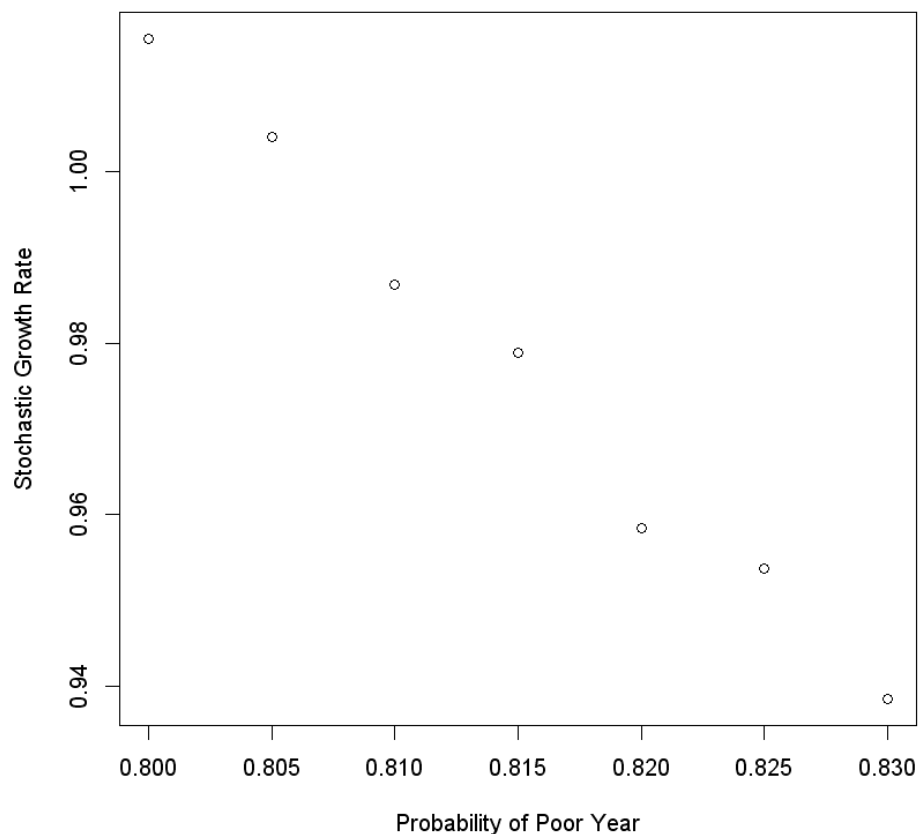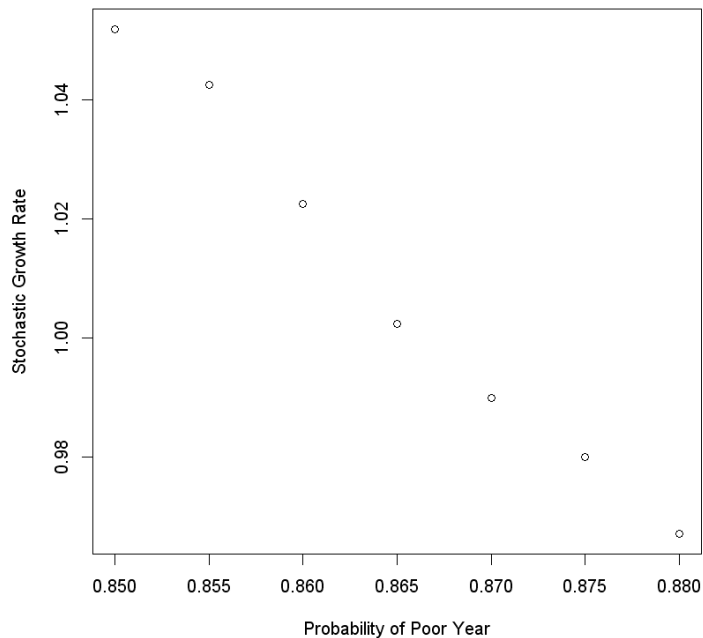
Ungrazed

Note that the Ungrazed sites can sustain a higher probability of Poor years and still stay viable (stochastic growth rate >= 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 calculationg 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 elastiticies 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 condtions that help enhance seed survival and germination rate would most affect the stochastic growth rate in common kidney vetch in ungrazed environments.

