Assignment 2 — Age-Structured Models

2019862s

Monday 14th March, 2016

Question 1. *Consider the Usher model*

$$\mathbf{N}_{t+1} = A\mathbf{N}_t,$$

where A is the $n \times n$ Usher matrix, and $\mathbf{N}_t$ is the $1 \times n$ column vector, given by

$$A = \begin{bmatrix} P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix}, \qquad \mathbf{N_t} = \begin{bmatrix} N_t^1 \\ N_t^2 \\ \vdots \\ N_t^n \end{bmatrix},$$

and $N_t^i \geq 0$ is the number of individuals in stage i at time t, $F_i \geq 0$ for $i \in [2,7]$ is the stage specific fecundity, $0 \leq P_i \leq 1$ for $i \in [1,7]$ is the probability of surviving and remaining in the same stage, and $0 \leq G_i \leq 1$ for $i \in [1,6]$ is the probability of surviving and growing to the next stage.

Solution 1. The Usher matrix for the tortoise population is given by

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.67 & 0.74 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.05 & 0.66 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.015 & 0.69 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.052 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.81 & 0.81 \end{bmatrix}$$

The following flow diagram illustrates the transitions between the age groups of the tortoise population.

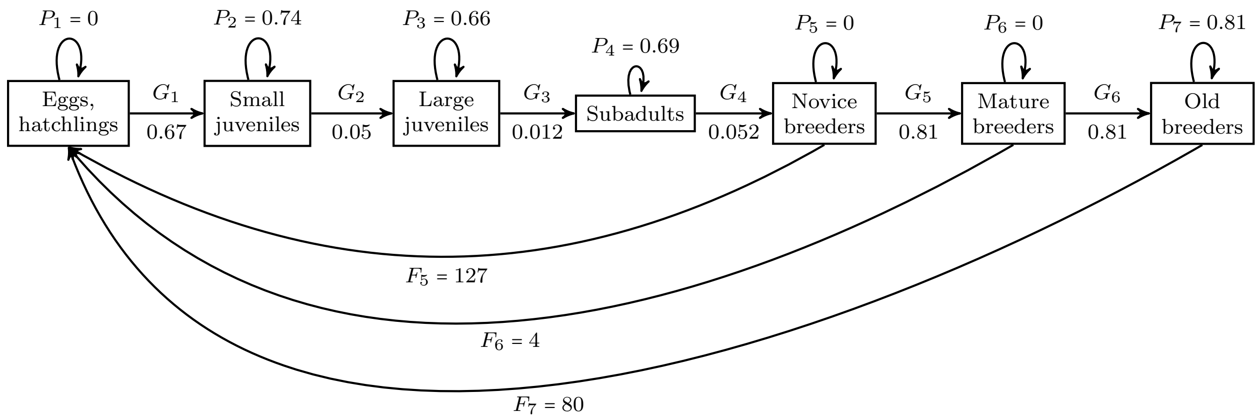

Figure 1: Flow diagram, illustrating the transitions between age groups.

Let N^1 be the eggs, hatchlings, N^2 — the small juveniles, N^3 — large juveniles, N^4 — subadults, N^5 — novice breeders, N^6 — mature breeders, and N^7 — old breeders. Considering the Usher matrix A and the diagram in Figure 1, we can make the following observations:

- Eggs, hatchlings N^1 — 67% survive and grow to small juveniles. The rest 33% die. As they have 0% chance of surviving and remaining as eggs, we can conclude that tortoise eggs take approximately one year to hatch.

- Small juveniles N^2 — 74% survive and remain as small juveniles; 5% grow to large juveniles; 21% die. This shows that small juvenile individuals take more than a single year to grow.

- Large juveniles N^3 — 66% survive and remain in the same age class; 1.5% survive and grow to subadults. The rest 32.5% die out. Again, it takes more than a year for a large juvenile to grow.

- Subadults N^4 — 69% survive and remain; 5.2% survive and grow to novice breeders. Remaining 25.8% die. Note that this class has no fecundity, i.e. does not breed.

- Novice breeders N^5 — none of the novice breeders survive and remain in the same class; 81% survive and grow to mature breeders, the rest 19% die. Each female novice breeder produces 127 female eggs per year.

- Mature breeders N^6 — 81% grow to old breeders, 19% die. Each female produces 4 eggs.

- Old breeders N^7 — 81% survive and remain old breeders, 19% die. Each female produces 80 female eggs.

□

Question 2. *Calculate the dominant eigenvalue λ of the Usher matrix A and the stable age distribution* $\mathbf{v}$.

Solution 2. The following MATLAB script `question2.m` calculates the dominant eigenvalue λ of the Usher matrix A and the stable age distribution vector $\mathbf{v}$.

Listing 1: Script for finding the dominant eigenvalue and corresponding eigenvector of the Usher matrix A.

```
%% Lab 2: 2019862s
% Question 2

% Find the dominant eigenvalue (growth rate) and
% the right eigenvector (stable age distribution).

A=[   0,      0,       0,       0,    127,      4,        80;...
   0.67,   0.74,       0,       0,      0,      0,         0;...
      0,   0.05,    0.66,       0,      0,      0,         0;...
      0,      0,   0.015,    0.69,      0,      0,         0;...
      0,      0,       0,   0.052,      0,      0,         0;...
      0,      0,       0,       0,   0.81,      0,         0;...
      0,      0,       0,       0,      0,   0.81,     0.81];
% Show the eigenvectors with corresponding eigenvalues
[V,D]=eig(A);
% Store all eigenvalues from the diagonal matrix
L=diag(D);
% The position of the dominant eigenvalue
j=find(abs(L)==max(abs(L)));
% Ensure there is a unique dominant eigenvalue
ndom=length(L);
% Display the eigenvalue
lambda=L(j);
disp(lambda);
% Stable age distirbution
v=V(:,j);
disp(v);


% Uncomment code below to estimate the
% stable age distribution at time t.
% % Set value for time we are interested in
% t = 40;
% % Approximate the population using Equation (2)
% Ntime=lambda^(t)*v;
% disp(Ntime);
```

Running the script yields a matrix V with columns all eigenvectors of A, and a diagonal matrix D with diagonal entries the corresponding eigenvalues of A. Then we extract the diagonal entries of D, i.e. the eigenvalues, in a vector L. The position of the dominant eigenvalue stored in the index j and hence, we store it as the variable λ. The corresponding eigenvector is the variable v. The output produced is shown in Figure 2.

```
lambda =

    0.9480


v =

    0.2925
    0.9421
    0.1636
    0.0095
    0.0005
    0.0004
    0.0026
```

Figure 2: Output from running the script `question2.m`.

