February 12, 1999

FW 662 Midterm Exam

This exam is a take-home, open-book exercise. There are 3 questions; you must answer all of them, including multiple parts. You may use any reference material (class notes, assigned reading, library material, etc.). Under NO circumstances are you to discuss this exam with classmates or any other individual. You are to work independently and you should not confer with others. If you need clarification on a question, please see the instructor, or send email with your question to gwhite@cnr.colostate.edu . This exam is to be turned in by 8:00 am Monday, 15 February, at the start of class. Turn in this sheet with your written answers and a disk that holds the spreadsheet models on which your answers are based. All questions require a written answer. In addition, some questions also require you to provide a spreadsheet demonstrating how you obtained your answer. Typed, short, concise answers will be graded more generously than hand-written, long, rambling responses. Your spreadsheets on a disk will be used to verify that your answers were obtained in a logical fashion, and provide you with partial credit in cases where you got the wrong solution, but just made a simple mistake in the spreadsheet. **Identify your answer sheets and disks with your SSN only.** Only put your name (via your signature) on this sheet.

By my signature below, I certify that I have not collaborated with anyone concerning any material related to this examination.

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SSN Signature Date

1. For an extensively-studied mule deer population, adult female over-winter (1 December until 15 June) survival averages 0.853, and over-winter fawn survival averages 0.444. Assume that no additional mortality occurs in adult females from the period 15 June until 1 December. No hunting mortality was inflicted on the female and fawn portions of the population during the time period of interest. Fawns per 100 adult females during the last 20 years follows the function:

$$\text{fawns/100 adult females} = 2952.8 - 1.4543 \times \text{year}\ ,$$

where year is from 1978 to 1998. This relationship was developed from helicopter surveys during December of each year.

Biological background. Mule deer are born approximately 15 June each year. Mule deer do not have fawns until their second birthday, and animals that are 1 year and 6 months old during the December counts cannot be distinguished from older animals. Thus, the December ratios of fawns per 100 does provide the newly produced animals in terms of all animals in the population, not just the animals that actually had young.

A. (25 pts) In what year did the population's rate of increase decline to 0, i.e., in what year did $\lambda = 1$? Describe how you answered this question, and provide me with your spreadsheet on a disk that you used to perform the calculations.

B. (15 pts) What assumptions did you have to make to obtain this estimate?

C. (15 pts) Nobody believes that adult and fawn survival is constant as described above. Estimates of temporal variation of this population are: adult female survival mean = 0.853, SD = 0.034; fawn over-winter survival mean = 0.444, SD = 0.217; with fawns/100 does assumed to have no temporal variation (other than the linear function given above) for the purposes of this question.. How would your conclusions about the year that $\lambda = 1$ change from part A above if you put this level of temporal variation in your model? Even if the mean value of λ is close to 1, does the population maintain itself? Again provide me with the spreadsheet you used to generate your answer. If you are unable to incorporate this temporal variation into your model, at least speculate on what you think the effect of temporal variation will be.

D. (5 pts) No demographic variation has been incorporated into either of your models. Do you think that demographic variation is needed to answer this question? Why or why not.

2. One group of researchers published an article on the decline of northern spotted owls. They based their conclusion that the population was declining at the rate of $\lambda = 0.809$ per year on the following Leslie matrix for the female segment of the population:

$$\underline{L} = \begin{bmatrix} 0 & 0 & 0.25 & 0.25 & 0.25 \\ 0.83 & 0 & 0 & 0 & 0 \\ 0 & 0.83 & 0 & 0 & 0 \\ 0 & 0 & 0.83 & 0 & 0 \\ 0 & 0 & 0 & 0.83 & 0 \end{bmatrix}$$

The parameter values they used were adult survival = 0.83, juvenile survival (from fledgling until 1-year old) = 0.25, and 1 female chick per nest. A second group published their model of owl population dynamics based on the same parameter estimates as the first group. However, they concluded that the population was only declining at the rate of $\lambda = 0.958$ per year. They also used a Leslie matrix:

$$\underline{L} = \begin{bmatrix} 0 & 0 & 0.25 & 0.25 & 0.25 & 0.25 & 0.25 & 0.25 & 0.25 & 0.25 \\ 0.83 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.83 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.83 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.83 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.83 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.83 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.83 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.83 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.83 & 0 \end{bmatrix}$$

A.(15 pts) Were the λ values published by each group correct? Use a spreadsheet to substantiate your answer, and provide me with the spreadsheet. If both groups were correct, how do you reconcile the differences in their estimates of λ?

B.(10 pts) What would you estimate as the correct value of λ? In other words, construct your own Leslie matrix model for this population. Provide your solution on a disk.

C.(5 pts) Are these matrices based on a pre-birth census or a post-birth census? Why?

3. (10 pts) Do the following Leslie matrices produce the same value of λ if $S_1 = S_2 = S_3$? Show your reasoning.

$$\begin{bmatrix} S_0 b_1 & S_1 b_2 & S_1 b_3 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_1 \end{bmatrix} \qquad \begin{bmatrix} S_0 b_1 & S_1 b_2 & S_2 b_3 & S_3 b_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & S_3 \end{bmatrix}$$

Helpful hints:

For the beta distribution,

mean = $\dfrac{\alpha}{\alpha + \beta}$, variance = $s^2 = \dfrac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)}$, mode = $\dfrac{\alpha - 1}{\alpha + \beta - 2}$ for $\alpha \geq 1$.

