1. Since 1973, the British Forestry Commission has surveyed for the presence of the American gray squirrel (*Sciurus carolinensis Gmelin*) and the native red squirrel (*Sciurus vulgaris L.*). From two consecutive years of data for 10 km square regions across Great Britain, data were collected on movement of the two types of squirrels. The transition matrix for red squirrels, gray squirrels, both, or neither in that order was given by

$$T = \begin{pmatrix} 0.8797 & 0.0382 & 0.0527 & 0.0008 \\ 0.0212 & 0.8002 & 0.0041 & 0.0143 \\ 0.0981 & 0.0273 & 0.8802 & 0.0527 \\ 0.0010 & 0.1343 & 0.0630 & 0.9322 \end{pmatrix}.$$

Find the equilibrium distribution of squirrels based on this transition matrix. Does this model suggest that the invasive gray species will significantly displace the native red squirrel over long periods of time?

2. An enclosed area is divided into four regions with varying habitats. One hundred tagged frogs are released into the first region. Earlier experiments found that on average the movement of frogs each day about the four regions satisfied the transition model given by

$$\begin{pmatrix} f_1(n+1) \\ f_2(n+1) \\ f_3(n+1) \\ f_4(n+1) \end{pmatrix} = \begin{pmatrix} 0.42 & 0.16 & 0.19 & 0.16 \\ 0.07 & 0.38 & 0.24 & 0.13 \\ 0.34 & 0.19 & 0.51 & 0.27 \\ 0.17 & 0.27 & 0.06 & 0.44 \end{pmatrix} \begin{pmatrix} f_1(n) \\ f_2(n) \\ f_3(n) \\ f_4(n) \end{pmatrix}.$$

a. Give the expected distribution of the tagged frogs after 1, 2, 5, and 10 days.

b. What is the expected distribution of the frogs after a long period of time? Which of the four regions is the most suitable habitat and which is the least suitable for these frogs?

c. These transitions are random events. Write a MatLab code for a Monte Carlo simulation of this experiment. (Show your code with comments to explain what the code is doing!) Run the experiment 1000 times, giving the mean and standard deviation of the distribution of frogs after 1, 2, 5, and 10 days. Compare these results to Part a.

3. In lecture, we saw that a stochastic birth only process could be given by the differential equation

$$\frac{dP_n}{dt} + \lambda N P_n = \lambda(N-1)P_{N-1},$$

with

$$P_N(0) = \begin{cases} 0 & N \neq N_0 \\ 1 & N = N_0 \end{cases},$$

where $P_N(t)$ is the probability that there are exactly N individuals in a population. The solution was given by

$$\begin{aligned} P_{N_0}(t) &= e^{-\lambda N_0 t} \\ P_{N_0+1}(t) &= N_0 e^{-\lambda N_0 t}(1 - e^{-\lambda t}) \\ &\cdots \\ P_{N_0+j}(t) &= \frac{N_0(N_0+1)\cdots(N_0+j-1)}{j!} e^{-\lambda N_0 t}(1-e^{-\lambda t})^j. \end{aligned}$$

Use mathematical induction to prove that this last formula holds for all j.

4. The expected population at time t, $E(t)$, is obtained from the formula

$$E(t) = \sum_{j=0}^{\infty} (N_0 + j) P_{N_0+j}(t).$$

a. Can you explain why this is valid using probabilistic ideas?

b. Show that $E(t) = N_0 e^{\lambda t}$. [Hint: Explicitly calculate the first few terms of the summation; compare this to the derivative of the binomial expansion.]

c. Explain the significance of Part b.

5. Consider the equation above for $P_{N_0+j}(t)$. Assume that $N_0 = 10,000$. Estimate λ, if it is observed that a total of 4500 births occur in 20 days. [Hint: See the previous exercise.]