Thus, the determining pair of eigenvalue and eigenvector of the Usher matrix A are

$$\lambda = 0.948, \qquad \mathbf{v} = \begin{bmatrix} 0.2925 \\ 0.9421 \\ 0.1636 \\ 0.0095 \\ 0.0005 \\ 0.0004 \\ 0.0026 \end{bmatrix}. \tag{1}$$

Observe that $\lambda < 1$, which means that the population is decreasing with a rate $\lambda^t = 0.948^t$, i.e. with $\approx 5\%$ each year. Note that this agrees with the formulation of the problem, since the tortoises are experiencing a rapid decline due to destruction of their habitat and vegetation. Now consider the vector $\mathbf{v}$. It shows the proportional distribution of the population among the age classes. Then the relative age distribution is

$$N^1 : N^2 : N^3 : N^4 : N^5 : N^6 : N^7 \approx 30 : 90 : 20 : 1 : 0.05 : 0.04 : 0.30.$$

Since the i^{th} entry of the stable age distribution corresponds to the i^{th} age class, we can see that the largest proportion of the population are the small juveniles, and the smallest — the mature breeders. Furthermore, note that the 'baby' age classes, N^1, N^2, N^3 form the majority of the population, while the adults, N^4, and the 'breeder' age classes, N^5, N^6, N^7, constitute a small proportion of the total population. Now observe the probabilities of surviving and growing to the next stage of the 'baby' age classes, $G_1 = 0.67$, $G_2 = 0.05$, and $G_3 = 0.015$. This shows that even though the three 'baby' classes form the largest proportion of the total population, they have a very small chance of surviving and proceeding to the next stages, which significantly decreases the chances of the tortoises to grow and stabilize. This might be caused by the destruction of vegetation. In general, the baby classes may die since the eggs are left unattended (usually in nests dug by the females) and juveniles are more vulnerable and unable to protect themselves from predators. Furthermore, environmental factors (such as heat and drought in the desert) decrease their probability of growing [1].

On the other hand, the 'breeder' classes form a much smaller part of the total population, but the fecundity rates of the novice N^5 and old N^7 breeders are quite high, namely $F_5 = 127$ and $F_7 = 80$. This is typical for species of the *Testudinidae* family, as the females lay a large number of eggs (usually turtles, not tortoises though). However, not all of them survive. Also bear in mind that while the novice breeders have a very high fecundity, their probability of surviving and remaining in the same class is $P_5 = 0$ and the probability of surviving and moving to the next age class is $G_5 = 0.81$, meaning that 81% of the novice breeders become mature breeders (who have a significantly low fecundity rate $F_6 = 4 << F_5 = 127$) and the rest 19% just die out. Thus, in summary the eigenanalysis makes sense, as really the population is dying out because:

- In general, the tortoises are unable to survive due to destruction of vegetation;
- Baby classes form a significantly larger proportion of the population, but have generally low probabilities to grow up to the breeder classes;
- Two out of the three breeding classes actually have 0% chance of surviving and remaining in the same age class, hence, the ability to reproduce decreases significantly;
- The breeding classes form a tiny proportion of the total population and the tortoises are unable to increase in numbers and stabilize.

As discussed in the lecture notes, if

$$|\lambda| = \max_{j=0,n}\{|\lambda_j|\},$$

then the population behaves as

$$\mathbf{N}_t \propto \lambda^t \mathbf{v}. \tag{2}$$

Let us examine what happens for different values of t, where the index of $\mathbf{N}$ denotes the corresponding time. The results are produced from running the script in Listing 1.

$$\mathbf{N}_{t=1} = \begin{bmatrix} 0.2773 \\ 0.8931 \\ 0.1551 \\ 0.0090 \\ 0.0005 \\ 0.0004 \\ 0.0025 \end{bmatrix}, \quad \mathbf{N}_{t=5} = \begin{bmatrix} 0.2240 \\ 0.7214 \\ 0.1253 \\ 0.0073 \\ 0.0004 \\ 0.0003 \\ 0.0020 \end{bmatrix}, \quad \mathbf{N}_{t=10} = \begin{bmatrix} 0.1715 \\ 0.5523 \\ 0.0959 \\ 0.0056 \\ 0.0003 \\ 0.0002 \\ 0.0015 \end{bmatrix}, \quad \mathbf{N}_{t=40} = \begin{bmatrix} 0.0346 \\ 0.1113 \\ 0.0193 \\ 0.0011 \\ 0.0001 \\ 0.0000 \\ 0.0003 \end{bmatrix}.$$

$$\mathbf{N}_{t=50} = \begin{bmatrix} 0.0203 \\ 0.0653 \\ 0.0113 \\ 0.0007 \\ 0.0000 \\ 0.0000 \\ 0.0002 \end{bmatrix}, \quad \mathbf{N}_{t=80} = \begin{bmatrix} 0.0041 \\ 0.0132 \\ 0.0023 \\ 0.0001 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}, \quad \mathbf{N}_{t=100} = \begin{bmatrix} 0.0014 \\ 0.0045 \\ 0.0008 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}, \quad \mathbf{N}_{t=128} = \begin{bmatrix} 0.0003 \\ 0.0010 \\ 0.0002 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}.$$

Hence, if the tortoise population remains under the same conditions and changes with rate $\lambda^t = 0.948^t$, the first age class to die out is the mature breeders N^6 and this happens at $t = 40$. The novice breeders N^5 then die out at $t = 50$, the old breeders N^7 at $t = 80$, and the subadults N^4 at $t = 100$. Hence, we observe that the critical time is $t = 40$, when one of the breeding classes of the tortoise population dies out. Naturally, if one age class becomes extinct, the chain of classes is seriously damaged. Then the total population starts decreasing extremely fast as it is unable to stabilize and eventually dies out. Ultimately, the population becomes extinct at $t \approx 129$. Notice that the first age class to die out are the mature breeders. Even though our previous analysis shows that their fecundity is very low, i.e. $F_6 = 4$, once they become extinct, all subclasses of the population start dying out. This shows that every class in the population is important for the overall dynamics and even if the 'least' reproductive class becomes extinct, the whole population eventually dies out.

