

**Problem set 1.** You may work in groups of up to 3 students. If you work in a group, turn in *one* set of answers with your group members listed and be sure that everyone agrees on the answers. Each person should understand how to reach the answer – you will work individually on the exam. Type or write legibly. You may e-mail a document with your answers or turn in a printed copy with the pages stapled together. Show how you obtain your answers; e.g., show the steps needed to find the answer and, when used, R code. Due by the start of class **Thursday, February 2.**

### Exponential growth:

1. A biologist counts 11.1 duckweed plants per m<sup>2</sup> on the surface of a pond at the beginning of summer. Twenty days later, there are 23.5 plants per m<sup>2</sup>. Assuming that the population is growing exponentially, what will the density of plants be after another 27 days (i.e., 47 days after the original count)?

2. The estimated population of Mexico (in 2015) is 121,005,000 growing at a rate of approximately 1.2% per year. The population of Ethiopia is 90,076,000 growing at a rate of 2.9% per year. Assuming that the population of each country grows exponentially at these rates, in what year will the population of Ethiopia reach that of Mexico?

3. Population growth can be modeled by the discrete difference equation:

$$N_T = \lambda^T N_0$$

(a) Assume that  $\lambda = 1.037$  per year, and that the original density is  $N_0 = 112$ . What will the population density be after seven years?

(b) What value of  $r$  produces the same result (the same population density at  $T = 7$ ) for the exponential growth equation in continuous time?

4. The numbers of collared doves in monitored for years its arrival in Great Britain.

Year	number
1955	4
1956	16
1957	45
1958	100
1959	205
1960	675
1961	1900
1962	4650
1963	10200
1964	18885

The data are from: Hengeveld, R. 1988. Mechanisms of biological invasions. Journal of Biogeography:819-828.

How closely can this increase be approximated by the exponential growth equation? Estimate the value of  $r$  from the numbers above. To do this, recall that  $r$  can be estimated as the slope of a plot of  $\ln(N)$  versus  $t$ . In R, `log()` finds the natural logarithm of a number and `lm(y ~ x)` fits a linear regression to a set of  $x$  and  $y$  values, yielding an estimate of the slope.

Plot  $\ln(N)$  versus time for this data set and calculate what the population sizes would be in each year, assuming exponential growth, given an initial size of 4 individuals in 1955 and the value of  $r$  estimated by regressing  $\ln(N)$  against year.