Exercise 6: Exploitation in a Matrix Model with Two Sexes

1. After carefully examining the respective files, deer.ulm or Exercise 6.r, describe the main demographic traits of this hypothetical red deer population that is based on the many studies of this charismatic species.

- 2 yr old females have a lower fecundity than older females (parameter a2), likely because not all 2 yr olds breed.
- Prime age males (until age 8) have a natural survival probability (q) that is higher than that of older males (d).
- The model population has an uneven sex-ratio at birth (parameter sr, 60% of females at birth), further made more unbalanced in favor of females by the lower survival (+ harvesting) of males.
- The ratio reproductive males /reproductive females is based on males aged 4 or more and females aged 2 or more. Although sexually mature at an earlier age, it takes time for a bull to gain the stature needed to eventually compete for females.
- The probability of reproduction p is modeled as a logistic (monotonic) function of this ratio, with an arbitray parameter b that could be estimate from field data.

2. Using the code in Exercise 6.r, use the two-sex matrix model for red deer and plot the relationship between male harvest rate and asymptotic population growth rate. Inspect the vector of harvest rates analyzed, and the resulting population growth rates, to find the harvest rate that lead to a stationary population. Denoting λ_0 as the asymptotic growth rate when h = 0, also calculate and plot $\lambda_0(1-h)$, which is the population growth rate assuming completely additive effects of the loss of males through harvest on the population growth rate. Comparing your two plots, what can you say about the degree of compensation in the harvest of male red deer at the population level?

The growth rate λ decreases much less rapidly than $\lambda_0(1-h)$, as shown by the figure at right, i.e; the harvest of males in such a polygynous species is highly compensatory at the population level. This would not be the case for harvest of females. When inspecting the vectors of examined harvest rates and corresponding population growth rates, the male harvest rate that leads to a stationary population is 0.23 , which can roughly be seen in the plot at right.
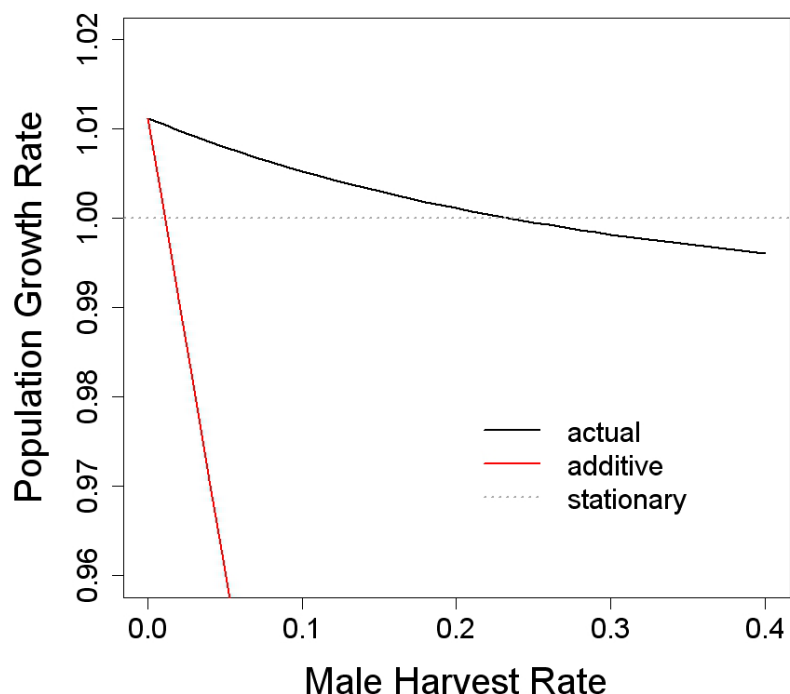
Exercise 7: Management of Overabundant Cormorant

1. Using the density-independent matrix model for cormorants in the Exercise 7.r file that is parameterized with the demographic parameters described above (as well as others described in the file), does an annual rate of growth of 15% per year seem plausible?