Our analysis so far yields the following predictions:

- The small juveniles N^2 form the largest proportion of the population, thus, their survivability may be crucial for the overall growth of the tortoise population;
- The 'baby' classes are most vulnerable to predation and death, so their conservation may be important;
- The old breeders have the second largest fecundity, but the fertility of most species decreases with age, so we have to apply additional analysis to conclude which breeding class has the most significant contribution to the growth rate of the population.

□

Question 3. *Investigate how changes to the matrix entry $a_{2,2}$ affects the growth rate.*

Solution 3. The following MATLAB script `question3.m` investigates the change in the eigenvalue λ while varying the values of the $a_{2,2}$ entry of the Usher matrix A. We are varying the value P_2 — the probability of survival and remaining in the same age class of the small juveniles. The probability P_2 is iterated in a `for` loop for values between 0 and 1 with a step 0.05. The code is a modified version of the answer provided by Bowers in [2].

Listing 2: Iterating the $a_{2,2}$ entry and storing dominant eigenvalues in a vector.

```
%% Lab 2: 2019862s
% Question 3

% Enter matrix entries, vary A_{2,2}=a, for
% a = [0,1] with increments of 0.05,
% calculate the dominant eigenvalues,
% and store them in a vector.
% Specify the initial matrix A
A=[    0,      0,       0,       0,    127,      4,        80;...
    0.67,   0.74,       0,       0,      0,      0,         0;...
       0,   0.05,    0.66,       0,      0,      0,         0;...
       0,      0,   0.015,    0.69,      0,      0,         0;...
       0,      0,       0,   0.052,      0,      0,         0;...
       0,      0,       0,       0,   0.81,      0,         0;...
       0,      0,       0,       0,      0,   0.81,    0.81];
% Pre-allocate the values we want to iterate
% over for the element in (2, 2)
a = (0:0.05:1)';
% Pre-allocate a vector to store the maximum eigenvalues
A22Vec = NaN * ones(length(a), 1);
% Loop over A22Vec
for i = 1:1:length(a)
    % Obtain the version of A for the current iteration
    A(2, 2) = a(i);
    % Obtain the maximum eigenvalue of the
    % current A, and store in gVec
    A22Vec(i, 1) = max(eig(A));
end
% Show the vector in the console
disp(A22Vec);
% Begin figure
figure
% Plot the vector with the stored eigenvalues
% vs. a=[0,1], i.e. how the eigenvalues change
% as we vary the A_{2,2} entry of the Usher matrix
plot(a, A22Vec);
xlabel('a=[0:0.05:1]')
ylabel('Dominant eigenvalues \lambda')
title('Dominant eigenvalues vs a')
```

The resulting vector, which stores the dominant eigenvalues from the iteration is displayed below, along with a plot of the graph of the dominant eigenvalue against $a_{2,2}$ in Figure 4.

```
>> question3
    0.8762
    0.8783
    0.8806
    0.8831
    0.8859
    0.8889
    0.8922
    0.8958
    0.8999
    0.9044
    0.9095
    0.9154
    0.9222
    0.9300
    0.9393
    0.9504
    0.9638
    0.9802
    1.0003
    1.0250
    1.0545
```

Figure 3: The dominant eigenvalues stored in a vector from running `question3.m`.

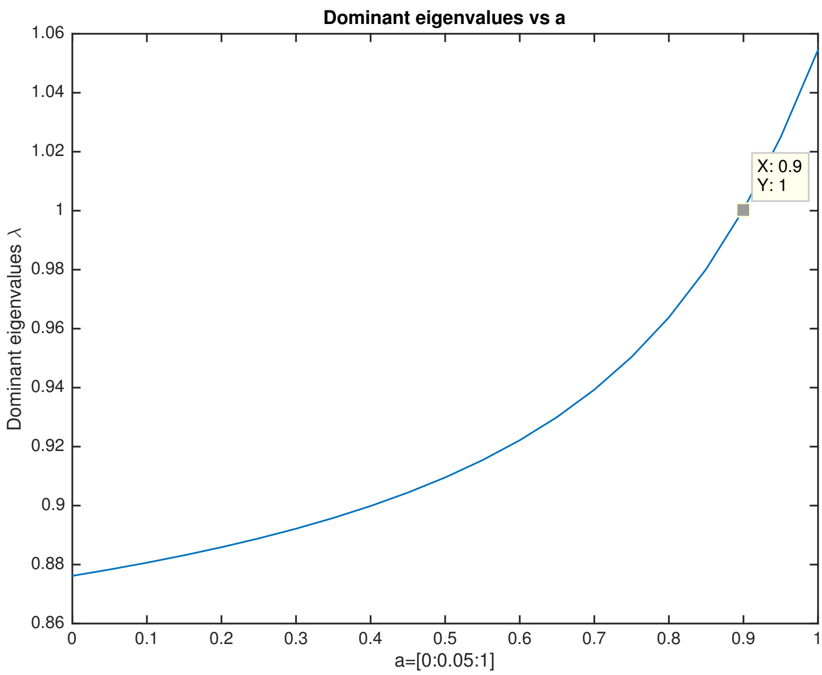

Figure 4: The dominant eigenvalues plotted against $0 \leq P_2 \leq 1$.

The plot in Figure 4 shows that when $a_{2,2} > 0.9$, the dominant eigenvector $\lambda > 1$ and thus, the population of tortoises exhibits a growth. The physical interpretation of $a_{2,2} = P_2$ is the probability of the small juveniles to survive and remain in the same class. When $P_2 = 0.9$, that is, the small juveniles have 90% chance of surviving and remaining small juveniles, the population is kept constant. Similarly, if $P_2 < 0.9$, then the population is decreasing, as the growth rate $\lambda < 1$. Therefore, if more than 90% of the small juveniles remain in the same class, the population eventually increases. If less than 90% of the small juveniles remain, the population decreases. Note that the probability of the small juveniles to grow to large juveniles is 5% and remains constant. Thus, we require more than 95% to remain alive in general in order for the population to stabilize. It is critical that sufficient conditions for the growth of the small juveniles are applied if we want to prevent extinction of the tortoise population. Note that this holds if and only if all the other parameters are kept constant.

