February 14, 1997

FW 662 Midterm Exam

This exam is a take-home, open-book exercise. There are 3 questions; you must answer all of them. 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. Your are to work independently and you should not confer with others. If you need clarification on a question, please see the instructor. This exam is to be turned in by 8:00 am Monday, 17 February, at the start of class. Turn in this sheet and the test questions with your answers, plus a disk with your computer solutions. Typed, short, concise answers will be graded more generously than hand-written, long, rambling responses. **Identify your answer sheets 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.

SSN	Signature	Date

1. (50 pts) Based on a 3-year radio-tracking study, David Freddy, Colorado Division of Wildlife researcher, has estimated the following values for an elk population in western Colorado.

Parameter	Value
Total Post-hunt Population Size in 1996	3700.00
Adult Male (24+ mos old) Summer-Fall Survival	0.99
Yearling Male (12-18 mos old) Summer-Fall Survival	0.99
Adult Female (24+ mos old) Summer-Fall Survival	0.99
Yearling Female (12-18 mos old) Summer-Fall Survival	0.99
Calf (0-6 mos old) Summer-Fall Survival	1.00
Adult Male (30+ mos old) Winter-Spring Survival	0.98
Yearling Male (18-24 mos old) Winter-Spring Survival	0.98
Adult Female (30+ mos old) Winter-Spring Survival	0.97
Yearling Female (18-24 mos old) Winter-Spring Survival	0.99
Calf (6-12 mos old) Winter-Spring Survival	0.90
Yearly Harvest %Rate Adult Males (24+ mos old)	0.80
Yearly Harvest %Rate Yearling Males (12-18 mos old)	0.10
Yearly Harvest %Rate Adult Females (24+ mos old)	0.10
Yearly Harvest %Rate Yearling Females (12-18 mos old)	0.10
Yearly Harvest %Rate Calves (0-6 mos old)	0.00
Calf Sex Ratio At 1 December Recruitment %Female	0.50

Post-season Sex/age Ratio Composition in 1996	
Adult Males >=2+ years	0.024
Yearling Males =1+ years	0.094
Adult and Yearling Females	0.588
Calves	0.294
Total	1.000

Note that calf survival is assumed to be 1 from June until the December age ratio of 0.294 calves per 0.588 adult and yearling females is measured (giving a recruitment rate of 50 calves per 100 adult and yearling females). This assumption is the same as used in the mule deer spreadsheet, i.e., that new animals are "born" into the population in December, when they are already 6 months old.

Develop a population model from these data, and answer the following questions. Turn in your population model on a disk so that I can examine it to determine how you answered these questions.

A. (10 pts) At what rate is the population increasing annually? Provide the spreadsheet model that computes your answer. So that you get off on the right track for parts B and C, I'll give you the numerical answer: $\lambda = 1.06809$.

B. (10 pts) At what rate do the adult and yearling females have to be harvested to hold this population stationary?

C. (20 pts) Biologists are worried that heavy female harvest will lower the mean age of the population, with a result of increased recruitment because of more "prime age" females.. To examine this question, estimate the stable age ratio for the population with enough female harvest to hold the population stationary and without any female harvest. Provide your estimates of the proportion of females aged 1 ½, 2 ½, 3 ½ - 8 ½, and ≥9 ½ for each of these models.

D. (10 pts) Discuss what you speculate will happen with this population if harvest rates are kept at the current levels.

2. (30 pts) The following data were collected on the Fraser River chum salmon population. Values are in thousands of fish.

Year	Spawners	Recruits
1961	164	236
1962	180	468
1963	325	1293
1964	185	579
1965	430	925
1966	212	325
1967	822	1933
1968	390	1434
1969	303	534
1970	356	361
1971	579	1239
1972	453	653
1973	565	1210
1974	235	386

Fit the Ricker equation in the form

$$R = aS\exp(-bS)$$

to the observed data. Answer the following questions about these data and your model.

