Mathematical Methods in Biology

Part 3

Exercises

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EXERCISES 1-7: CONSTRUCTION OF MATRIX MODELS

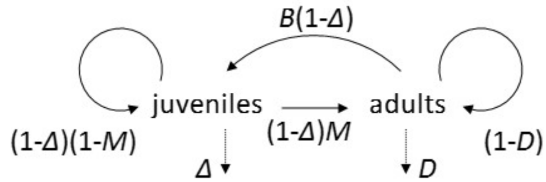
Exercise 1. *Spatial movement.* Suppose that individuals can move between two locations. Reproduction and death (other than the mortality risk in (c) and (d)) are negligible during the time frame of interest, so that the numbers of individuals in locations 1 and 2, denoted respectively with N_1 and N_2, change only due to movement. We monitor the population on a daily basis. Build matrix models to project N_1 and N_2 for the following situations:

(a) Symmetric movement with probability m (the probability to go from location 1 to 2 in one day is the same as to go from 2 to 1)
(b) Unidirectional movement: it is possible to go from location 1 to 2 but not the other way
(c) Symmetric movement at a survival cost: migrating individuals survive the transfer with probability s (which is less than 1)
(d) Symmetric movement with asymmetric cost: the probability to go from location 1 to 2 is the same as to go from 2 to 1, but the probability of surviving the transfer is different (s_1 when moving out of location 1 and s_2 when moving out of location 2).

Exercise 2. *Stage-structured populations in discrete time.* We count ("census") the population at the beginning of spring, just before reproduction. Let N_1 and N_2 respectively denote the number of juveniles and adults. Till the next census time at the beginning of next spring, the following events take place:

- Juveniles die during the year with probability Δ. Those juveniles who stay alive mature with probability M and remain juveniles with probability $1 - M$.
- Each adult produces B offspring and subsequently a fraction D of the adults die. Of the newborns, a fraction Δ dies during the year (so that it is never seen at census). The surviving newborns become juveniles by the next census.

This life cycle is summarized in the graph below, where each arrow represents a full year's time. (Note that it takes at least two years to get from adults to adults, i.e., offspring can become adults by their second census at the earliest. The dotted arrows could be omitted.)



(a) Construct the projection matrix **A** that corresponds to this life cycle.
(b) Modify the model such that instead of maturing with probability M every year, all juveniles mature exactly by their second census.
(c) Modify the model such all juveniles mature exactly by their third census.

Exercise 3. *Membrane channels.* Suppose that a membrane channel can open only if it has bound an agonist (helper) molecule. The chemical reactions that lead to the opening of the channel are thus

$$X_1 + A \underset{k_{12}}{\overset{ak_{21}}{\rightleftharpoons}} X_2 \underset{k_{23}}{\overset{k_{32}}{\rightleftharpoons}} X_3$$

where X_1 denotes the channel without the agonist (and hence closed), X_2 denotes the channel with the agonist A bound but still closed, and X_3 is the open channel. X_1 binds the agonist molecule A at a rate ak_{21} (note that according to mass action, this rate is proportional to the concentration of the agonist, a; we assume that a is kept constant). The channel-agonist complex X_2 either dissociates (at a rate k_{12}) or opens (at a rate k_{32}). The open channel cannot release the agonist before closing, and closes at a rate k_{23}.

Let the vector

$$\mathbf{n} = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}$$

contain the number of channels in states X_1, X_2 and X_3 (with $n_1 + n_2 + n_3$, the total number of channels, being constant over time). Determine the matrix **K** such that the dynamics of the channels is given by

$$\frac{d\mathbf{n}}{dt} = \begin{pmatrix} dn_1/dt \\ dn_2/dt \\ dn_3/dt \end{pmatrix} = \mathbf{Kn}$$

Exercise 4. *Age-structured populations.* Modify or apply the Leslie matrix to model a population of

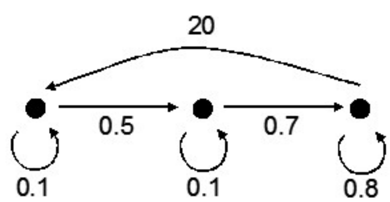
(a) a strictly biennial plant (it reproduces only at age 2 and dies after reproduction);
(b) an organism that has no upper limit of lifetime, but from age 3 years onwards, its effective fecundity is F and its probability of survival is P in every year;
(c) a hitherto unknown species of Magicicada, which reproduces at age 7, dies immediately afterwards, and the offspring have the same probability of survival each year until they become 7 years old and reproduce (real Magicicada is similar but with 13 or 17 years).

Exercise 5. *Order of life history events.* Consider an annual species in a metapopulation of 4 local populations. Let F_i and s_i denote respectively the number of offspring produced per parent and the probability that an offspring survives in habitat $i = 1, 2, 3, 4$.

During dispersal, a fraction m of individuals leave their habitat and enter a dispersal pool; from the dispersal pool, the individuals get into any of the four habitats with equal probabilities ("global dispersal"). Construct the projection matrix if the order of events is

(a) (census -) reproduction - survival - dispersal (- census)
(b) (census -) reproduction - dispersal - survival (- census).

Exercise 6. *Size-structured populations.* For many organisms, fecundity and survival depend on body size rather than on age. The life cycle graph below shows a size-structured population with three size classes (small, medium, large). After one year, a surviving individual may have grown one class larger or may stay in the same class as before; nobody shrinks in size. Death means that some individuals do not appear in any class after one year: For example, 10% of the smallest class remains in the smallest class, 50% grows, and the remaining 40% dies (does not go anywhere). Only the largest class reproduces, and all offspring enter the smallest class. Construct the corresponding projection matrix and compare its structure with the Leslie matrix of age-structured populations.