The demographic parameters and density-independent matrix model lead to a growth rate of 1.187, equal to 18.7 % growth per year, quite compatible with those estimated from winter surveys of abundance (15 %). This result confirms what are surprisingly high rates of population growth for such a large bird, but nevertheless possible given the combination of high survival and high fecundity. The high fecundity is thought to be associated to the fish diet that makes it possible to raise a large brood of large chicks that survive well.

2. To limit the increase in numbers, a manager might be quite interested in knowing if it would be more efficient to remove eggs from nests or cull individuals capable of flight. By lowering the cs and cf variables, one at a time (e.g., changing each one from 1 to 0.9), which type of management action would lead to the largest reduction in population growth rate given equivalent percentage changes in clutch size vs. survival? What is the general rule explaining your findings?

Taking the baseline scenario as a starting point, removing 10 % of the eggs (cf = 0.9) leads to an annual growth rate of 1.1705. The decrease in λ is 1.43 % (from 1.187 to 1.170). The ratio of the relative change in growth rate to the relative change in fecundity is thus only 0.14. In a similar fashion, removing 10% of individuals capable of flight (changing cf back to 1 and then cs to 0.9 for example) changes the annual growth rate from 1.187 to 1.069, a relative change in λ exactly equal to 10%.
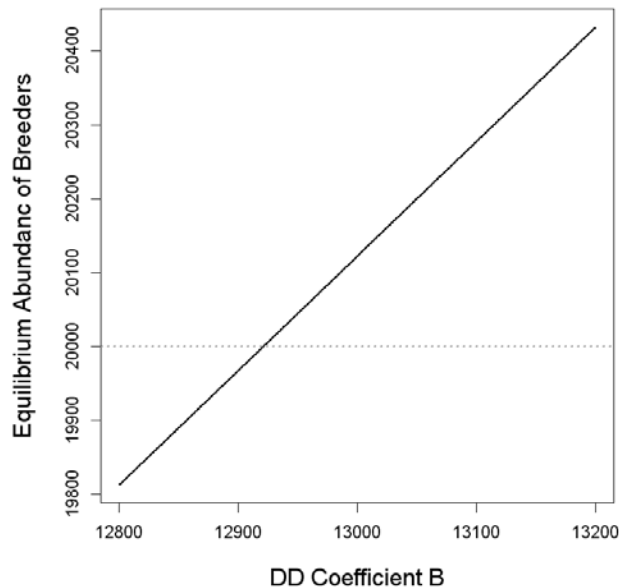
As discussed before, we know this result is linked to generation time T, equal to 7.17 years in the baseline scenario. Its inverse, 0.14 is the elasticity of λ to a change in fecundity, while the elasticity to a change in survival (of all age classes) is 1; thus the 1:1 relationship between a percentage change in survival and the percentage response in λ.

It is not surprising that similar results were obtained by Bédard et al. (Colonial Waterbirds, 1995) in Canada for the double-crested cormorant *Phalacrocorax auritus*.

The intuitive explanation is that removing an egg or chick is not equivalent to removing an adult because few 'eggs' actually result in breeding adults. By removing flighted birds, including breeding adults, one removes their 'remaining lifetime production of offspring'. The effect of culling is thus stronger than egg removal.

3. The assumption of exponential growth is strong and will not be relevant in the long-term. There is no doubt that regulation through a density-dependent reduction of fertility or survival should eventually occur. Indeed, such a regulation may have already been present in Northern Europe after the year 2000. In order to model a density-dependent process, we can multiply nestling survival (commonly limited by per capita food availability) by a function that decreases exponentially as a function of the number of breeding females. By looping through alternative values of the density-dependent coefficient for nestling survival B, use the second piece of code

in Exercise 7.r to find the value of B that would lead to an equilibrium number of breeding females (nbc) equal to 20,000.

Using the graph, we can look more closely at the simulate values of B, the density-dependent coefficient affecting nestling survival, to see which value confers an equilibrium abundance of breeding females = 20,000.

```
eqnbc[100:200]
Bseq[122]
```
B = 12921 confers nbc = 20,000

4. In the density-dependent environment, estimate the percentage reduction in fecundity or survival required to decrease the equilibrium population size by approximately 20 % (i.e., ~20,000×0.8; use the value of B that resulted in your answer for problem 3 above).