A. (5 pts) What is K in terms of the parameters a and b? Provide an analytical solution and show your work.

B. (15 pts)What are your estimates of a and b for these data? Provide your computer model on disk as will as your written description of how you did the estimates.

C. (10 pts) Do these data support density dependence? Explain why or why not, and discuss how you might strengthen this conclusion about density dependence if you were responsible for managing this population.

3. (20 pts) The Denver Zoo has decided to develop an onager exhibit in one of the large corrals available. Onagers are difficult to maintain because they become very aggressive towards other after 2 years of age. Hence, the decision is made to remove all animals from the exhibit 6 months after their second birthday, when their offspring (if any) can survive on their own. Further, all males are removed after they are 6-months old, and one mature male is provided each year for breeding purposes. New-born animals are assumed to survive with probability 0.77 to their first birthday, and then with probability 0.95 to their second birthday. Females give birth to 1 offspring on their first birthday with probability 0.9, and to 2 offspring on their second birthday with 0.95. Otherwise, they have no foals. The probability that a foal is female, and hence stays in the exhibit is 0.5. Assume that the zoo buys 5 females aged 1-year old, and 4 of them have foals.

Note: onagers really don't ever have 2 foals, but I had to make the question fit the problem.

Again, provide your computer model on a disk so that I can see how you computed your solutions.

a. (10 pts) What is the expected population size of females in the exhibit in 20 years from the day of the first introduction?

b. (10 pts) What is the probability that the zoo will have onagers in the exhibit in 20 years from the day of the first introduction?

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The spreadsheet `answers.wb2` provides solutions to all the problems on this midterm.

1. This problem was difficult because there were 3 sources of mortality: Spring-Fall, Harvest, and then Winter-Spring. You have to keep the different sources straight for each age class. To set up the difference equations, create the following table at the top of your spreadsheet.

Age-Sex Class	Spring-Fall Survival	Harvest Rate	Winter-Spring Survival
Calves			$S_{WS,C}$
Yearling Females	$S_{SF,YF}$	H_{YF}	$S_{WS,YF}$
Adult Females	$S_{SF,AF}$	H_{AF}	$S_{WS,AF}$
Yearling Males	$S_{SF,YM}$	H_{YM}	$S_{WS,YM}$
Adult Males	$S_{SF,AM}$	H_{AM}	$S_{WS,AM}$

Define the following population classes:

Calves	N_C
Yearling Females	N_{YF}
Females Aged 2 ½	N_{2F}
Females Aged 3 ½	N_{3F}
Females Aged 4 ½	N_{4F}
Females Aged 5 ½	N_{5F}
Females Aged 6 ½	N_{6F}
Females Aged 7 ½	N_{7F}
Females Aged 8 ½	N_{8F}
Females Aged 9 ½ and older	N_{9F}
Yearling Males	N_{YM}
Adult Males	N_{AM}

The reason I'm defining all these adult female age classes is to be able to answer part C of the question, i.e., I want to be able to calculate the age ratios.

Next, register strongly in your mind that you want the census time for the population to be 1 December, after the harvest, but before the winter mortality period. The N_C animals are the newly recruited calves.

Now, start setting up the difference equations. First lets increment all the ages before we try to set up the reproduction. Start with female calves that will become yearling females. Apply the over-winter survival rate of calves ($S_{WS,C}$), times the sex ratio (0.5 females) times the spring to fall survival of yearling females ($S_{SF,YF}$) times the probability of not being harvested (1 - H_{YF}). Note that the spring to fall survival is not for calves, but for yearlings. They had their first birthday in the spring. The spring-fall survival is for yearlings, as is the fall harvest rate,

$$N_{YF}(t+1) = N_C(t)\ S_{WS,C}\ 0.5\ S_{SF,YF}\ (1 - H_{YF}).$$

The nearly identical equation works for yearling males, but with 1 minus the proportion of calves that are female:

$$N_{YM}(t+1) = N_C(t)\ S_{WS,C}\ (1 - 0.5)\ S_{SF,YM}\ (1 - H_{YM}).$$

To increment yearling females to 2 ½ years old, we again apply the over-winter survival rate ($S_{WS,YF}$) times the spring-fall survival rate of adults ($S_{SF,AF}$ — remember, they just had a birthday) times the probability of surviving the harvest (1 - H_{AF}), giving

$$N_{2F}(t+1) = N_{YF}(t)\ S_{WS,YF}\ S_{SF,AF}\ (1 - H_{AF}).$$

Similarly, for 3 ½ year-old females,

$$N_{3F}(t+1) = N_{2F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}),$$

and so forth for females up to 8 ½ years old:

$$N_{4F}(t+1) = N_{3F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}),$$

$$N_{5F}(t+1) = N_{4F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}),$$

$$N_{6F}(t+1) = N_{5F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}),$$

$$N_{7F}(t+1) = N_{6F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}), \text{ and}$$

$$N_{8F}(t+1) = N_{7F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}).$$

For 9 ½ years old and older, females in $N_{9F}(t)$ are included, using Lefkovitch's method of limiting the number of age classes:

$$N_{9F}(t+1) = [N_{8F}(t) + N_{9F}(t)]\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF}).$$

Adult males don't require all the age classes that I've constructed above for females, because we're not interested in their age structure as part of question C. Thus, yearling males at time *t* are moved into the adult male age class at time *t*+1 with yearling male winter-spring survival, and adult males at time *t* are also continued into the adult male age class at time *t*+1 with adult male winter-spring survival. However, once the animals have their birthday in the spring, both groups undergo adult male spring-fall survival and then adult male harvest rates. The following equation defines this operation:

$$N_{AM}(t+1) \;=\; [N_{YM}(t)\; S_{WS,YM} \;+\; N_{AM}(t)\; S_{WS,AM}]\; S_{SF,AM}\; (1 \;-\; H_{AM}).$$

Now comes the trickiest part. New animals are entered into the population as calves after the hunting season based on a ratio of 0.5 (=0.294/0.588) calves per adult <u>and</u> yearling female. In other words, the number of calves is 0.5 times the number of yearling and adult females. Thus, the equation for calves is

$$N_C(t+1) \;=\; 0.5\;[N_{YF}(t+1) \;+\; N_{2F}(t+1) \;+\; N_{3F}(t+1) \;+\; N_{4F}(t+1)$$
$$+\; N_{5F}(t+1) \;+\; N_{6F}(t+1) \;+\; N_{7F}(t+1) \;+\; N_{8F}(t+1) \;+\; N_{9F}(t+1)].$$

I used the numbers of yearling and adult females at time *t*+1 because that is how reproduction was defined in the problem. Yearlings don't actually have calves, but because observers can't reliably tell yearling females from adult females when determining calf:cow ratios, yearlings are included in the ratio.

Once you program these equations into a spreadsheet, you're ready to answer the questions.

A. You should get λ = 1.06809 with the above model. If you don't, something is wrong with your spreadsheet model.

B. By adjusting the adult and yearling female harvest (assuming that they are the same — something I didn't make clear in the question), you should find that $H_{YF} \;=\; H_{AF} \;=\; 0.157375$, or 15.74% harvest is needed to achieve λ = 1. You can't specify a different harvest rate for yearling females from adult females because hunters can't tell them apart. You could argue that one age class is more vulnerable, and hence has a higher harvest rate, but this argument is not well supported with observed harvest data. A question for discussion: design an experiment to detect this possible difference in vulnerability.

C. To obtain the requested age ratios (yearlings, 2 ½, 3 ½ - 8 ½, and 9 ½ and more), you have to sum the 3 ½ - 8 ½ classes. First, set the harvest rate in your model for adult and yearling females to zero. Compute the total number of females for your last year, where the age structure is stationary. Use this total to compute the proportion of the total that each age class comprises. Then, do the same thing when you set yearling and adult female harvest back to 0.1573 to simulate the second part of the question. The results for both harvest levels are identical:

Age Class	$H_{YF} = H_{AF} = 0$	$H_{YF} = H_{AF} = 0.1574$
Yearlings	0.1877	0.1877
2 ½	0.1550	0.1550
3 ½ - 8 ½	0.4728	0.4728
9 ½ and older	0.1845	0.1845

This result seems a little counter-intuitive until you think about how the harvest is implemented. That is, harvest is equal for all these age classes. Thus, we reduce each age class by exactly the same proportion. The result is that age ratios do not change. This would not have been the case if we had not used the Lefkovitch method, and thus allowed senility in the model, or if you allowed different yearling and adult female harvest rates.