### Life tables and projection matrices:

5. Here is a life-table for females of an imaginary mammal:

Age in years ( $x$ )	$S(x)$	$b(x)$
0	740	0
1	280	0.4
2	105	1.3
3	32	3.8
4	0	

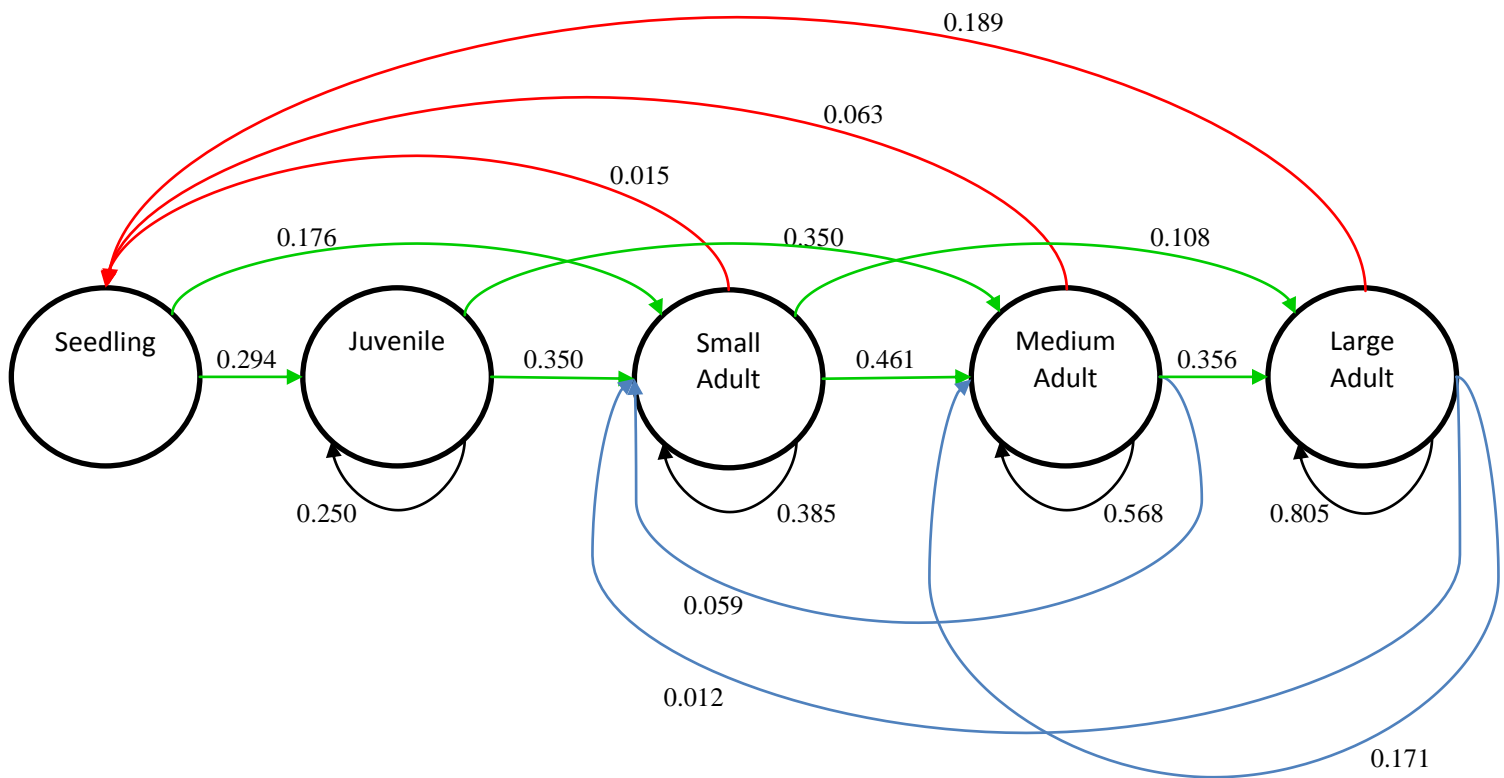
Calculate  $l(x)$  and  $g(x)$  for all age classes; also,  $R_0$ , and  $G$ .

6. Imagine a population of the mammal whose life table you generated in problem 6. Suppose that at the start of one year, there are 70 new-born females, 40 females that are one year old, 20 females that are two years old, and 10 females that are three years old. Construct the Leslie matrix for this population and project the number in each age class for the next two years.

7. For this question, you will need to install the `popbio` package for R on your computer. Instructions for doing are on the course web site. (See “Matrices in PopBio.pdf”). Follow the example, then create a new projection matrix to match the loop diagram shown below, which summarizes demographic rates for *Prunella vulgaris*, an understory plant studied in an English forest.

Valverde, T., and J. Silvertown. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology* 86:545-562.

Notice that red arrows represent fecundity values, green arrows represent probabilities of growth to a larger size class, black arrows represent probabilities of remaining in the same size class, and blue arrows represent probabilities of transition to a smaller size class.



Use the popbio package to answer the following:

- What is the value of  $\lambda$ ?
- What is the stable-age distribution for this population?
- Calculate the sensitivities and elasticities of  $\lambda$  to the matrix elements. For which demographic value is the elasticity of  $\lambda$  the greatest?
- If the fecundities of the adult trees (of all sizes – the values indicated by the red arrows) are cut in half, how do the value of  $\lambda$  and the stable age distribution change?
- If the probabilities that the adult trees stay in the same size-class (for all sizes – the values indicated by the black arrows) are cut in half, how do the value of  $\lambda$  and the stable age distribution change?