The higher elasticity to the cull of flighted indivudals is again confirmed in the density-dependent environment. A drop of survival by only 2.5 % (cs=0.975) is sufficient to bring the equilibrium number of breeders to 16,226, close to a 20 % decrease (which would be an equilibrium abundance of 16,000), while it takes the removal of 25% of the eggs (cf = 0.75) to reach a similar level (16,223).

This density-dependent model is a bit arbitrary. Models with density-dependence in survival should show a stronger compensation of the management actions than does this one, precisely because of the higher elasticity to survival.

## Exercise 8: The Ricker Model of Density Dependence

1. Using the first part of the code in Exercise 8.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.
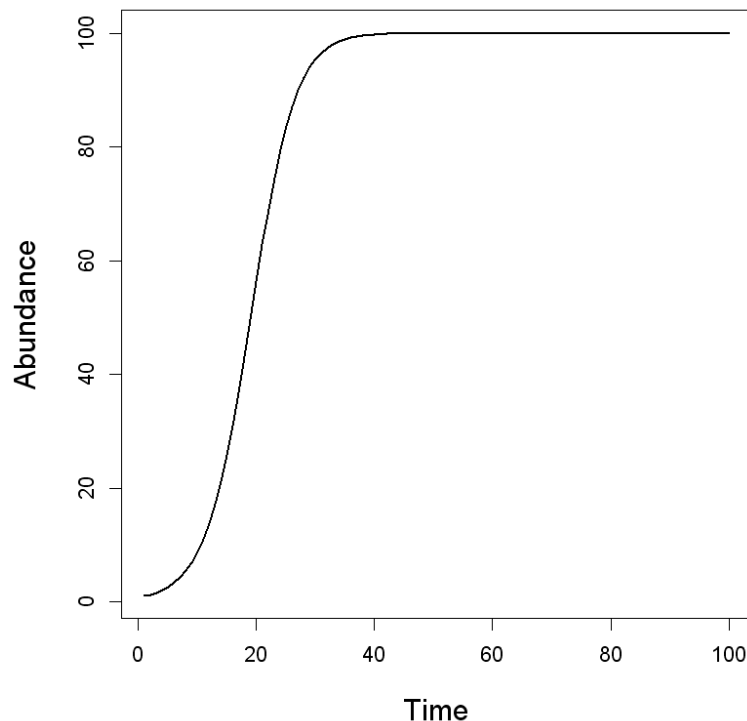
2. Keeping K fixed at 100, now explore the effects of progressively increasing values of r. Start from r = 1.7 and increase it by 0.2 each time you re-run the code. What happens when r > 2?
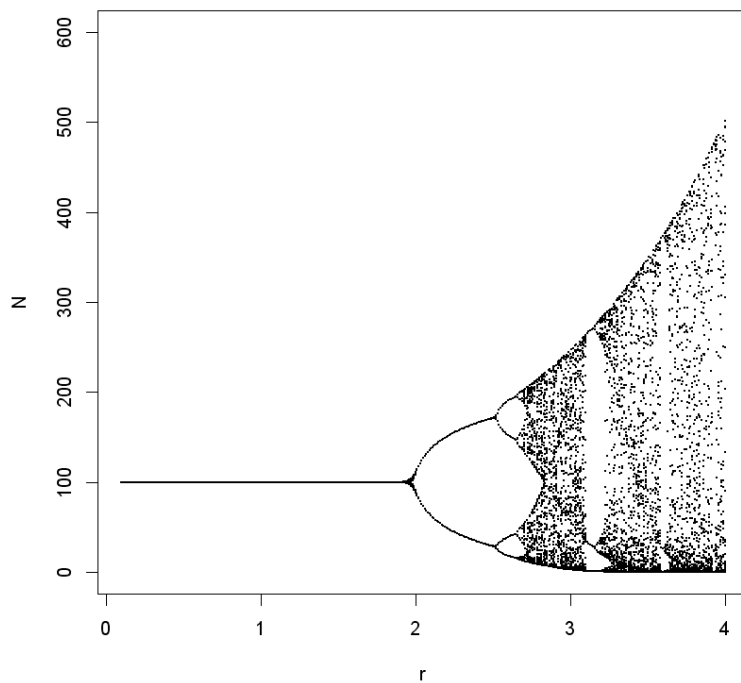
At first we observe damped cycles that stabilize, then perpetual cycles that do not disappear, then cycles with two different types of peaks and troughs (a 4-cycle), and eventually the cycles become erratic where the values of abundance at the peaks and troughs never repeat themselves, which is called "chaos" (shown below in the example plot). For structured populations, chaotic dynamics can form beautiful "Fractals" (*sensu* Benoit Mandelbrot).
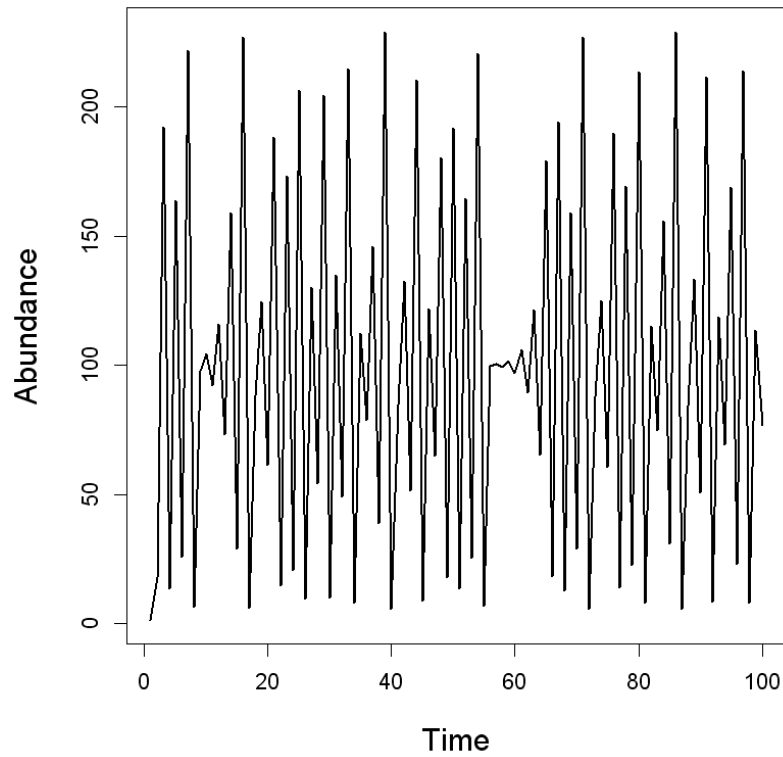
Shown for r = 2.9