Exercise 7. *Biennial plants with seed bank.* Consider a population of biennial plants. Each year, half the seeds in the soil seed bank germinate in March. 10% of the germinating seeds survive till March next year and become a 1-year-old rosette (vegetative plant; in early March, it is mainly an underground storage of nutrients e.g. in a thick root, as a carrot). 80% of the surviving rosettes will start flowering in May and produce on average 100 seeds. 40% of the seeds fall in suitable soil and survive from seed production till next March. Seeds in the soil seed bank that do not germinate in March survive till next March with 90% probability. Draw the life cycle graph and construct the projection matrix for census at the beginning of March.

Exercise 8. *Important patterns in matrix multiplication.* Do the following multiplications and observe the resulting patterns:

(a)

$$\begin{bmatrix} 3 & 8 & 9 \\ 1 & 2 & 7 \\ 6 & 4 & 5 \end{bmatrix} \begin{bmatrix} 3 & 1 & 6 \\ 8 & 2 & 4 \\ 9 & 7 & 5 \end{bmatrix}$$

The result is a *symmetric* matrix: The element in the first row second column is the same as the element in the second row first column, etc., such that for all i, j we have that the number in the ith row, jth column is the same as in the jth row, ith column. Do you see why?

(b) The following is a very common structure: a matrix "sandwiched" between two vectors. The result is a number:

$$\begin{bmatrix} 5 & 2 \end{bmatrix} \begin{bmatrix} 3 & 4 \\ 2 & 0 \end{bmatrix} \begin{bmatrix} 6 \\ 3 \end{bmatrix}$$

(c) Pre-multiplying a column vector with a row vector of 1's calculates the sum of the vector's elements:

$$\begin{bmatrix} 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}$$

(d) This 4×4 matrix "falls apart" into two matrices of size 2×2:

$$\begin{bmatrix} a_{11} & a_{12} & 0 & 0 \\ a_{21} & a_{22} & 0 & 0 \\ 0 & 0 & a_{33} & a_{34} \\ 0 & 0 & a_{43} & a_{44} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \end{bmatrix}$$

in the sense that the result of the multiplication above looks like the results of $\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$ and $\begin{bmatrix} a_{33} & a_{34} \\ a_{43} & a_{44} \end{bmatrix} \begin{bmatrix} x_3 \\ x_4 \end{bmatrix}$ "glued" together into one vector. The 4×4 matrix is *block-diagonal*.

Exercise 9. *Diagonal matrix.* A matrix of the form

$$\mathbf{\Lambda} = \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix}$$

is called a *diagonal matrix* because the only non-zero elements are in its diagonal.

(a) Investigate the emerging pattern when you pre- or post-multiply an arbitrary matrix $\mathbf{A}$ by a diagonal matrix $\mathbf{\Lambda}$. Let thus $\mathbf{A}$ be the arbitrary matrix

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

and compute both $\mathbf{\Lambda A}$ and $\mathbf{A\Lambda}$.

(b) Calculate the square of the diagonal matrix $\mathbf{\Lambda}$. The square of a matrix is the product with itself: $\mathbf{\Lambda}^2 = \mathbf{\Lambda\Lambda}$.

Exercise 10. *Exercises to practice matrix multiplication* Perform the following multiplications when possible:

(a) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 3 \\ 5 \end{bmatrix}$

(b) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 2 \\ 1 \end{bmatrix}$

(c) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 3 & 2 \\ 5 & 1 \end{bmatrix}$

(d) $\begin{bmatrix} -3 & 2 & -1 \\ 6 & 0 & 1 \\ 0 & 5 & -2 \end{bmatrix} \begin{bmatrix} 7 & 1 & 3 \\ 6 & 4 & -2 \\ -3 & -1 & 1 \end{bmatrix}$

(e) $\begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} 2 & 4 \\ 6 & 8 \end{bmatrix}$

(f) $\begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} -3 & 2 & -1 \\ 6 & 0 & 1 \\ 0 & 5 & -2 \end{bmatrix}$

(g) $\begin{bmatrix} -2 & 0 \\ 1 & 8 \end{bmatrix}^2$

(h) $\begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix} \begin{bmatrix} 9 & 10 \\ 11 & 12 \end{bmatrix}$

Exercise 11. *Find out the matrix* Construct the matrix $\mathbf{A}$ such that the following holds true for every vector $\mathbf{x}$:

(a) $\mathbf{A} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 2x_1 \\ 2x_2 \end{bmatrix}$

(b) $\mathbf{A} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} x_1 \\ 0 \end{bmatrix}$

(c) $\mathbf{A} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} x_1 \\ -x_2 \end{bmatrix}$

(d) $\mathbf{A} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} = \begin{bmatrix} -x_1 \\ 2x_2 \\ 0 \end{bmatrix}$

EXERCISES 12-15: ANALYSIS OF MATRIX MODELS

Exercise 12. *Long-term dynamics of age-structured populations.* For simplicity, in this exercise we consider an age-structured population with maximum age of only 2, i.e., a population described with a 2×2 Leslie-matrix

$$\mathbf{L} = \begin{bmatrix} F_1 & F_2 \\ P_1 & 0 \end{bmatrix}$$

Larger matrices would behave similary.

(a) Take the parameter values $F_1 = 2$, $F_2 = 5$, $P_1 = 0.25$, and the initial population vector

$$\mathbf{N}(0) = \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

Calculate $\mathbf{N}(1)$, $\mathbf{N}(2)$,... for a number of generations and observe the behaviour of the population vector. It is a good idea to monitor total population size (the sum of the elements of $\mathbf{N}$) and the fraction of the population belonging to different age classes. *Hint:* You may want to use Excel, MatLab or any other suitable software to do the calculations, but it is also feasible by hand as it is sufficient to calculate $\mathbf{N}(t)$ for 5-6 years.