D. Your model is predicting that the population will grow to infinity. Obviously, this can't happen. You might suggest 2 different scenarios. First, the population will grow to some level, where food resources are completely exhausted, and then the population will crash. The second scenario is that density-dependence will continue to have a stronger effect, and a decline in reproduction and an increase in calf mortality will eventually cause the population to stop growing. I would bet on the second option. However, before carrying capacity is reached, the Colorado Division of Wildlife will be broke from paying game damage claims.

2. A. Remember that the number of spawners (*S*) equals the number of recruits (*R*) at *K*. Substituting *K* for both *S* and *R* gives $K = aK\exp(-bK)$. The solution for *K* has 2 answers, *K* = 0 is trivial, and $K = \log(a)/b$.

B. You needed to construct a spreadsheet model to estimate the parameters *a* and *b* from the observed data. If you assumed normally-distributed residuals, you got the estimates $\hat{a} = 2.1459$ and $\hat{b} = -7.4E{-5}$, with SSE = 1079983. If you assumed lognormally-distributed residuals, you got the estimates $\hat{a} = 1.9348$ and $\hat{b} = -0.00018$, with SSE = 1.9277.

C. These data do not support density-dependence because the parameter *b* is not different than zero. Construct an *F* test with 1 and 12 degrees of freedom. The reduced model is the Ricker equation with *b* = 0. For lognormally-distributed residuals, the *F* statistic is 0.087, with *P* = 0.773. Thus, there is no evidence of a decline in number of recruits per number of spawners. Further, looking at the graph of recruits versus spawners does not suggest any tendency for the data to "tip over". To really test this hypothesis, managers need to let the population grow to higher levels, where density dependence might be observed.

3. A. I didn't clarify that the 4 foals were all meant to be females. Hence, I accepted different answers depending on how you classified the foals. One way to compute the mean population size after 20 years is to use a deterministic Leslie matrix model. Depending on how you treated the 4 foals, you get the following answers:

Scenario	Male foals not counted	Male foals counted
4 foals = 2 females	15.36	21.64
4 foals = 4 females	20.16	28.40

I accepted the above answers. However, one of the purposes of the question was to demonstrate to you that the estimate based on a deterministic model is greater than the mean of a large number of stochastic simulations. This result is because of Jensen's Inequality, $E[f(x)] \leq f(E[x])$. That is, the expected value of a complicated function where the parameters are random variables is less or equal to the expected value of the parameters plugged into the function. In this case, our complicated function is a Leslie matrix, and x is the vector of population growth parameters. However, as it turns out, the demographic stochasticity is not enough to cause the < part of the inequality to be true. As I show below, the stochastic model generates exactly the same answer.

B. To determine the probability that the zoo would have onagers in the exhibit after 20 years, I expected you to develop a Leslie Matrix model with demographic stochasticity. You had to assume that temporal stochasticity and individual heterogeneity were negligible, especially because I didn't give you any values to work with. The easiest approach incorporating demographic stochasticity was to assume that survival rates, reproductive rates, and sex ratios were all binomially distributed. Many of you didn't allow the sex ratio to be stochastic, so ended up with fractions of animals. Seeing half an onager in your model should have made you think twice — how can a binomial distribution handle half an animal?