6. a. Consider an animal that lives four years and reproduces annually. Animals that are 0-1 years old don't reproduce and only 40% ($s_1 = 0.4$) of them survive to the next year. Animals that are 1-2 years old produce on average $b_2 = 1.5$ offspring and 70% ($s_2 = 0.7$) of them survive to the next year. Animals 2-3 years old produce on average $b_3 = 2.2$ offspring and 75% ($s_3 = 0.75$) of them survive to the next year. Finally, animals 3-4 years old produce $b_4 = 3.4$ offspring. Create a model using a Leslie matrix, L, of the form:

$$P_{n+1} = LP_n.$$

Find the steady-state percentage of each age group. Determine how long it takes for this population to double after it has reached its steady-state distribution.

b. Assume that a fraction of 2-4 year olds are harvested. That is, the survival rates s_2 and s_3 are reduced. If the survival rates are reduced by a fraction α, so that the survival rate of 1-2 year olds is $0.7\,\alpha$ and the survival rate of 2-3 year olds is $0.75\,\alpha$. Determine the value of α that leaves the population at a constant value. For this value of α (to at least 3 significant figures), if there are 550 mature (3-4 year olds), then determine the total population and number in each population age group. How many animals are harvested annually under these conditions?

7. One problem with the Leslie matrix models is that they are linear and so result in either exponentially growing or exponentially declining populations. One modification adds a logistic growth factor, creating a nonlinear model, known as the Leslie matrix model with density-dependent recruitment (LMMDDR). The model is given by

$$X(n+1) = q(x(n))LX(n),$$

where L (an $m \times m$ matrix) has a dominant eigenvalue $\lambda_1 > 1$ and q satisfies

$$q(x(n)) = \frac{K}{K + (\lambda_1 - 1)x(n)},$$

where K is the carrying capacity and $x(n) = \sum_{i=1}^{m} x_i(n)$, with $X(n) = (x_1(n), x_2(n), ...x_m(n))^T$.

a. Suppose that

$$L = \begin{pmatrix} 0 & 2.95 & 4.1 \\ 0.5 & 0 & 0 \\ 0 & 0.3 & 0 \end{pmatrix}$$

and $K = 100$. Find the dominant eigenvalue and associated eigenvector for L. Write the LMMDDR model.

b. Begin with a population $X(0) = (5, 5, 5)^T$, then simulate the model for 20 generations. Graph the populations of each age group and the total population. Determine the limiting populations in each of the age classes for this population model. Give a brief biological description of this model.

8. An age-structured population of birds was surveyed over 4 years. The researchers determined the number of birds in each age class for each of the 4 years and found out how many nestlings fledged from each of the different age classes each year. The researchers divided the population of birds into the birds 0-1 years old, 1-2 years old, and those that are older. This age-structured population forms a Leslie model of the following form:

$$\begin{pmatrix} P_1(n+1) \\ P_2(n+1) \\ P_3(n+1) \end{pmatrix} = \begin{pmatrix} 0 & b_2 & b_3 \\ s_{12} & 0 & 0 \\ 0 & s_{23} & s_{33} \end{pmatrix} \begin{pmatrix} P_1(n) \\ P_2(n) \\ P_3(n) \end{pmatrix}.$$

a. The table below shows how many birds in each age class survived to the next year (and gives the total number of birds that fledged). The researchers determined that the survival of the 1-2 year old birds is roughly equal to the survival of the older birds. Thus, we can assume that $s_{23} = s_{33}$. Use the data below to compute the average values for each of the survival parameters s_{12} and $s_{23} = s_{33}$.

Bird Age	Year 1	Year 2	Year 3	Year 4
0-1	175	237	258	311
1-2	42	59	89	92
older	97	104	128	145

They also collected data on the success rate of nesting of each of the different age classes of birds. The table below shows the number of fledglings raised by each of the age classes over the 4 year period. (Note that these columns total to the number of 0-1 year old birds the next year.) Use the data below to compute the average birth rates for each of the age classes b_2 and b_3. (One year old birds of this species don't nest.)

Bird Age	Year 1	Year 2	Year 3	Year 4
1-2	38	47	66	74
older	199	211	245	293

b. Write the Leslie matrix for this species of bird using the average values computed above (to **4 significant figures**). Use your Leslie matrix to estimate the population of each of the age classes for the next 3 years. (Use the last surveyed data as your starting point for this simulation.)

c. Find the eigenvalues and eigenvectors for this model, then give the limiting percent population in each of the age classes. What is the approximate annual rate of growth for this species of bird and how long would it take for the total population to double?