### Probability of extinction in stochastic models

8. For a population undergoing exponential growth with demographic stochasticity, the probability of extinction can be estimated by

$$P(\text{extinction}) = \left( \frac{d}{b} \right)^{N_0}$$

where  $d$  = the per capita death rate,  $b$  = the per capita birth rate, and  $N_0$  = the initial population size (Gotelli. 2008. A Primer of Ecology. 4<sup>th</sup> edn. Sinauer: Sunderland, Mass.)

Thus, for a population with  $d = 0.5$  and  $b = 0.55$ , the probability of extinction is  $(0.5/0.55)^{10} = 0.386$  if the initial population size is 10 and  $(0.5/0.55)^{20} = 0.149$  if the initial population size is 20.

Exponential growth with demographic stochasticity can be modeled in R using the function listed below. (You can cut and paste these lines into your R editor, then send them to R.)

```
StochasticSim <- function(steps,b,d,N0){
  # Create vectors to hold population size and time
  # The length is = steps + 1 to hold the initial value
  #   and all the updates
  N <- numeric(steps + 1);
  t <- numeric(steps + 1);
  # Assign N0 (the initial population size) to the first element of N
  N[1] <- N0;
  # Assign time = 0 to the initial element of t
  t[1] <- 0;
  # for each step, update N and t
  for(i in 1:steps){
    # check that the population is not extinct
    if (N[i]>0) {
      # The time to the next event is drawn from an exponential
      # distribution in which the rate is the product of the population
      # size and the sum of the per capita birth and death rates.
      eventTime <- rexp(1,(b+d)*N[i])
      # The new value of t is the old value plus
      # the time to the next event.
      t[i+1] <- t[i] + eventTime
      # The probability that the next event is a birth is b/(b+d)
      # Draw a random number between 0 and 1 and see if it is
      #   less than b/(b+d)
      if (runif(1) < (b/(b+d))) {
        # If the event is a birth, population size increases by 1
        N[i+1] <- N[i] + 1
      } else {
        # Otherwise, the event is a death, and population size
        # decreases by 1
        N[i+1] <- N[i] - 1
      }
    }
    else {
      # if the population is extinct, N is 0 and time is unchanged
      N[i+1] <- 0
      t[i+1] <- t[i]
    }
  }
  # Plot N versus t
  plot(N~t,type="l")
  # Output the final population size
  return(N[steps+1])
}
```

After the function has been entered in R, a simulation is executed by calling the function as follows:

```
StochasticSim( steps, birth_rate, death_rate, initial_N)
```

with appropriate numbers substituted for the four inputs (steps, birth\_rate, death\_rate, initial\_N). For example, to simulate 1000 events (births or deaths) in an exponentially with  $b = 0.55$  and  $d = 0.5$ , and initial population size = 10, execute this line in R:

```
StochasticSim( 1000, 0.55, 0.50, 10)
```

A plot of  $N$  versus  $t$  is produced, and the final population size is shown in the console.

Use this function to conduct 50 simulations with initial population sizes of 10 and 50. What proportion of the 50 simulations lead to extinction (final population size = 0)? We will collect the numbers across the class to see how closely they match the values predicted by the formula above. You may also try varying  $b$ ,  $d$ , and  $N_0$  to see the effect on the probability of extinction.

### **Plant laws.**

9. A forester grows pine trees, which are to be harvested and used to manufacture paper. Two plots are established. Plot A is planted with 16 seedlings per  $\text{m}^2$ , while plot B is planted with 4 seedling per  $\text{m}^2$ . Both plots are so crowded that plants soon begin to compete with their neighbors. After a few years, competition has caused considerable mortality, and both plots have reached the self-thinning limit. Assume that the  $-3/2$  self-thinning law applies. Plot A has declined to 1.0 tree per  $\text{m}^2$  and plot B has declined to 0.5 tree per  $\text{m}^2$ . If trees on plot A weigh an average of 24 kg, how much does the average tree on plot B weigh? For each plot, what is the total weight of the plants?