(b) Experiment with the long-term dynamics of strictly biennial plants, which have the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 0 & F \\ P & 0 \end{bmatrix}$$

(see exercise 4a above). Assume values for the parameters F and P as you wish. Is any equilibrium achieved? Why or why not? *Hint:* Since the Leslie matrix is small and has many zeros, this part can easily be done also by hand.

Exercise 13. *Backward projection.* The demography of an age-structured population with maximum age 3 is described with the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{bmatrix}$$

(a) Suppose that $F_1 = 0$, $F_2 = F_3 = 2$ and $P_1 = P_2 = 0.6$. In year t, the population vector is

$$\mathbf{N}(t) = \begin{bmatrix} 12 \\ 3 \\ 2 \end{bmatrix}$$

Find out what was the population vector in the previous year, $\mathbf{N}(t-1)$.

(b) Find parameter values in the Leslie matrix such that $\mathbf{N}(t-1)$ cannot be determined. Explain in biological terms why this is the case.

Exercise 14. *Equilibrium allele frequencies under mutation.* Let the vector $\mathbf{p}_t$ contain the frequencies of alleles in generation t and the matrix model

$$\mathbf{p}_{t+1} = \mathbf{Q}\mathbf{p}_t$$

give the dynamics of allele frequencies from generation to genration. Find the equilibrium allele frequencies for the transition probability matrices

$$\text{(a) } \mathbf{Q} = \begin{bmatrix} 0.8 & 0.2 & 0.15 \\ 0.06 & 0.7 & 0.1 \\ 0.14 & 0.1 & 0.75 \end{bmatrix} \qquad \text{(b) } \mathbf{Q} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0.8 & 0.1 \\ 0 & 0.2 & 0.9 \end{bmatrix}$$

Hint: Use also the fact that the allele frequencies must add up to 1.

Exercise 15. *The Hawk-Dove game.* The Hawk-Dove game is a famous model of evolutionary game theory, and many other game theory models (collectively known as matrix games) follow the same basic setup. Envisage a population where pairwise interactions take place between randomly chosen individuals. At each interaction, each player can choose between a number of actions. The reward or *pay-off* gained from the interaction depends on the actions of both players, but one player does not know what action the other player will choose.

Suppose there are only two actions to choose from (labelled as action 1 and action 2, respectively) and let a_{ij} denote the pay-off I receive if I choose action i and my opponent chooses action j (where i and j can be 1 or 2). The matrix

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

is called the pay-off matrix of the game. Suppose all individuals other than the focal one (whom is described here as "I") choose action 1 with probability p_1 and action 2 with probability p_2, and let

$$\mathbf{p} = \begin{bmatrix} p_1 \\ p_2 \end{bmatrix}$$

(a) Show that the vector $\mathbf{x} = \mathbf{Ap}$ contains the expected payoffs of the focal individual: if I choose action 1, then on average I receive payoff x_1, whereas if I choose action 2, then I can expect payoff x_2.

The Hawk-Dove game envisages two players fighting over a resource of value V. Hawk players escalate the fight such that if both myself and my opponent choose the action Hawk, then with probability 1/2 I win the resource and therefore get pay-off V, but with probability 1/2 I lose and suffer an injury of cost C. In a Hawk-Hawk interaction, therefore, the payoff is $\frac{1}{2}V - \frac{1}{2}C$. The alternative action Dove does not escalate the fight. If I play Hawk and my opponent plays Dove, then I win and get the pay-off V; if I play Dove and my opponent plays Hawk, then my opponent wins but I have no injury, so that I get zero pay-off. Finally, if both players choose Dove, then each wins with probability 1/2 without an injury and the pay-off is $\frac{1}{2}V$. The pay-off matrix is thus

$$\mathbf{A} = \begin{bmatrix} \frac{1}{2}(V-C) & V \\ 0 & \frac{1}{2}V \end{bmatrix}$$

(b) Show that if $V > C$, then it is always better for me to play Hawk than to play Dove, no matter what $\mathbf{p}$ is.

(c) Suppose now that $V < C$. Find a vector $\mathbf{p}$ such that I get the same payoff whether I play Hawk or Dove. This particular $\mathbf{p}$ represents a so-called Nash-equilibrium. If the pay-off to Hawk is higher than the pay-off to Dove, then Hawk players will spread in the population; and vice versa, if the pay-off to Dove is higher, then Dove will spread. If, however, the two actions get the same pay-off, then neither spreads, i.e., the population is at equilibrium.

EXERCISES 16-17: DETERMINANTS

Exercise 16. *Expansion of determinants.* Calculate the determinants of the matrices used in exercise 14.

Exercise 17. *Special determinants.* Calculate the determinant of the following special matrices (*hint:* expand using a row or a column such that the calculation is the simplest). The results are worth noting:

(a) A diagonal matrix: $\begin{bmatrix} \lambda_1 & 0 & 0 & 0 \\ 0 & \lambda_2 & 0 & 0 \\ 0 & 0 & \lambda_3 & 0 \\ 0 & 0 & 0 & \lambda_4 \end{bmatrix}$

(b) A triangular matrix: $\begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ 0 & a_{22} & a_{23} & a_{24} \\ 0 & 0 & a_{33} & a_{34} \\ 0 & 0 & 0 & a_{44} \end{bmatrix}$

EXERCISES 18-23: EIGENVALUES AND EIGENVECTORS

Exercise 18. *Stable age distribution.* Calculate all eigenvalues and eigenvectors of an age-structured population with Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 2 & 5 \\ 0.25 & 0 \end{bmatrix}$$

Compare the results with the numerical experiment carried out with the same matrix in exercise 12a.

