Introduction to Mathematical Biology
Exercises 7.1-7.5

7.1. *Spatial structure.* Suppose a population lives in two habitats (two separate spatial locations, like butterflies in two meadows, fish in two bays of a lake, etc.). Two events take place in each year: (1) the population grows ρ_i-fold in habitat i ($i = 1, 2$); and (2) a fraction m of the individuals disperse, i.e., leave their habitat and move towards the other. Dispersal is a risky process: Dispersing individuals enter the opposite habitat with probability s and die with probability $1 - s$.
(a) Construct the projection matrix of this population.
(b) Suppose that dispersal is very risky, $s \to 0$. What is the condition for viability, which ensures that the population does not die out?

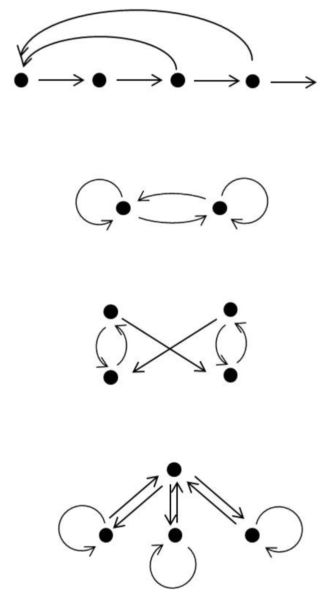
7.2. *Plant reproductive strategies.* Plants can reproduce via seeds as well as via vegetative propagules. In the latter case, rhizomes (underground stems) or runners (horizontally growing stems) grow new roots at some distance from the parent plant, and subsequently sever the connection to the parent plant such that the propagule becomes an independent individual. Suppose that full-sized flowering plants produce S seeds and V vegetative propagules each year. All seeds germinate and become small seedlings by the next census, whereas the vegetative propagules (which start much bigger than seeds) become intermediate-sized juvenile plants by the next census. Unless they die, the seedlings reach juvenile size by the second census of their life. Juvenile plants may die, may remail juvenile-sized or may grow into full-sized flowering plants. Flowering plants remain in the same state until they die. Construct the projection matrix of this population.

7.3. *Powers of primitive matrices.* Diagonalize the Leslie matrix

$$\mathbf{L} = \begin{pmatrix} 0.6 & 1.1 \\ 0.5 & 0 \end{pmatrix}$$

and use the diagonalized form to compute the ten-year projection matrix $\mathbf{L}^{10}$. Is the result close to a singular matrix? Why? What is the stable age distribution of this population?

7.4. *Life cycle graphs.* Decide for each of the life cycle graphs whether the corresponding projection matrix is irreducible and whether it is primitive. Describe possible biological scenarios that lead to these graphs. Summarize what type of qualitative behaviour these populations would show and what predictions can be made if the nonzero elements of the projection matrices are given.



7.5. *Reproductive value.* The element a_{ij} of a population projection matrix $\mathbf{A}$ denotes the expected number of *descendants* in state i produced in one year's time by an individual in state j. Descendants include the individual itself if it survives and moves from state j to state i, plus any surviving offspring who are in state i. Suppose that the projection matrix is primitive. Recall that the reproductive value of an individual in state j is the jth element of the leading left eigenvector $\mathbf{v}^T$ used in the diagonalization of $\mathbf{A}$.

(a) Show that the reproductive value of an individual equals the sum of the reproductive values of all its descendants in the next year divided with the annual growth rate λ (leading eigenvalue). The reproductive value measures the contribution of an individual to the population in the far future (cf. lecture). In this light, explain in words why the descendants' reproductive value is discounted by the division with λ. (In simpler terms, explain why the division is there; why a descendant in state i contributes v_i/λ rather than v_i to the individual's own reproductive value.)

(b) Suppose the population has achieved its stable state distribution. Let v denote the reproductive value of a randomly chosen individual. Show that the expected value of v is 1.

(c) Suppose again that the population has achieved its stable state distribution. Choose an individual at random and calculate the expected reproductive value of its descendants in the next year. Show that this equals the population growth rate λ.