In reality, however, every age class is dependent on the others so we cannot say that the probability of the small juveniles to survive and remain as such is sufficient to analyze the population dynamics and is critical for the overall increase or decrease of the tortoise population. We need to consider how the other age classes' probabilities and fecundities affect the stability of the population. To summarize, in theory if more than 90% of the small juveniles survive and remain in this age class, the population will increase and stabilize. In real life, however, this depends on other factors, such as the fecundities of the breeding classes, the probabilities of the eggs to survive and move to the small juveniles, predation by other species, mortality rates, various environmental and external forces, etc. □

Question 4. *In this question we calculate the proportional sensitivity (or "elasticity") of λ to changes in a matrix element a_{ij}, given by*

$$\frac{\partial \ln \lambda}{\partial \ln a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda}\left(\frac{w_i v_j}{\sum_k w_k v_k}\right),$$

where λ is the dominant eigenvalue of A, $\mathbf{v}$ the corresponding eigenvector and $\mathbf{w}$ is the corresponding left eigenvector $\mathbf{w}A = \lambda\mathbf{w}$.

Solution 4. Consider the definition of the right eigenvector

$$A\mathbf{v} = \lambda\mathbf{v}.$$

We are interested in the rate of change of both the matrix, the eigenvalue, and the eigenvector, hence, we need to compute the total derivative of the system with respect to the ij^{th} entry, that is

$$\frac{d}{da_{ij}}(A\mathbf{v}) = \frac{d}{da_{ij}}(\lambda\mathbf{v}).$$

Using the Product Rule, we obtain

$$\frac{\partial A}{\partial a_{ij}}\mathbf{v} + A\frac{\partial \mathbf{v}}{\partial a_{ij}} = \frac{\partial \lambda}{\partial a_{ij}}\mathbf{v} + \lambda\frac{\partial \mathbf{v}}{\partial a_{ij}}, \tag{*}$$

as required. Now let us compute the dot product of $\mathbf{w}$ and Equation *.

$$\mathbf{w}\cdot\left(\frac{\partial A}{\partial a_{ij}}\mathbf{v} + A\frac{\partial \mathbf{v}}{\partial a_{ij}}\right) = \mathbf{w}\cdot\left(\frac{\partial \lambda}{\partial a_{ij}}\mathbf{v} + \lambda\frac{\partial \mathbf{v}}{\partial a_{ij}}\right)$$

$$\therefore \quad \mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v} + \underbrace{\mathbf{w}\cdot A}_{\text{left eigenvector}}\frac{\partial \mathbf{v}}{\partial a_{ij}} = \mathbf{w}\cdot\frac{\partial \lambda}{\partial a_{ij}}\mathbf{v} + \underbrace{\mathbf{w}\cdot\lambda}_{\text{left eigenvector}}\frac{\partial \mathbf{v}}{\partial a_{ij}}.$$

Notice that the two underbraced terms are the precise definition of the left eigenvector, so they are equal. Thus, we can cancel them to obtain

$$\mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v}+\underbrace{\mathbf{w}\cdot A}_{=\mathbf{w}\lambda}\frac{\partial \mathbf{v}}{\partial a_{ij}}=\mathbf{w}\cdot\frac{\partial \lambda}{\partial a_{ij}}\mathbf{v}+\underbrace{\mathbf{w}\cdot\lambda}_{=\mathbf{w}A}\frac{\partial \mathbf{v}}{\partial a_{ij}}$$

$$\implies \mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v}+\cancel{\mathbf{w}\cdot A\frac{\partial \mathbf{v}}{\partial a_{ij}}}=\mathbf{w}\cdot\frac{\partial \lambda}{\partial a_{ij}}\mathbf{v}+\cancel{\mathbf{w}\cdot\lambda\frac{\partial \mathbf{v}}{\partial a_{ij}}}$$

$$\therefore\quad \mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v}=\mathbf{w}\cdot\frac{\partial \lambda}{\partial a_{ij}}\mathbf{v}.$$

Since $\dfrac{\partial \lambda}{\partial a_{ij}}$ is a scalar, we can rearrange the above equation to obtain

$$\mathbf{w}\cdot\mathbf{v}\frac{\partial \lambda}{\partial a_{ij}}=\mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v}, \tag{3}$$

as required. Finally, writing out the LHS explicitly yields

$$\begin{aligned}\mathbf{w}\cdot\mathbf{v}\frac{\partial \lambda}{\partial a_{ij}}&=[w_1,\dots,w_i,\dots,w_n]\cdot\begin{bmatrix}v_1\\ \vdots\\ v_j\\ \vdots\\ v_n\end{bmatrix}\frac{\partial \lambda}{\partial a_{ij}}\\ &=\sum_k w_k v_k\frac{\partial \lambda}{\partial a_{ij}}\end{aligned} \tag{4}$$

Similarly, writing out the RHS explicitly yields

$$\begin{aligned}\mathbf{w}\cdot\frac{\partial A}{\partial a_{ij}}\mathbf{v}&=[w_1,\dots,w_i,\dots,w_n]\cdot\begin{bmatrix}0&\dots&0&\dots&0\\ \vdots&\ddots&\vdots&\iddots&\vdots\\ 0&\dots&1_{ij}&\dots&0\\ \vdots&\iddots&\vdots&\ddots&\vdots\\ 0&\dots&0&\dots&0\end{bmatrix}\begin{bmatrix}v_1\\ \vdots\\ v_j\\ \vdots\\ v_n\end{bmatrix}\\ &=[w_1,\dots,w_i,\dots,w_n]\cdot\begin{bmatrix}0\\ \vdots\\ v_j\\ \vdots\\ 0\end{bmatrix}\\ &=w_i v_j,\qquad \text{for } i\neq j.\end{aligned} \tag{5}$$

By Equation 3, we know that the expressions 4 and 5 are equal. Thus,

$$\sum_k w_k v_k\frac{\partial \lambda}{\partial a_{ij}}=w_i v_j\quad\therefore\quad \frac{\partial \lambda}{\partial a_{ij}}=\frac{w_i v_j}{\sum_k w_k v_k},$$

as required. □

Question 5. *Finding the dominant left eigenvector, corresponding to the matrix A.*

Solution 5. The following MATLAB script `question5.m` is used to find the dominant left eigenvector of A.