Exercise 19. *The role of initial conditions.* Consider an age-structured population with maximum age 2 where only 1-year-old females reproduce, and therefore the Leslie matrix has the form

$$\mathbf{L} = \begin{bmatrix} F & 0 \\ P & 0 \end{bmatrix}$$

(a) Show that the eigenvalues and eigenvectors of this matrix are

$$\lambda_1 = F \text{ with } \mathbf{u_1} = k \begin{bmatrix} F \\ P \end{bmatrix} \quad \text{and} \quad \lambda_2 = 0 \text{ with } \mathbf{u_2} = \begin{bmatrix} 0 \\ u \end{bmatrix}$$

where k and u are arbitrary numbers (cf. the eigenvectors are determined only up to a constant).

(b) Find all initial vectors $\mathbf{N}(0)$ for which
(i) the population grows eventually exponentially with annual growth rate F;
(ii) the population goes extinct.
Hint: write the initial vector as a linear combination of the eigenvectors ($\mathbf{N}(0) = \alpha_1\mathbf{u_1} + \alpha_2\mathbf{u_2}$) and use this to investigate the long-term dynamics given by $\mathbf{L}^t\mathbf{N}(0)$.

(c) Are there any initial conditions from which the population of exercise 18 will go extinct?

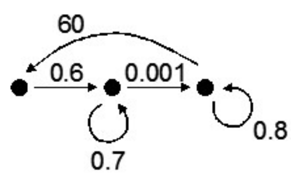
Exercise 20. *Biennial plants.* As seen in exercise 4a, the population growth of a strictly biennial plant population is given by the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 0 & F \\ P & 0 \end{bmatrix}$$

(a) Calculate all eigenvalues. Is there a *unique* dominant eigenvalue? Why does a population of biennials not converge to a stable distribution?

(b) Calculate $\mathbf{L}^2$, the matrix that projects the current population vector into the vector *two* years later. Calculate the eigenvalues and eigenvectors of this matrix and use these results to interpret the numerical experiment in exercise 12b.

Exercise 21. *Large matrices.* Sea turtles have size-structured populations with three stages: juveniles (< 10 cm), sub-adults (between 10 cm and 85 cm) and adults (> 85 cm). Only adults reproduce, and all offspring enter the smallest (juvenile) stage. The life cycle graph (simplified from Crouse et al. 1987[1]) is as follows:



Construct the projection matrix and determine its dominant eigenvalue and the corresponding eigenvector (the other eigenvalues/eigenvectors are not necessary).

Hint: plot the determinant of $\mathbf{A} - \lambda\mathbf{I}$ as a function of λ and get an estimate of λ_1 visually from the graph. You can obtain the eigenvalue more precisely using the bisection method or using software like MatLab.

Exercise 22. *State transitions in continuous time.* Let the vector $\mathbf{p}$ contain the fractions of individuals belonging to states $1, ..., n$, and let the system of equations

$$\frac{d\mathbf{p}}{dt} = \mathbf{M}\mathbf{p}$$

give the dynamics of state transitions. We assume that the total number of individuals is constant, and the elements of $\mathbf{p}$ (fractions) sum to 1. A concrete example for a system like this appeared in exercise 3, where the "individuals" were membrane channels with $n = 3$ different states. Recall that each column of matrix $\mathbf{M}$ sums to zero (why?).

[1]Crouse D. T., L. B. Crowder & H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68: 1412-1423.

(a) Show that $\lambda_1 = 0$ is an eigenvalue of $\mathbf{M}$ and the equilibrium $\mathbf{p}$ is the eigenvector corresponding to $\lambda_1 = 0$.

(b) Calculate the equilibrium eigenvector for the matrix

$$\mathbf{M} = \begin{bmatrix} -\alpha & \beta & \gamma \\ \alpha & -\beta & \delta \\ 0 & 0 & -(\gamma+\delta) \end{bmatrix}$$

and explain why p_3 is zero in equilibrium.

Exercise 23. *Migration into a sink.* A metapopulation consists of two local populations. In the first population, each individual produces F offspring every year and survives with probability P to the next year (independently of age). The first population is thus an unstructured local population where every individual replaces herself in the next year on average with $G = F + P > 1$ descendants (F offspring plus, in fraction P of the parents, herself). In the second population there is no reproduction at all and survival occurs with probability $Q < 1$. The second population would thus be not viable in itself. However, every year a fraction μ of the individuals migrates from the first population to the second, and fraction ν migrates from the second to the first. Migration takes place after reproduction and survival (i.e., migration is the last event before census).

(a) Construct the life cycle graph and the corresponding projection matrix.
(b) Determine the largest value of μ such that the metapopulation does not die out. Investigate how this critical value depends on G, Q and ν. *Hint:* The metapopulation dies out if it's dominant eigenvalue is less than 1. A clever solution is to substitute the critical value $\lambda = 1$ already in the characteristic equation and solve for μ.

EXERCISES 24-27: AGE-STRUCTURED POPULATIONS

Exercise 24. *The effect of increasing fecundity.* Find the stable age structure and the growth rate of a baseline population with the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 1 & 1 \\ 0.75 & 0 \end{bmatrix}$$

Compare the speed of growth and the stable age structure of this baseline population with a population where the fecundity of each age class is increased twofold:

$$\mathbf{L} = \begin{bmatrix} 2 & 2 \\ 0.75 & 0 \end{bmatrix}$$

Does the speed of growth also increase twofold? How does the stable age structure change if fecundity increases or decreases?