Define the 3 age classes: N_0, N_1, and N_2 for young, 1-year-olds, and 2-year olds. The following parameters are needed:

Parameter	Description	Value
S_0	Probability of survival from birth to 1 year old	0.77
S_1	Probability of survival from 1 year old to 2 years old	0.95
B_1	Probability of giving birth to 1 foal on first birthday	0.9
B_2	Probability of giving birth to 2 foals on second birthday	0.95
R	Probability of a foal being female	0.5

Now, define the deterministic model first. Assume an after-birth census. The number of females reaching their first birthday is

$$N_1(t+1) = N_0(t)\ S_0\ R,$$

and the number of animals reaching their second birthday is

$$N_2(t+1) = N_1(t)\ S_1.$$

The number of new-born foals in the exhibit is

$$N_0(t+1) = B_1\ N_1(t+1) + 2\ B_2\ N_2(t+1),$$

where animals just having their first birthday give birth to 1 foal with probability B_1 and animals just having their second birthday give birth to 2 foals with probability B_2. Hence, the value 2 in the second part of the equation. This equation predicts the total number of foals, both male and female. Males are removed before they become 1 year old.

For this model, λ = 1.0246.

Now, add demographic stochasticity. Where each of the parameters are multiplied times a population size, (including *R*) a binomial process is assumed. In Quattro, the `@CRITBINOM` function is implemented. The model now generates 1 realization of the stochastic process. To answer the question, you need to generate ~100 realizations, and compute the proportion of times the model predicted no onagers left in the exhibit. For the case of 4 foals being female, and males not included in the exhibit count, I found a mean number of 20.157 (SE = 0.006) for 10,000,000 realizations of the process. The probability of onagers still in the exhibit was 82.4% (SE = 0.00012). I used a SAS code to do this — spreadsheets are too cumbersome to do that many simulations.

Two take-home messages from this problem.

1. Jensen's Inequality — didn't happen to make a good demonstration here, but we'll see cases where it makes a big difference.

2. Even though the deterministic model says λ = 1.0246, the probability of extinction is still 17.6%. Thus, with stochastic models, positive population growth does not always result in zero probability of extinction.

Age-Sex Class	**Spring-Fall Survival**	**Harvest Rate**	**Winter-Spring Survival**
Calves			$S_{WS,C}$
Yearling ♀	$S_{SF,YF}$	H_{YF}	$S_{WS,YF}$
Adult ♀	$S_{SF,AF}$	H_{AF}	$S_{WS,AF}$
Yearling ♂	$S_{SF,YM}$	H_{YM}	$S_{WS,YM}$
Adult ♂	$S_{SF,AM}$	H_{AM}	$S_{WS,AM}$

Assume after-birth census on December 1.

$$N_{YF}(t+1) = N_C(t)\ S_{WS,C}\ 0.5\ S_{SF,YF}\ (1 - H_{YF})$$

$$N_{YM}(t+1) = N_C(t)\ S_{WS,C}\ (1 - 0.5)\ S_{SF,YM}\ (1 - H_{YM})$$

$$N_{2F}(t+1) = N_{YF}(t)\ S_{WS,YF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{3F}(t+1) = N_{2F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{4F}(t+1) = N_{3F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{5F}(t+1) = N_{4F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{6F}(t+1) = N_{5F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{7F}(t+1) = N_{6F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{8F}(t+1) = N_{7F}(t)\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$N_{9F}(t+1) = [N_{8F}(t) + N_{9F}(t)]\ S_{WS,AF}\ S_{SF,AF}\ (1 - H_{AF})$$

$$\begin{aligned} N_{AM}(t+1) = {} & [N_{YM}(t)\ S_{WS,YM} + N_{AM}(t)\ S_{WS,AM}] \\ & \times S_{SF,AF}\ (1 - H_{AF}) \end{aligned}$$

$$\begin{aligned} N_{C}(t+1) = 0.5\ [& N_{YF}(t+1) + N_{2F}(t+1) + N_{3F}(t+1) \\ & + N_{4F}(t+1) + N_{5F}(t+1) + N_{6F}(t+1) \\ & + N_{7F}(t+1) + N_{8F}(t+1) + N_{9F}(t+1)] \end{aligned}$$