Listing 3: Determining the dominant left eigenvector of A.

```
%% Lab 2: 2019862s
% Question 5

% Enter matrix entries, calculate the eigenvalues,
% and find the dominant eigenvalue.

A=[    0,      0,       0,       0,    127,      4,      80;...
    0.67,   0.74,       0,       0,      0,      0,       0;...
       0,   0.05,    0.66,       0,      0,      0,       0;...
       0,      0,   0.015,    0.69,      0,      0,       0;...
       0,      0,       0,   0.052,      0,      0,       0;...
       0,      0,       0,       0,   0.81,      0,       0;...
       0,      0,       0,       0,      0,   0.81,    0.81];
% Show the eigenvectors with corresponding eigenvalues
[V,D,W]=eig(A);
% Store all eigenvalues from the diagonal matrix
L=diag(D);
% The position of the dominant eigenvalue
j=find(abs(L)==max(abs(L)));
% Ensure there is a unique dominant eigenvalue
ndom=length(L1);
% Display the eigenvalue
lambda=L(j);
disp(lambda);
% Left eigenvector
w=W(:,j)';
disp(w);
```

The output from running the script `question5.m` is displayed below.

```
>> question5

lambda =

    0.9480


w =

    0.0010    0.0015    0.0062    0.1183    0.5869    0.5228    0.6067
```

Figure 5: The left dominant eigenvector of A.

Note that MatLab calculates the left eigenvectors as columns of the matrix W, so we explicitly require the transpose of the left eigenvector corresponding to the dominant eigenvalue λ. Hence, the left dominant eigenvector is

$$\mathbf{w} = [0.0010, 0.0015, 0.0062, 0.1183, 0.5869, 0.5228, 0.6067]. \tag{6}$$

The left eigenvector $\mathbf{w}$ corresponding to the dominant eigenvalue λ gives the reproductive value of the different age classes [3]. In contrast with the right eigenvector $\mathbf{v}$, which gave us information about the proportional distribution of the population, the left eigenvector $\mathbf{w}$ indicates the proportional reproductive contribution of each age class. We can think of the reproductive values as a very crude approximation of how much does the respective age class contribute to the production of eggs. However, bear in mind that we define the fecundities as 'the average number of daughters born per female in class i per time step t' according to the Lecture Notes. Thus, it is important to note that:

- We consider the number of eggs a female tortoise produces per year, while tortoises may mate several times a year, depending on many internal and external factors, which may vary the values from year to year;
- Tortoises are generally polygamous (one male can breed with many females) and we do not measure the fertility of the males precisely [1];
- We take into account the 'female' eggs produced by a female per year, so we do not approximate the male eggs;
- We assume that the individuals reach sexual maturity at a particular age, while they may start breeding at a younger age [1].

Nevertheless, we can now examine the reproductive values. Following the same line of thought as in analyzing the right eigenvector, the proportional reproductive values are

$$N^1 : N^2 : N^3 : N^4 : N^5 : N^6 : N^7 \approx 0 : 0 : 1 : 10 : 60 : 50 : 60.$$

Note that in our model, the breeding classes are N^5, N^6, N^7. This illustrates that our fecundities are an approximation to what happens in reality. The reproductive values in the left eigenvector show that the breeding classes N^5, N^6, N^7 have the largest contribution to the overall reproduction (not surprising at all), but the subadults N^4 have a small contribution as well, which may be the result of some individuals reaching sexual maturity (or copulating) at a younger age as discussed above. Also, the contribution of the mature breeders N^6 is approximately the same as of the novice and old breeders, even though their fecundity is quite low $F_6 = 4$ compared to $F_5 = 127$ and $F_7 = 80$. So we can conclude that despite their low fecundity rate, the mature breeders have a large impact on the production of eggs. Nevertheless, we proceed with analyzing solely the fecundity rates as given in the Usher matrix. □

Question 6. *Calculate the elasticity of λ to changes in each value of P_i, G_i, and F_i.*

Solution 6. The following MATLAB script `question6.m` is used to calculate the elasticity of λ to changes in P_i, G_i, and F_i.

Listing 4: Calculating the elasticity of λ to changes in the the probabilities and fecundities.

```
%% Lab 2: 2019862s
% Question 6

% Calculate the elasticity of the eigenvalue
% to changes in each entry of the matrix A

% Specify the initial matrix A
A=[    0,      0,       0,       0,    127,      4,       80;...
    0.67,   0.74,       0,       0,      0,      0,        0;...
       0,   0.05,    0.66,       0,      0,      0,        0;...
       0,      0,   0.015,    0.69,      0,      0,        0;...
       0,      0,       0,   0.052,      0,      0,        0;...
       0,      0,       0,       0,   0.81,      0,        0;...
       0,      0,       0,       0,      0,   0.81,     0.81];
% Eigenspace of the Usher matrix A
[V,D,W]=eig(A);
% Store the eigenvalues in a vector
L=diag(D);
% Indicate position of dominant eigenvalue
k=find(abs(L)==max(abs(L)));
% Obtain dominant eigenvalue
lambda=L(k);
% Corresponding left eigenvector
w=W(:,k);
% Corresponding right eigenvector
v=V(:,k);
% Calculate the length of the eigenvector
n=length(v);
% Define the vector dot product of v and w
vdotw=dot(v,w);
% Iterate over the columns
for i=1:n;
    % Iterate over the rows
    for j = 1:n;
        % Calculate the sensitivity of
        % the eigenvalue
        sensitivity(i,j)=v(j)*w(i)/vdotw;
    end;
end;
% Calculate the elasticity
elasticity=(sensitivity.*A)/lambda
% Store and plot the elasticity of
```

```
% the eigenvalue for the probabilities
% and fecundities
probabilityStay=diag(elasticity);
probabilityGrow=[diag(elasticity,-1);0];
fecundity=[0,elasticity([1],[2:7])];
figure
plot(1:n,probabilityStay,'k')
axis([1 7 0 0.3])
hold on
plot(1:n,probabilityGrow,'k:')
plot(1:n,fecundity,'k--')
xlabel('Age class i')
ylabel('Elasticities of \lambda to changes in Pi, Gi, Fi')
legend('Pi - probability of staying',...
    'Gi - probability of growing',...
    'Fi - fecundity')
```

The output from running the script is a matrix, which contains all the calculated elasticities and is displayed below in Figure 6.

```
>> question6

elasticity =

         0         0         0         0    0.0123    0.0003    0.0388
    0.0514    0.1827         0         0         0         0         0
         0    0.0514    0.1177         0         0         0         0
         0         0    0.0514    0.1374         0         0         0
         0         0         0    0.0514         0         0         0
         0         0         0         0    0.0391         0         0
         0         0         0         0         0    0.0388    0.2275
```

Figure 6: The resulting elasticities for each entry.