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* ≈ 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.
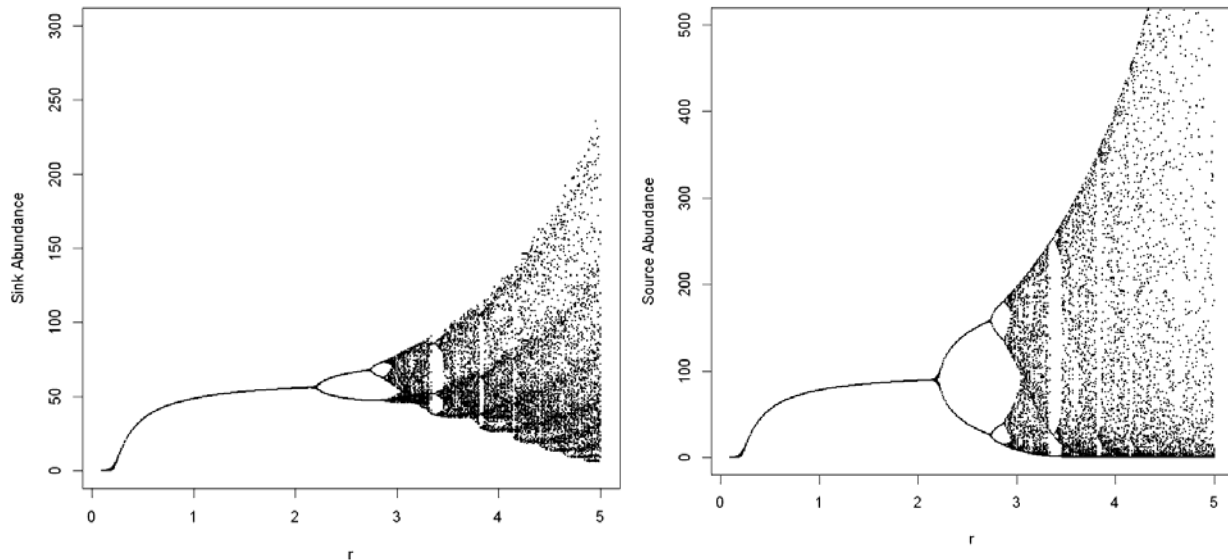
Exercise 9: Demographic Stochasticity in the House Sparrow