Given a mean (μ) and standard deviation (s),

$\alpha = \dfrac{-\mu(\mu^2 - \mu + s^2)}{s^2}$, and $\beta = \dfrac{(\mu - 1)(\mu^2 - \mu + s^2)}{s^2}$.

February 17, 1999

FW 662 Midterm Exam – Answers

1. A. Year was 1984.861, obtained by optimizing the spreadsheet to get a value of the year that made lambda exactly 1. I got this value by removing male fawns after their first year, i.e., only putting female yearlings into the population. Most of you didn't do the optimization that I show in my answer, but just modeled fawn ratios as th linear function I gave you, and picked out the year when λ became <1. This approach is okay as long as your model had reached stable age distributions before $\lambda < 1$.

B.

1. System is assumed to not change from 1978-1998, e.g., no habitat changes that would change survival.
2. Deterministic, no process stochasticity (individual heterogeneity, temporal, spatial, or demographic).
3. No senility of older adults, in either reproduction or survival
4. No age-specific reproduction.
5. Density-independent, i.e., no density dependence, so that parameters are assumed to stay the same regardless of population density.
6. Closed population, i.e., no immigration or emigration.
7. Sex ratio of fawns is assumed to be 50:50.
8. No time lags built into the model.

I usually took off a few points on this answer, just because I don't want too many perfect scores on my tests. Ruins my reputation!

C. This question wasn't as clear as I thought. When you incorporated temporal variation into the model with a beta distribution, λ bounces all around, as it should, so you couldn't give a definitive answer. As long as you built the model correctly, I gave you full credit. I built a stochastic model with the exact fawn:doe ratio (0.662162) that gives $\lambda = 1$ for the deterministic model, and then ran the model for 1000 years. By incorporating temporal variation into the model, the average of λ for 1000 years is still close to one. However, the population always declines, because a down-swing in the population causes a larger absolute change in size than a corresponding up-swing of the same relative magnitude. That is, a 10% decrease is not equivalent in absolute numbers of animals to a 10% increase. Temporal variation causes the population to decline, even with the average $\lambda = 1$. This latter interesting phenomena is what I wanted this question to get at, but I missed my mark.

D. The need for demographic variation in the model will depend on the population size at the start of the time frame to be modeled. If the population size is in the thousands, demographic variation would not be important. However, if the population size is <100, then demographic variation should be incorporated. The actual size of the population in this question is not specified, so a definitive answer cannot be given.

2. A. Both groups reported the correct λ for the Leslie matrix they gave. However, group 1 is assuming that all adults die after reproducing at age 5. Group 2 assumes all adults die after reproducing at age 10. Neither of these models is realistic.

B. The correct value of λ based on the information given in the problem is 1.0017, based on the following matrix:

$$\underline{L} = \begin{bmatrix} 0 & 0 & 0.25 \\ 0.83 & 0 & 0 \\ 0 & 0.83 & 0.83 \end{bmatrix}$$

Adults are not all assumed to die after a set age that is dictated by the size of the matrix, but rather continue in the population with a 0.83 survival rate indefinitely. That is, I applied the Lefkovitch "corner trick", and this is what I was expecting. Some of you incorporated demographic stochasticity (which was okay), but some of you incorporated temporal stochasticity without any idea of what variability was reasonable. Another common misconception was to extend the group 2 matrix a bunch more years, like to 17 age classes to supposedly achieve a model where the mean life span is 17 years. The error in this thinking is that mean life span is not equal to the number of age classes in the model. Mean life span is -1/ln(S), which for S=0.83 gives 5.4 years, even with the Lefkovitch matrix shown above. Notice that by 5 years, only 39% of the birds starting the cohort are still alive, i.e., $0.83^5 = 0.394$.

C. Pre-birth. The age of animals in the first element of the population vector is 1 year old, just prior to reproduction. Survival rates in the top row are juvenile survival rates. The first survival rate in the second row is an adult (actually yearling) survival rate.

3. Yes. In the smaller matrix, all animals over 2 years of age reproduce with rate b_3, and survive with rate S_1. If S_2 and S_3 are replaced with S_1 in the larger matrix, then all animals over 2 years of age will also reproduce with rate b_3, and survive with rate S_1. Thus, the matrices would produce the same results. Many of you plugged in values in spreadseet models, which was okay. Note, however, you have to be smart about what values you plug in. If you used zeros for any of the parameters, you could get into big trouble. Don't use "nice" values when you want to test for differences in 2 matrices by plugging in numerical values. If you want to get sophisticated, you can show that both matrices have the characteristic polynomial

$$b_1\lambda S_0(\lambda - S_1) + b_2 S_0 S_1(\lambda - S_1) + b_3 S_0 S_1^2 - \lambda^2(\lambda - S_1),$$

although I have not been able to solve for the analytic expression for λ because it is a cubic equation that has a nasty formula for its roots..