Let E_{P_i} denote the elasticity of λ to changes in P_i. Let E_{G_i} be the elasticity of λ to changes in G_i. Finally, let E_{F_i} be the elasticity of λ with respect to changes in F_i. Hence, the non-zero elasticities of $\lambda_{i,j}$ are as follows:

$E_{P_2} = 0.1827$, $\quad E_{P_3} = 0.1177$, $\quad E_{P_4} = 0.1374$, $\quad E_{P_7} = 0.2275$,

$E_{G_1} = E_{G_2} = E_{G_3} = E_{G_4} = 0.0514$, $\quad E_{G_5} = 0.0391$, $\quad E_{G_6} = 0.0388$,

$E_{F_5} = 0.0123$, $\quad E_{F_6} = 0.0003$, $\quad E_{F_7} = 0.0388$.

The resulting plot of the elasticity of λ to changes in P_i, G_i, and F_i is shown below in Figure 7.

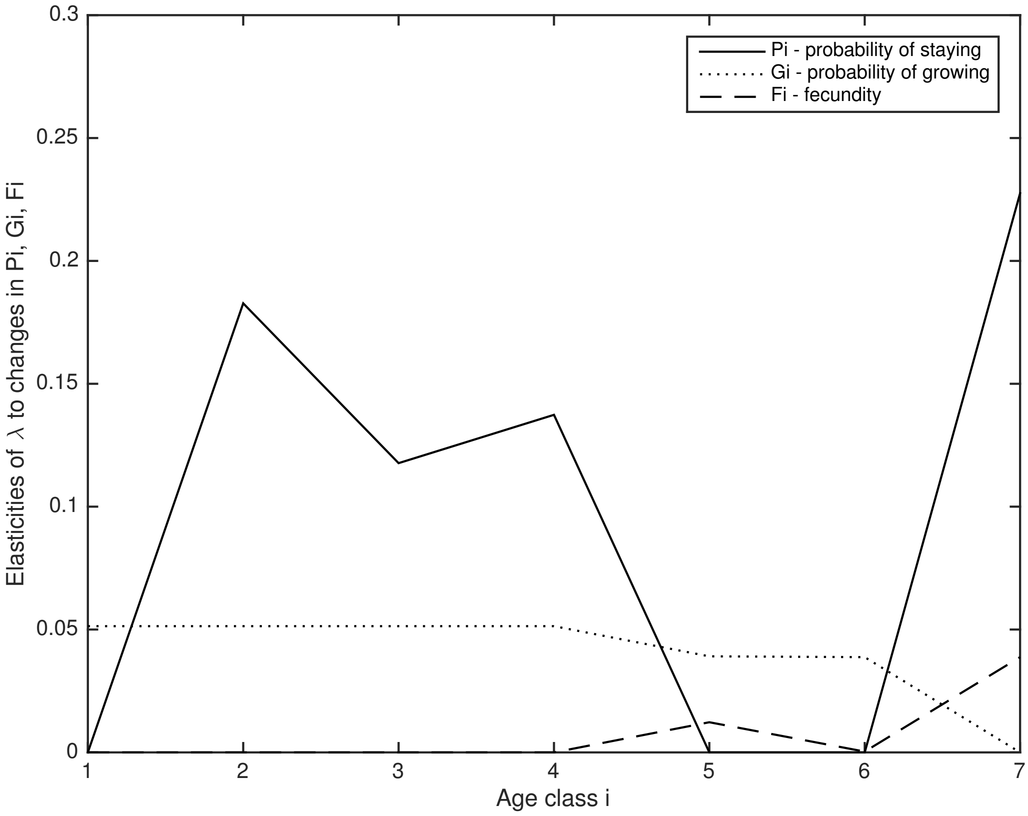

Figure 7: Plotting the elasticity of λ to changes in the probabilities and fecundities.

Now consider Figure 7. The curves represent the elasticity of λ in the following way:

- Solid curve — probability of surviving and remaining in the same class;
- Dotted curve — probabilities of surviving and growing to the same class;
- Dashed curve — fecundities.

First consider the P_i curve (i.e. the solid curve). The graph indicates that proportional changes in λ due to varying the P_1, P_5, and P_6 parameters (or the $a_{1,1}$, $a_{5,5}$, and $a_{6,6}$ entries of the Usher matrix respectively), do not affect the dominant eigenvalue. However, the probabilities P_2, P_3, P_4, and P_7 do have an effect on the dominant eigenvalue, and in particular, these four parameters have the largest net effect. Going back to our original Usher matrix, P_1, P_5, and P_6 are actually zeros. Thus, even if in reality they are not precisely zero, it makes sense to approximate them to zero, since they have negligible effect on the growth of the population.

In biological terms, this means that changes in the eggs and hatchlings, novice breeders, and mature breeders do not affect the growth rate of the tortoise population. However, if we manage to conserve as many small and large juveniles, subadults and old breeders, (i.e. increase their probability of survival and remaining), the population may start increasing and stabilizing.

It is important to note that the sum $P_j + G_j \leq 1$ for $j = [1, 6]$, and $P_7 \leq 1$, so we can think of $(P_i + G_i)$ as the general probability of survival, say S_i for $i = [1, 6]$. Note $S_7 = P_7$ as the mature breeders cannot grow to a next stage (there is no such age class). However, we do not impose such conditions in the iterative process in the code, so there might be some flaws of our analysis. It does not make biological sense to have more than 100% small juveniles, say, survive in total (remaining and growing), as the tortoises are a fixed number and random new small juveniles do not appear out of nowhere. More generally, the number of individuals in each class either remains the same (if the sum of the probabilities is equal to 1), or decreases due to mortality (if the survival probability is less than 1).

Now consider the G_i curve (i.e. the dotted curve). We observe that the elasticities of G_1, G_2, G_3, and G_4 are the same and all equal to 0.05. Then the elasticities of G_5 and G_6 are approximately equal — $E_{G_5} = 0.0391$ and $E_{G_6} = 0.0388$. Examining the plot in Figure 7 we see that the probabilities of growing G_i have some effect on the elasticity of the dominant eigenvalue, but compared with the probabilities of staying P_i, these are lower for $i = [1, 4] \cup \{7\}$. However, the effect on the elasticity of λ of G_5 and G_6 is higher than E_{P_5} and E_{P_6}.

