Introduction to Mathematical Biology
Exercises 8.1-8.4

8.1. *Age-structured populations.* Consider an age-structured population with a primitive Leslie-matrix. Denote, as usual, the fecundity and survival probability of age class i with F_i and P_i, respectively. Let $l_1 = 1$, $l_i = \prod_{j=1}^{i-1} P_j$ for $i = 2, ..., \omega$, and let λ, $\mathbf{u}$, and $\mathbf{v}$ be respectively the dominant eigenvalue and the corresponding right and left eigenvector of the Leslie-matrix. Prove that

(a) at the stable age distribution, the frequency of age class i is proportional to l_i/λ^i;

(b) the reproductive value of age class i can be written as $v_i = \frac{1}{\lambda}(F_i v_1 + P_i v_{i+1})$ (with P_ω defined to be zero such that the second term is zero for $i = \omega$). This means that the reproductive value of age i is the reproductive value represented by the offspring produced at age i (given by $F_i v_1$) plus the reproductive value of the next age class in case the individual survives ($P_i v_{i+1}$), discounted by factor λ because one year of time is spent (cf. exercise 7.5).

Use the above results to demonstrate that

(i) all post-reproductive age classes have zero reproductive value ($v_j = 0$ for all j such that $F_i = 0$ for $i \geq j$);

and, assuming $\lambda \geq 1$ (the population does not die out),

(ii) the frequency of age classes decreases with age;

(iii) if there are k pre-reproductive age classes ($F_i = 0$ for $i = 1, ..., k$ but $F_i > 0$ for some $i > k$), then the reproductive value increases from age 1 through age k.

8.2. *Elasticity.* The lecture introduced the sensitivity of the population growth rate λ to an element of its projection matrix $\mathbf{A} = [a_{ij}]$,

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = v_i u_j$$

where v_i and u_j are the ith and jth elements of the leading left and right eigenvectors, respectively, with scaling such that $\mathbf{v}^T\mathbf{u} = 1$. Elasticity is a related measure that expresses the relative ("percentage") change of λ with respect to a relative change in a_{ij}:

$$e_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \frac{a_{ij}}{\lambda}$$

Prove that $\sum_{i,j} e_{ij} = 1$. Because elasticities are non-negative and the sum of all elasticities is 1, it is easy to judge if a certain elasticity value is high or low (i.e., relative to 1).

8.3. *Conservation of endangered species* (simplified from Crouse et al. 1987). As for many species, survival and fecundity of sea turtles depend on their size. The population is divided into three classes: the smallest individuals (<10 cm) are called juveniles, these are all 1-year old; the intermediate class (10-85 cm) contains sub-adults, an individual remains sub-adult possibly for many years; and the fully grown individuals (>85 cm) are adults. Only adults reproduce, and an adult female produces 60 female juveniles by the next year. Juveniles survive with probability 0.6 and become sub-adults when they are 2-year old. Sub-adults grow slowly: with probability 0.7, sub-adults remain sub-adults also in the next year, and only with probability 0.001 they become adults (the rest of sub-adults die). Once in the adult class, the turtles survive till the next year with probability 0.8.

The leading eigenvalue of the projection matrix is $\lambda = 0.95$, which means that the turtles are dying out. There are two possible policies to save the population: (i) we can protect the beaches where the eggs are laid to avoid that the newborn die before they reach the sea, and thereby increase the (effective) fecundity; or (ii) we can apply a special device on fishing nets to avoid catching adults, and thereby increase adult survival. Suppose increasing the survival of the newborn (and therefore the effective fecundity) by 1% costs A, whereas increasing adult survival by 1% costs B. Evaluate the elasticities to judge which policy is more effective; should we invest the available money into protecting the beaches or protecting the adults?

8.4. *Next generation matrix.* Consider the plant population described in exercise 7.2 with the projection matrix

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & S \\ s_1 & (1-p)s_2 & V \\ 0 & ps_2 & s_3 \end{pmatrix}$$

where S and V are respectively the number of seedlings and number of vegetatively produced juveniles per adult plant, s_1 is the probability that a seedling survives (in which case it becomes a juvenile), s_2 is the probability that a juvenile survives, in which case it matures into an adult plant with probability p and remains a juvenile with probability $1-p$, and s_3 is the probability that an adult survives (in which case it remains an adult).

(a) Consider producing a seedling and producing a new juvenile by an adult as "birth", so that there are two birth states (seedling, juvenile). Formulate the next generation matrix (it is enough to obtain the 2×2 block that corresponds to the birth states, i.e., $\mathbf{K_1}$ in the notation of the lecture) and obtain R_0.

Hint 1: You can calculate the elements k_{ij} of the next generation matrix directly (so that you can avoid inverting a 3×3 matrix). For k_{11}, calculate from the life cycle graph the probability that a seedling ever becomes an adult, the expected lifetime of an adult, and from these, the expected number of new seedlings produced per one seedling at the start; and analogously for the other elements k_{ij}. To find out what is the probability of getting through the juvenile phase (which may last for several years), use the method of *first step analysis*. Let q be the probability that a juvenile ever becomes an adult (i.e., does not die as a juvenile). A juvenile becomes an adult in the next year with probability ps_2, whereas with probability $(1-p)s_2$ the juvenile remains a juvenile in the next year and hence has probability q to become an adult some time later. Therefore we have the equation $q = ps_2 + (1-p)s_2q$ for q.

Hint 2: Notice that the resulting next generation matrix is singular. This is nice because it is easy to find the eigenvalues. But you may want to contemplate why we get a singular next generation matrix in this model.

(b) Alternatively, consider only seedling production as "birth", so that there is only one birth state (seedlings). Here we need to assume that V is not too large. Write the projection matrix as $\mathbf{A} = \mathbf{F} + \mathbf{T}$ with only seedling production as birth, and find the condition that V has to satisfy for the next generation formalism to be applicable (cf. lecture). Find R_0.

Hint 3: With a single birth state, the block $\mathbf{K_1}$ is 1×1, i.e., a single number, which is R_0 itself. It is possible to calculate this number directly as suggested in (a). If this seems too complicated and you resort to inverting a 3×3 matrix, notice that in this problem you will use only the last row of the inverse, so it is enough to calculate the three elements of the last row.

(c) Somewhat surprisingly, (a) and (b) yield different expressions for R_0. Intuitively, the reason is that a generation is shorter in (a) than in (b), so that the same real-time population growth gives a lower value for R_0 in (a) than in (b). However, for both versions $\lambda \gtreqless 1 \Leftrightarrow R_0 \gtreqless 1$ must be true (where λ is the leading eigenvalue of the projection matrix $\mathbf{A}$; cf. lecture). Show that indeed R_0 obtained in (a) is greater than 1 if and only if R_0 obtained in (b) is greater than 1, so that the two versions make the same prediction as to whether the population grows or declines. (Recall that predicting growth vs decline is the goal of calculating R_0; if we need the actual speed of growth or decline, we need to obtain the annual growth rate, i.e., λ itself.)