1. … Examine the first piece of code to get a feel for how the scalar recurrence equation for house sparrow demography is implemented with demographic stochasticity. Run the first piece of code (including that for the plot) a few times to visualize the random impact of demographic stochasticity (coin flipping) on the dynamics of a small population.

Demographic stochasticity is implemented in the code using Poisson and binomial distributions for the demographic outcomes of N individuals experiencing the expected value of a given vital rate. We can see that there are few individuals (low N enforced by the DD), the outcomes are quite random and different across simulations (and thus quite different than what your neighbor is seeing on their computer).
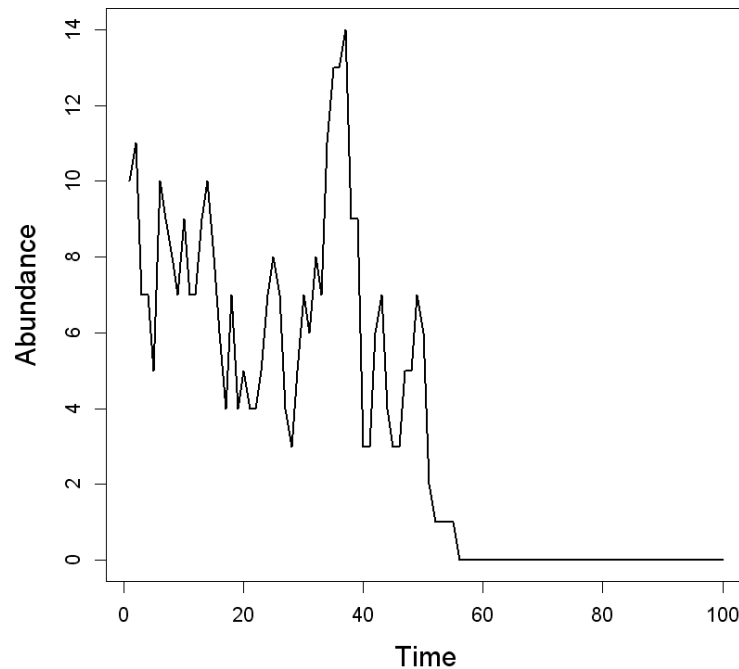
2. Obtain a formula for the deterministic equilibrium of the house sparrow model in the absence of demographic stochasticity, but in the presence of density dependence (N*).

To attain the solution we start with $N(t+1) = N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}$, then replace all values of N with N*, the equilibrium abundance, $N^* = N^*(s_{0,low}f + s_{1,low})e^{-bN^*}$. We then solve for N*

$N^* = \frac{1}{b}\log(s_{0,low}f + s_{1,low}) = \frac{\log(\lambda_{max})}{b}$. Note that $\lambda_{max} = s_{0,low}f + s_{1,low}$.

3. The population size conditional on non-extinction is distributed as the "Quasi-Stationary Distribution", and the stochastic equilibrium mean is denoted as lim E(Nt+1/ Nt >0). Part two of the code has lines of code to estimate moments (e.g., the mean) of the Quasi-Stationary Distribution, extinction probabilities, and extinction times (also conditional on E[N] > 0) across 10,000 simulations. Inspect and then run part two of the code to attain estimates of each of these 'population viability' parameters over 100, 200, 300, and 400 years.