Exercise 25. *Timing of reproduction.* Compare the speed of growth and the stable age structure of the baseline population in the previous exercise with a population where reproduction is delayed by one year. For simplicity, assume that all individuals survive the first year such that the delay does not imply extra mortality (in reality, of course, it would):

$$\mathbf{L} = \begin{bmatrix} 0 & 1 & 1 \\ 1 & 0 & 0 \\ 0 & 0.75 & 0 \end{bmatrix}$$

Hint: Plot the characteristic polynomial and obtain an approximate value of the dominant eigenvalue visually from the graph.

Exercise 26. *Stable age structure.* Show that in a Leslie model with two age classes, the proportion of 2-year-old individuals can exceed the proportion of 1-year-olds in the stable age distribution only if the population is dying out. (This is true also in general: in the stable age distribution, the fraction of individuals in a higher age class can exceed the fraction of individuals in a lower age class only if the population is declining.)

Exercise 27. *Reproductive value.* Suppose that in an age-structured population, the maximum age is ω but females of age m and older do not reproduce (m is the age of menopause). Show that the reproductive value of the post-menopausal age groups is zero. *Hint:* use the eigenvector equation $\mathbf{v}^T\mathbf{L} = \lambda\mathbf{v}^T$. You may want to try first an example with a small Leslie matrix.

EXERCISE 28: THE PERRON-FROBENIUS THEORY

Exercise 28. *Irreducibility and primitivity.* Determine whether the projection matrices of the following examples are irreducible and primitive, and characterize the long-term behaviour of the models:

(a) the Leslie matrices in exercises 4, 18, 19 and 25;
(b) the spatially structured population in exercise 1;
(c) the projection matrices of allele frequencies under mutation in exercise 14;
(d) the stage-structured population in exercise 2;
(e) the size-structured population in exercise 21;
(f) biennial plants with a seed bank;
(g) age-structured populations with post-reproductive age classes (as in humans).

SOLUTIONS

1. (a) $\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 1-m & m \\ m & 1-m \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix}$

(b) $\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 1-m & 0 \\ m & 1 \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix}$

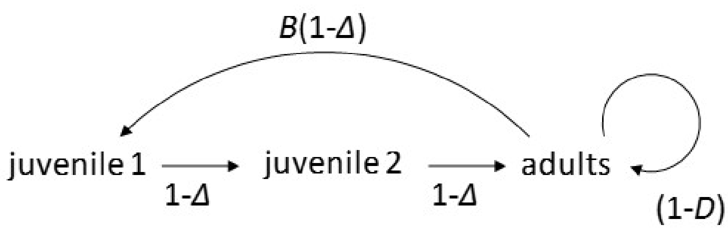
(c) $\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 1-m & sm \\ sm & 1-m \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix}$

(d) $\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 1-m & s_2 m \\ s_1 m & 1-m \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix}$

2. (a) $\mathbf{A} = \begin{bmatrix} (1-\Delta)(1-M) & B(1-\Delta) \\ (1-\Delta)M & 1-D \end{bmatrix}$

(b) The same as in (a) but with $M = 1$.

(c) One needs to distinguish between 1-year old juveniles and 2-year old juveniles:



The projection matrix is $\mathbf{A} = \begin{bmatrix} 0 & 0 & B(1-\Delta) \\ 1-\Delta & 0 & 0 \\ 0 & 1-\Delta & 1-D \end{bmatrix}$

3. $\mathbf{K} = \begin{bmatrix} -ak_{21} & k_{12} & 0 \\ ak_{21} & -(k_{12}+k_{32}) & k_{23} \\ 0 & k_{32} & -k_{23} \end{bmatrix}$

4. (a) $\begin{bmatrix} 0 & F \\ P & 0 \end{bmatrix}$

(b) Because all 3 year-old and older individuals have the same parameters, it suffices to distinguish three age classes: 1-year-old, 2-year-old and 3-year-old-and-older. The corresponding projection matrix

$$\begin{bmatrix} F_1 & F_2 & F \\ P_1 & 0 & 0 \\ 0 & P_2 & P \end{bmatrix}$$

is not a Leslie matrix because the last group is composite.

(c) Even though the probability of survival is P every year, the age classes cannot be grouped because we need to know exactly who become 7-year-olds:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & F \\ P & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & P & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & P & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & P & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P & 0 \end{bmatrix}$$

5. (a) $$\begin{bmatrix} (1-\frac{3}{4}m)F_1s_1 & \frac{1}{4}mF_2s_2 & \frac{1}{4}mF_3s_3 & \frac{1}{4}mF_4s_4 \\ \frac{1}{4}mF_1s_1 & (1-\frac{3}{4}m)F_2s_2 & \frac{1}{4}mF_3s_3 & \frac{1}{4}mF_4s_4 \\ \frac{1}{4}mF_1s_1 & \frac{1}{4}mF_2s_2 & (1-\frac{3}{4}m)F_3s_3 & \frac{1}{4}mF_4s_4 \\ \frac{1}{4}mF_1s_1 & \frac{1}{4}mF_2s_2 & \frac{1}{4}mF_3s_3 & (1-\frac{3}{4}m)F_4s_4 \end{bmatrix}$$

(b) $$\begin{bmatrix} (1-\frac{3}{4}m)F_1s_1 & \frac{1}{4}mF_2s_1 & \frac{1}{4}mF_3s_1 & \frac{1}{4}mF_4s_1 \\ \frac{1}{4}mF_1s_2 & (1-\frac{3}{4}m)F_2s_2 & \frac{1}{4}mF_3s_2 & \frac{1}{4}mF_4s_2 \\ \frac{1}{4}mF_1s_3 & \frac{1}{4}mF_2s_3 & (1-\frac{3}{4}m)F_3s_3 & \frac{1}{4}mF_4s_3 \\ \frac{1}{4}mF_1s_4 & \frac{1}{4}mF_2s_4 & \frac{1}{4}mF_3s_4 & (1-\frac{3}{4}m)F_4s_4 \end{bmatrix}$$