Biologically, the above analysis means that changes in the probability of surviving and growing to the next age class of the 'baby' classes and the subadults have approximately three times less effect on the growth of the population compared to the probabilities of surviving and remaining in the same age class. Nonetheless, we can deduce that the overall survivability of the juveniles, subadults, and old breeders is of great importance for the growth of the population.

As discussed above, the two probabilities, P_i and G_i, are closely related. Inspecting the graph we have two candidates for the largest effect on the elasticity of λ to changes in the overall survivability S_i, namely, the small juveniles N^2 and the mature breeders N^7. The survivability of the small juveniles is $S_2 = 0.1827 + 0.0514 = 0.2341$, while the survivability of the old breeders is $S_7 = 0.2275$. At this point we note that S_2 has the greatest significance for the value of the dominant eigenvalue, i.e. the joint probability of survival of the small juveniles has the largest effect on the growth rate of the population. However, we need to consider the effect of the fecundities of the breeder classes as well before we proceed making any general conclusions about the effect of each parameter on the dynamics of the tortoise population.

Finally, consider the F_i curve (i.e. the dashed curve). Note that the $a_{1,2}$, $a_{1,3}$ and $a_{1,4}$ entries in our Usher matrix are zeros, which makes sense in reality as the respective age classes do not breed. The only classes which are breeders are N^5, N^6, and N^7 — the novice, mature, and old breeders, respectively. Inspecting the graph, we see that the elasticity of the eigenvalue λ to changes in F_5 and F_7 is higher than the one in F_6.

The biological interpretation of the elasticity curve of the fecundities is that the old breeders have the largest impact on the growth of the population. The proportional rate of change of the growth rate with respect to varying the fecundity of the old breeders is 0.0388, which is much higher compared to the one of the novice breeders (0.0123) and the mature breeders (0.0003). Hence, an increase in the number of individuals in the old breeders, will lead to an increase in their fecundity and will result in growth of the population. This confirms our analysis of Equations 1 and 6 — the old breeders constitute the largest proportion of the breeders and contribute the most to egg production. $\square$

Question 7. *State with reasons whether the model supports egg protection, identifying which parameters are affected by egg protection.*

Solution 7. Taking into account the discussion in the previous question, we can summarize our observations in Table 1 below.

Table 1: Summary of elasticity analysis.

Approximate effect of the parameters on the growth rate.		
Age class	Effect of general survival probability S_i	Effect of fecundity F_i
Eggs, hatchlings	0.0514	N/A
Small juveniles	0.2341	N/A
Large juveniles	0.1691	N/A
Subadults	0.1888	N/A
Novice breeders	0.0391	0.0123
Mature breeders	0.0388	0.0003
Old breeders	0.2275	0.0388

In order to be concise, we shall first analyze the variables, which *do not* affect the population growth or have a negligible impact. The plot in Figure 7 tells us the following:

- The probability of survival and remaining in the same stage of the eggs, the novice breeders, and the mature breeders has no effect on the growth rate;
- The fecundity of the mature breeders has a negligible effect on the growth rate.

Next consider the parameters which have *some* effect on the growth:

- The probability of surviving and growing to the next age class of all groups has some effect on the growth rate of the population;
- The fecundity of the novice breeders has some effect, but it is considerably smaller than the one of the old breeders;
- The general survivability of the large juveniles and subadults has some effect on the growth of the tortoise population.

Ultimately, we discuss the age classes with the *largest* effect on the elasticity of the growth rate:

- The joint probability of survival of the small juveniles has the largest effect on the growth rate of the population. An increase in the survival probability, or a decrease in the mortality of the small juveniles, may result in the tortoise population growing and stabilizing;
- The survival probability of the old breeders has the second highest impact on the growth rate. Taking into account their highest contribution in terms of fecundity, makes the old breeders crucial to the growth of the tortoise population.

Thus, we can conclude that the two classes with largest impact on the growth of the tortoise population are the small juveniles and the old breeders. Protecting the eggs and hatchlings is important, of course, since if a large proportion of them die, there will be less tortoises moving to the next age classes. However, we cannot change the probability of remaining of the eggs, because they hatch for one year. In other words, the eggs either die out, or hatch and move to the small juveniles very fast. Thus, our results suggest that more conservation efforts should be invested in preserving the small juveniles.

Let us now carefully analyze the parameters affected by egg protection, in order to conclude whether egg conservation efforts are effective in stabilizing the population. We perform the same analysis as in Question 3, but this time we vary the $a_{2,1}$ entry of the Usher matrix — the probability of surviving and growing of the eggs and hatchlings class. If we protect the eggs, this means that more tortoises will grow to the small juveniles class, as they hatch for one year. Thus, the only parameter affected by egg conservation is the probability of growing G_1. Varying the probability G_1 from 0 to 1 affects the growth rate of the population as shown in Figure 8.