Because of the use of loops, the code takes quite a while to run. The loops explicitly show you the demographic and probabilistic process but there are ways to not depend on loops and significantly speed up the computation. Below are the results passed from R.

sumtable
```
      [,1]    [,2]     [,3]
[1,] 0.8716 39.54234  9.85493
[2,] 0.9890 51.09909 10.63333
[3,] 0.9987 51.98488 12.33333
[4,] 1.0000 53.16040     NaN
```

4. Using what you have learned above, and the third piece of code, complete rows 1-4 in the table below by manually changing the vital rate values to those specified in the table. Each time you change a vital rate, re-run the entire third piece of code (it takes time to run).

$s_{0,low}$	$s_{1,low}$	λ_{max}	Deterministic equilibrium N^*	Cumulative Pr(extinction) over 1000 time steps	Stochastic equilib. lim $E(N_{t+1} / N_t{>}0)$
0.20	0.50	1.1	9.53	1	Not defined
0.25	0.50	1.25	22.31	0.5152	19.9
0.30	0.50	1.4	33.65	0.0028	32.2
0.30	0.60	1.5	40.55	0.0002	39.3
Beta(18.5,55.5)	0.50	1.25	22.31	0.7582	19.3

5. Given an infinite time horizon, what would be the overall probability of extinction in each scenario above? For the mathematically inclined: Why is the stochastic equilibrium smaller than the deterministic equilibrium?

Given an infinite time horizon, the overall probability of extinction is always = 1; all populations will eventually go extinct. However, the probability of extinction over a finite time horizon does vary markedly, as does its complement, the probability of reaching the quasi-stationary distribution.

For the math-stat fans, the stochastic equation is $E[N(t+1)] = N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}$, which implies $E[N(t+1)] = E[N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}]$. When $N(t)$ is distributed as the QSD and P is the probability of extinction in one time step, then $E[N(t+1)] = (1-P)E[N(t)]$; the population goes extinct with probability P or transitions to a new population size distributed according the QSD with probability $1-P$. By Jensen's inequality, the convexity of the model function $\lambda_{max} xe^{-bx}$ in the domain considered is such that $E[N(t)](s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > E[N(t)(s_{0,low}f + s_{1,low})e^{-bN(t)}]$, and hence $E[N(t)](s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > (1-P)E[N(t)]$. This implies that $(s_{0,low}f + s_{1,low})e^{-bE[N(t)]} > 1$ because the variance of the QSD makes the effect of the convexity much larger than that of P.

Then $(s_{0,low}f + s_{1,low})e^{-bE[N(t)]} < 1 = (s_{0,low}f + s_{1,low})e^{-bN^*}$ which finally implies for the QSD mean taht $E[N(t)] < N^*$.

6. Given the effect of λ_{max} on the risk of extinction over a finite time horizon, what do you think about the concept called the "extinction vortex"?

From the table above, the shift in extinction probabilities over a finite time horizon is very sharp with the change in λ_{max}, and nearly creates a sharp borderline between populations rapidly doomed to extinction and those for which the probability of extinction is very small or even negligible, so the vortex may largely result from the fact that a population is on one side or the other of the borderline. This result does not imply that other factors contributing to accelerated extinciton in small populations (e.g., Allee effects) should be neglected.

7. What happens when $s_{0,low}$ is additionally subject to random environmental variation? Keep $s_{1,low}$ at 0.5 and replace the numerical value for $s_{0,low}$ in the R code with "rbeta(1,18.5,55.5)", which specifies a Beta distribution for the environmental stochasticity in $s_{0,low}$ with a mean of 0.25 and variance of 0.0025. Then re-run part three of the code and complete row 5 of the table in problem 4 (note: you just need to un-comment a line of code within the time loop and comment out the original line for $s_{0,low}$).

The population abundance varies quite a bit, and the risk of extinction over 1000 years increases notably (shown in the last line of the Table for problem 4 above). As a result of the larger variance of population size, the average number of individuals in the QSD is even smaller than in the absence of random environmental variation. The combined effects of environmental and demographic stochasticity on population viability can be biologically significant for small populations of conservation concern.

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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.

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