6. $$\begin{bmatrix} 0.1 & 0 & 20 \\ 0.5 & 0.1 & 0 \\ 0 & 0.7 & 0.8 \end{bmatrix}$$

7. At the beginning of March, only two life stages are present: seeds and surviving rosettes (with stored nutrients in their roots). The projection matrix is therefore a 2×2 matrix:

$$\begin{bmatrix} 0.45 & 32 \\ 0.05 & 0 \end{bmatrix}$$

8. (a) $\begin{bmatrix} 154 & 82 & 95 \\ 82 & 54 & 49 \\ 95 & 49 & 77 \end{bmatrix}$

(b) 174

(c) $x_1 + x_2 + x_3$

(d) $\begin{bmatrix} a_{11}x_1 + a_{12}x_2 \\ a_{21}x_1 + a_{22}x_2 \\ a_{33}x_3 + a_{34}x_4 \\ a_{43}x_3 + a_{44}x_4 \end{bmatrix}$

9. (a) $\mathbf{\Lambda A}$: each element in the ith row of $\mathbf{A}$ is multiplied with λ_i; $\mathbf{A\Lambda}$: each element in the ith column of $\mathbf{A}$ is multiplied with λ_i

(b) $\mathbf{\Lambda} = \begin{bmatrix} \lambda_1^2 & 0 & 0 \\ 0 & \lambda_2^2 & 0 \\ 0 & 0 & \lambda_3^2 \end{bmatrix}$ (also higher powers are like this)

10. (a) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 3 \\ 5 \end{bmatrix} = \begin{bmatrix} 7 \\ 10 \end{bmatrix}$

(b) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 7 \\ 2 \end{bmatrix}$

(c) $\begin{bmatrix} 4 & -1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 3 & 2 \\ 5 & 1 \end{bmatrix} = \begin{bmatrix} 7 & 7 \\ 10 & 2 \end{bmatrix}$ (compare with (a) and (b)!)

(d) $\begin{bmatrix} -3 & 2 & -1 \\ 6 & 0 & 1 \\ 0 & 5 & -2 \end{bmatrix} \begin{bmatrix} 7 & 1 & 3 \\ 6 & 4 & -2 \\ -3 & -1 & 1 \end{bmatrix} = \begin{bmatrix} -6 & 6 & -14 \\ 39 & 5 & 19 \\ 36 & 22 & -12 \end{bmatrix}$

(e) $\begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} 2 & 4 \\ 6 & 8 \end{bmatrix} = \begin{bmatrix} 4 & 4 \end{bmatrix}$

(f) this multiplication is not possible

(g) $\begin{bmatrix} -2 & 0 \\ 1 & 8 \end{bmatrix}^2 = \begin{bmatrix} 4 & 0 \\ 6 & 64 \end{bmatrix}$

(h) $\begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix} \begin{bmatrix} 9 & 10 \\ 11 & 12 \end{bmatrix} = \begin{bmatrix} 413 & 454 \\ 937 & 1030 \end{bmatrix}$

11. (a) $\mathbf{A} = \begin{bmatrix} 2 & 0 \\ 0 & 2 \end{bmatrix}$

(b) $\mathbf{A} = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$

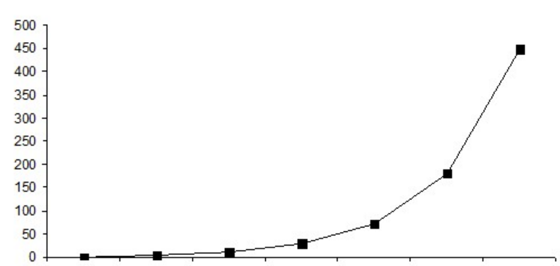
(c) $\mathbf{A} = \begin{bmatrix} 1 & 0 \\ 0 & -1 \end{bmatrix}$

(d) $\mathbf{A} = \begin{bmatrix} -1 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 0 \end{bmatrix}$

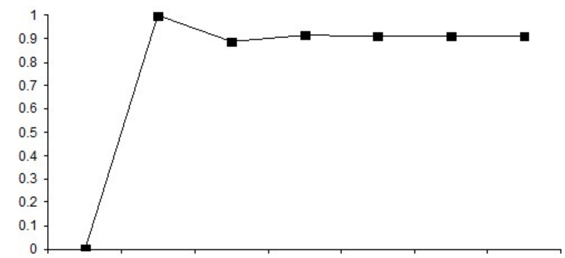
12. (a) The table shows the numbers of 1- and 2-year-olds in the initial year (first column) and in six subsequent years:

$t = 0$	$t = 1$	$t = 2$	$t = 3$	$t = 4$	$t = 5$	$t = 6$
0	5	10	26.25	65	162.8125	406.875
1	0	1.25	2.5	6.5625	16.25	40.70313

The graph of total population size shows approximately exponential growth:



whereas the fraction of 1-year-olds stabilizes in time:



The stabilization of the population structure, i.e., the fractions of individuals that belong to various classes is the typical behaviour of matrix models, the case of biennial plants in (b) is exceptional.

(b) The population structure, i.e., the fraction of 1- and 2-year olds, keeps oscillating. Individuals born in even years and in odd years form two separate populations.

13. (a) $\mathbf{N}(t-1) = \begin{bmatrix} 5 \\ 3\frac{1}{3} \\ 2\frac{2}{3} \end{bmatrix}$

(b) If $F_3 = 0$, then $\mathbf{N}(t-1)$ cannot be determined. This is because all individuals who were 3 year old in year $t-1$ are dead by year t, and if they do not leave any offspring, then they vanish without any trace, i.e., it is impossible to tell how many 3 year old individuals were present in year $t-1$. (A similar situation arises if P_1 or P_2 is zero, but then the maximum age is not 3.)