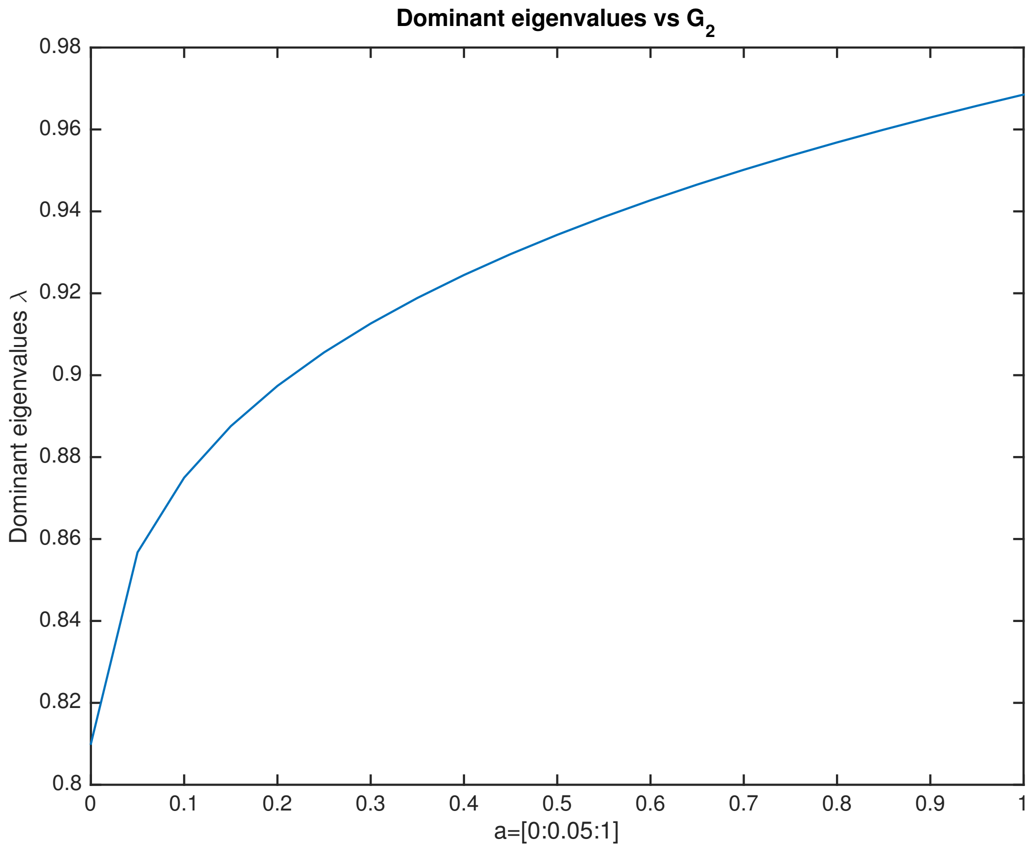

Figure 8: The growth rate λ plotted against $0 \leq G_1 \leq 1$.

The plot in Figure 8 shows that even if $G_1 = 1$, the dominant eigenvalue is still $\lambda < 1$. In other words, even if 100% of the eggs grow to become small juveniles, the population still *does not* exhibit growth. In real life, this is impossible since some eggs are unable to hatch [3]. Note that we only iterate through the values of the probability of surviving and growing, as the eggs take one year to hatch, so it does not make sense to increase the probability of surviving and remaining as eggs. Thus, egg protection, which directly affects the G_1 parameter is not the most effective strategy for ensuring growth of the tortoise population.

Both the sensitivity analysis and varying the G_1 parameter show that *not all* conservation efforts should focus on the egg life stage. Surely eggs and hatchlings should be protected, since if they die, there will be no tortoises to continue growing, but our results suggest that egg protection efforts *will not* ultimately prevent extinction. Instead, we should focus on conserving the small juveniles and the old breeders. □

Question 8. *State with reasons whether the model supports reduction in juvenile and/or adult (breeder) mortality.*

Solution 8. We can think of the mortality rate of the class N^i as the difference $1-(G_i+P_i)$. The two parameters P_i and G_i denote probabilities, bounded above by the value 1, which denotes 100% of the individuals in the particular class. That is why it makes sense to bound their sum $P_i + G_i = S_i$ above by 1 as well. Hence, we shall now analyze the mortalities of each age class, which we denote $M_i = 1 - (G_i + P_i)$. Table 2 summarizes the mortalities of each age class.

Table 2: Mortality rates of each age class, calculated from the initial Usher matrix.

Age class	Mortality M_i
Eggs, hatchlings	0.3300
Small juveniles	0.2100
Large juveniles	0.3250
Subadults	0.2580
Novice breeders	0.1900
Mature breeders	0.1900
Old breeders	0.1900

Table 2 shows that the eggs and the large juveniles have the highest mortalities, which partially justifies why almost all conservation efforts focus on the conservation of eggs. Also, in general we can deduce that the 'baby' classes have higher mortality rates compared to the breeders, which in reality makes sense as small tortoises are much more vulnerable to predation.

In terms of elasticity analysis, we can deduce the following:

- If a parameter has a significant effect on the elasticity analysis, so does its complementary value.

This means that an increase in the probabilities of survival ,S_i, is equivalent to a decrease in the mortality rate, M_i, but the net effect on the elasticity of the growth rate is the same. Thus, taking into account the elasticity plot in Figure 7 produced in Question 5, the two classes with the largest effect on the growth rate are the small juveniles ($E_{S_2} = 0.2341$)

and the old breeders ($E_{S_7} = 0.2275$). The effect of the eggs is $E_{S_1} = 0.0514$, which is significantly smaller than the elasticity of the small juveniles. Further, the effect of the old breeders is approximately 6 times higher than the other two breeder classes. Thus, if we decrease the mortality rate of the small juveniles, and hence, increase their general probability of survival, the growth rate λ will significantly increase and the population will exhibit a growth. The parameters affected are an increase in P_2 and G_2, and a decrease in M_2. Furthermore, if we decrease the mortality rate of the old breeders, and increase their probability of survival and remaining old breeders, the population will again exhibit a growth, as the effect of the fecundity F_7 is largest as well. The parameter which will be affected is P_7. In other words, if we conserve the old breeders, who have the largest contribution to the production of eggs, more old breeders will be able to continue reproducing and thus, the population will grow and stabilize.

In summary, based on our model, *conservation of the small juveniles and old breeders is crucial in order to prevent the extinction of the population.*

Again, the protection of all age classes is necessary and contributes to the overall protection of the tortoise population. By conservation of the small juveniles and old breeders, we mean that more efforts should be made towards the protection of these two classes, when compared with the other classes. This does not imply that we need to focus only on the small juveniles and old breeders — it means we need to come up with protection strategies explicitly for these two.

Tortoises are mostly vulnerable to predation by ravens, habitat destruction due to urbanization, and vandalism [4]. These threats can be mitigated if

- Larger areas of desert tortoise habitats are protected by legislation and conservation organizations;
- Regular inspection of the well-being of the tortoises and aid when necessary is provided;
- Tortoises can be held in shelters or wild-life centers while they are most vulnerable to threats [4];
- Stricter laws and lawsuits are applied in cases of illegal domestication, collection, and vandalism;
- People in general become more considerate of endangered species, ecological impacts, and environmental sustainability.

□

References

[1] K. Berry, T. Duck, Answering Questions about Desert Tortoises: A Guide for People who Work with the Public, (2010), http://www.deserttortoise.org/nsweringquestions/index.html.

[2] C. Bowers, Update only one matrix element for iterative computation, (2012), http://stackoverflow.com/questions/12488005/update-only-one-matrix-element-for-iterative-computation.

[3] H. Caswell, A General Formula for the Sensitivity of Population Growth Rate to Changes in Life History Parameters, *Theoretical Population Biology* **14**, 215-230 (1978).

[4] Desert tortoise (Wikipedia), (2016). https://en.wikipedia.org/wiki/Desert_tortoise#Predation_and_conservation_status.