14. (a) $\mathbf{p} = \begin{bmatrix} 65/142 \\ 29/142 \\ 48/142 \end{bmatrix} \approx \begin{bmatrix} 0.458 \\ 0.204 \\ 0.338 \end{bmatrix}$

(b) We have that $p_3 = 2p_2$ and $p_1 + p_2 + p_3 = 1$ such that $p_2 = (1-p_1)/3$ and $p_3 = 2(1-p_1)/3$. p_1 is however arbitrary and therefore there are infinitely many solutions. Biologically, the reason for this is that allele A_1 is "isolated" from the other two alleles so that the other two alleles do not mutate into A_1 and A_1 does not mutate into any other allele. Hence the initial value of p_1 is preserved, whatever it was, and only the other two alleles equilibrate.

15. (a) If I choose action 1, then my pay-off is either a_{11} or a_{12}, depending on whether my opponent chose action 1 or action 2. The former happens with probability p_1 and the latter happens with probability p_2. Hence the expected pay-off to action 1 is $a_{11}p_1 + a_{12}p_2$. The first element of $\mathbf{x} = \mathbf{A}\mathbf{p}$ is $x_1 = a_{11}p_1 + a_{12}p_2$, which is indeed the expected pay-off to action 1. The same logic applies to each element of $\mathbf{x}$, also in games with larger matrices.

(b) In the Hawk-Dove game, $x_1 = \frac{1}{2}(V-C)p_1 + Vp_2$ and $x_2 = \frac{1}{2}Vp_2$. If $V - C$ is positive, then x_1 is certainly greater than x_2 because the second term of x_1 is the double of x_2 and the first term is positive.

(c) We have to solve

$$\begin{bmatrix} x \\ x \end{bmatrix} = \begin{bmatrix} \frac{1}{2}(V-C) & V \\ 0 & \frac{1}{2}V \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix}$$

Writing out the equations, we have

$$\begin{aligned} x &= \tfrac{1}{2}(V-C)p_1 + Vp_2 \\ x &= \tfrac{1}{2}Vp_2 \end{aligned}$$

x is unknown, all what we know is that it is the same in both equations. It is thus best to eliminate x and write

$$\tfrac{1}{2}(V-C)p_1 + Vp_2 = \tfrac{1}{2}Vp_2$$

This is one equation for p_1 and p_2, but since p_1 and p_2 must add up to 1, we can write $p_2 = 1 - p_1$ to obtain

$$\tfrac{1}{2}(V-C)p_1 + V(1-p_1) = \tfrac{1}{2}V(1-p_1)$$

which easily solves to $p_1 = V/C$. Note that this is a probability if $V < C$, as assumed in this part. The Nash equilibrium is therefore at $p_1 = V/C$ and $p_2 = 1 - p_1 = 1 - V/C$.

16. (a) 0.392; (b) 0.7

17. (a) $\lambda_1\lambda_2\lambda_3\lambda_4$; (b) $a_{11}a_{22}a_{33}a_{44}$

18. Eigenvalues: $\lambda_1 = 2.5$ and $\lambda_2 = -0.5$; eigenvectors $\mathbf{u_1} = \begin{bmatrix} 10 \\ 1 \end{bmatrix}$ and $\mathbf{u_2} = \begin{bmatrix} -2 \\ 1 \end{bmatrix}$. (Recall that eigenvectors are determined only up to a constant, so for example $\mathbf{u_1}$ could also be $\begin{bmatrix} 20 \\ 2 \end{bmatrix}$ or any other vector where the ratio of the two elements is 10:1.)

The population grows asymptotically (=after a long enough time) $\lambda_1 = 2.5$-fold each year and the age structure converges to the first eigenvector $\mathbf{u_1}$. It is convenient to scale the eigenvector such that its elements sum to 1: we then obtain $\mathbf{u_1} = \begin{bmatrix} 10/11 \\ 1/11 \end{bmatrix}$, i.e., 10/11 of the population is of age 1 and the remaining fraction 1/11 is of age 2.

19. (b) If $\mathbf{N}(0)$ is such that in $\mathbf{N}(0) = \alpha_1\mathbf{u_1} + \alpha_2\mathbf{u_2}$ the coefficient α_1 is zero, then the population grows at the rate $\lambda_2 = 0$, i.e., it goes extinct. α_1 is zero when $\mathbf{N}(0) = \begin{bmatrix} 0 \\ u \end{bmatrix}$ (where u is any positive number). Hence the population goes extinct when the initial population contains only 2-year-old individuals, who do not reproduce anymore. From any other initial population vector, the population grows with $\lambda_1 = F$.

(c) In exercise 18, no initial population can have $\alpha_1 = 0$ because this would mean a negative number of individuals in one of the age classes. Hence the population eventually grows with $\lambda_1 = 2.5$ from any initial condition.

20. (a) The eigenvalues are $\lambda_{1,2} = \pm\sqrt{FP}$ and they are equal in absolute value. This is why the population does not converge to a stable age distribution: neither term in $\mathbf{N}(t) = \mathbf{L}^t\mathbf{N}(0) = \alpha_1\lambda_1^t\mathbf{u_1} + \alpha_2\lambda_2^t\mathbf{u_2}$ dominates for large t.

(b) $\mathbf{L}^2 = \begin{bmatrix} FP & 0 \\ 0 & FP \end{bmatrix} = FP\mathbf{I}$. Because any vector is an eigenvector of the identity matrix $\mathbf{I}$, any vector is an eigenvector also of $\mathbf{L}^2$. For any initial vector $\mathbf{N}(0)$ hence we have $\mathbf{L}^2\mathbf{N}(0) = FP\mathbf{N}(0)$. Over 2-year intervals, the population preserves its initial structure (whatever it was) and grows FP-fold.

21. The projection matrix is

$$\begin{bmatrix} 0 & 0 & 60 \\ 0.6 & 0.7 & 0 \\ 0 & 0.001 & 0.8 \end{bmatrix}$$

which yields the characteristic equation $-\lambda^3 + 1.5\lambda^2 - 0.56\lambda + 0.036 = 0$. The dominant eigenvalue is $\lambda_1 = 0.951$ (you may get it with various precision depending on the method used to solve the characteristic equation) and the dominant eigenvector (scaled such that its elements add up to 1) is

$$\mathbf{u_1} = \begin{bmatrix} 0.2933 \\ 0.7020 \\ 0.0046 \end{bmatrix}$$

22. (a) Because the columns of $\mathbf{M}$ sum to zero, $\mathbf{M}$ is singular and its determinant is $|\mathbf{M}| = 0$. $\lambda = 0$ is an eigenvalue because the characteristic equation $|\mathbf{M} - \lambda\mathbf{I}| = 0$ is satisfied for $\lambda = 0$: $|\mathbf{M} - \lambda\mathbf{I}| = |\mathbf{M}| = 0$. The eigenvector corresponding to $\lambda = 0$ satisfies $\mathbf{Mp} = \lambda\mathbf{p} = \mathbf{0}$, and this is the vector that makes $d\mathbf{p}/dt = \mathbf{Mp} = \mathbf{0}$ (no change in equilibrium).

(b) After scaling such that the elements of $\mathbf{p}$ sum to 1, $\mathbf{p} = \begin{bmatrix} \beta/(\alpha+\beta) \\ \alpha/(\alpha+\beta) \\ 0 \end{bmatrix}$.

23. (a) $\mathbf{A} = \begin{bmatrix} (1-\mu)G & \nu Q \\ \mu Q & (1-\nu)Q \end{bmatrix}$

(b) The characteristic equation is

$$\lambda^2 - \lambda[(1-\mu)G + (1-\nu)Q)] + (1-\mu-\nu)GQ = 0$$

Substitute $\lambda = 1$:

$$1 - [(1-\mu)G + (1-\nu)Q)] + (1-\mu-\nu)GQ = 0$$

and solve this equation for μ to obtain

$$\mu = \frac{G-1}{G} \cdot \frac{1-(1-\nu)Q}{1-Q}$$

If μ is greater than the critical value given by this formula, the metapopulation goes extinct. As expected, the critical value increases with G (a fast-growing population can tolerate more loss to emigration), increases with Q (emigration to the sink is not so bad if survival in the sink is high) and increases with ν (emigration to the sink is not so bad if one has a high chance of getting back).

24. In the baseline population, the annual growth rate is $\lambda = 1.5$ and the stable age distrubution is $\mathbf{u} = \begin{bmatrix} 2/3 \\ 1/3 \end{bmatrix}$. In the population with twofold fecundity, $\lambda = 2.581$ and $\mathbf{u} = \begin{bmatrix} 0.775 \\ 0.225 \end{bmatrix}$. The speed of growth increased less than twofold because the twofold increase in the fecundity at age 2 will be realized only by those who live till age 2. The stable age distribution is skewed towards the young when fecundity increases, and towards the old when fecundity decreases (cf. the pension crisis of ageing societies).

25. The 3×3 Leslie matrix has the dominant eigenvalue $\lambda = 1.263$ and the stable age distribution $\mathbf{u} = \begin{bmatrix} 0.442 \\ 0.350 \\ 0.208 \end{bmatrix}$. The comparison to the baseline population of the previous exercise ($\lambda = 1.5$) shows that delayed reproduction slows down population growth even if survival is 100% during the delay. This is because the offspring produced early in life start start reproducing quickly; early offspring are like invested money that produces interest. Late offspring are discounted like money received late and missing the gain of interest. If survival is less than 100% during the delay, then the speed of growth diminishes further.

26. At the stable age distribution, $\mathbf{LN} = \lambda\mathbf{N}$ and therefore $PN_1 = \lambda N_2$. Rearrange this into $N_2/N_1 = P/\lambda$. N_2/N_1 is greater than 1 if $\lambda < P$. Since P is less than 1, this implies that λ must be less than 1 and therefore the population is declining.

27. From the eigenvector equation $\mathbf{v}^T\mathbf{L} = \lambda\mathbf{v}^T$, we get $F_\omega v_1 = \lambda v_\omega$ for the last element v_ω of the left eigenvector. If F_ω is zero (the last age group does not reproduce), then v_ω must be zero. The last but one element of the left eigenvector must satisfy the equation $F_{\omega-1}v_1 + P_{\omega-1}v_\omega = \lambda v_{\omega-1}$. If both F_ω and $F_{\omega-1}$ are zero, then v_ω is zero as above, so that $F_{\omega-1}v_1 + P_{\omega-1}v_\omega$ is zero and therefore $v_{\omega-1}$ must also be zero. By repeating the same argument, one can see that v_i is zero for every post-reproductive age i.

28. (a) Exercise 4a: imprimitive, 4b: primitive, 4c: imprimitive; exercise 18: primitive; exercise 19: reducible; exercise 25: primitive
(b) Exercise 1a: primitive (assuming $0 < m < 1$); 1b: reducible; 1c: primitive (assuming that s is not zero); 1d: primitive (assuming that s_1 and s_2 are not zero)
(c) Exercise 14a: primitive; 14b: reducible
(d) Exercise 2: primitive
(e) Exercise 21: primitive
(f) biennial plants with a seed bank: primitive
(g) age-structured populations with post-reproductive age classes: reducible