A Periodic Matrix Population Model

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The following exercises are based on the paper written by Hunt and Tongen:

Problem 1. *As done in the paper, assume $F_1 = F_2 = F$, $C_1 = C_2 = C$, $L_1 = L_2 = L$, and $y = z = 6$. Use the parameters in Table 1 and determine the matrix M in Eqn. (3). (You may, and I think you should, do this numerically, of course, using MATLAB or whatever software you prefer.) By examining the form of M, find the eigenvalues of M. Find an associated eigenbasis for M. (An eigenbasis is a basis of $\mathbb{R}^3$ consisting of eigenvectors of M.) Show you work. (Do this calculation by hand). Under what conditions, will the population survive? What is the long-term structure of the population?*

Solution. The model is given by

$$P_{t+1} = MP_t \tag{1a}$$
$$M = M_4 M_3 M_2^y M_1^z, \tag{1b}$$

where M_n is the matrix associated with the n^{th}-stage of the migration process, and the powers y and z are the number of 2-week periods in Stage 2 and Stage 1, respectively. The vector P_t encodes the total population at generation t:

$$P_t = \begin{bmatrix} p_\ell \\ p_c \\ p_a \end{bmatrix},$$

where

$$\begin{aligned} p_\ell &= \text{monarch population of larvae;} \\ p_c &= \text{chrysalis population;} \\ p_a &= \text{adult monarch butterflies .} \end{aligned}$$

Under the assumptions $F_1 = F_2 = F$, $C_1 = C_2 = C$, $L_1 = L_2 = L$, $y = z = 6$, and using the table

Symbol	Description	Initial Parameter
A_1	Adult survival per 2-week period (Stage 1)	0.125
A_2	Adult survival per 2-week period (Stage 2)	0.2458
A_3	Adult survival for the entire fall migration (Stage 3)	0.586
A_4	Adult survival for the entire winter (Stage 4)	0.85
F	The fecundity of a single monarch butterfly per 2-week period	45
L	The survival rate of the eggs to the chrysalis stage per 2-week period	0.03426
C	The survival of the chrysalis into a butterfly per 2-week period	0.85

Eq. (1b) becomes (c.f., Listing 1)

$$\begin{aligned} M &= M_4 M_3 M_2^6 M_1^6 \\ &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & A_4 \end{bmatrix} \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & A_3 \end{bmatrix} \begin{bmatrix} 0 & 0 & F \\ L & 0 & 0 \\ 0 & C & A_2 \end{bmatrix}^6 \begin{bmatrix} 0 & 0 & F \\ L & 0 & 0 \\ 0 & C & A_1 \end{bmatrix}^6 \\ &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0.85 \end{bmatrix} \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0.586 \end{bmatrix} \begin{bmatrix} 0 & 0 & 45 \\ 0.03426 & 0 & 0 \\ 0 & 0.85 & 0.2458 \end{bmatrix}^6 \begin{bmatrix} 0 & 0 & 45 \\ 0.03426 & 0 & 0 \\ 0 & 0.85 & 0.125 \end{bmatrix}^6 \\ &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0.0248 & 0.3382 & 1.6218 \end{bmatrix}. \end{aligned} \tag{2}$$

Since M is in lower-triangular form, and we know that the eigenvalues of a triangular matrix are exactly its diagonal entries, the eigenvalues of M are 0 (multiplicity 2) and 1.6218 (multiplicity 1). Now, the eigenvector $\boldsymbol{v}$ corresponding to an eigenvvalue λ lives in the nullspace of $M - \lambda I$; i.e., it must satisfy

$$(M - \lambda I)\,\boldsymbol{v} = \mathbf{0}.$$

Thus we have, for $\lambda_1 = \lambda_2 = 0$,

$$\begin{aligned} \mathbf{0} &= M\boldsymbol{v} \\ \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} &= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0.0248 & 0.3382 & 1.6218 \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix} \\ \implies 0 &= 0.0248 v_1 + 0.3382 v_2 + 1.6218 v_3 \\ v_3 &= -0.0152917\, v_1 - 0.208534\, v_2. \end{aligned}$$

Thus we have two free variables, from which a linear combination yields the remaining component. In other words, any vector in the eigenspace corresponding to $\lambda = 0$ is of the form

$$\boldsymbol{v} = \begin{bmatrix} \alpha \\ \beta \\ -0.0152917\alpha - 0.208534\beta \end{bmatrix} = \alpha \begin{bmatrix} 1 \\ 0 \\ -0.0152917 \end{bmatrix} + \beta \begin{bmatrix} 0 \\ 1 \\ -0.208534 \end{bmatrix}, \qquad \alpha, \beta \in \mathbb{R}. \tag{3}$$

Hence the eigenspace of $\lambda = 0$ is spanned by the eigenvectors

$$\left\{ \begin{bmatrix} \alpha \\ 0 \\ -0.0152917\,\alpha \end{bmatrix}, \begin{bmatrix} 0 \\ \beta \\ -0.208534\,\beta \end{bmatrix} \right\}, \qquad \alpha, \beta \in \mathbb{R}.$$

Similarly, for $\lambda_3 = 1.6218$,

$$\begin{aligned} \mathbf{0} &= (M - 1.6218I)\,\boldsymbol{v} \\ \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} &= \begin{bmatrix} -1.6218 & 0 & 0 \\ 0 & -1.6218 & 0 \\ 0.0248 & 0.3382 & 0 \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix} \\ \implies 0 &= v_1 = v_2; v_3 \in \mathbb{R}. \end{aligned}$$

Thus any vector of the form

$$\boldsymbol{v} = \alpha \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}, \qquad \alpha \in \mathbb{R} \tag{4}$$

is an eigenvector of $\lambda = 1.6218$.

Now, since the dominant eigenvalue $\lambda = 1.6218 \geq 1$, we know that the population is thriving, per Eq. (1a). Moreover, we see from the corresponding dominant eigenvector (4) that the remaining population of monarchs is composed entirely of adults, since

$$P_{t_{\text{final}}} = \begin{bmatrix} p_\ell \\ p_c \\ p_a \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ \alpha \end{bmatrix}, \qquad \alpha \in \mathbb{R}.$$

It makes sense that we are left with adults only, since the overwintering stage (where no more eggs are being laid and only adults remain) is given by M_4, which is the last matrix acting on the population vector from the previous generation (c.f., Eq. (1b)). $\square$

Problem 2. *We will do the same calculations except, instead of computing M, we will compute $\widetilde{M} = M_1^z M_4 M_3 M_2^y$. We can't simply report the eigenvalues by examining the form of $\widetilde{M}$. Because $\widetilde{M}$ is a positive matrix, $\widetilde{m}_{i,j} > 0$ for $1 \leq i, j \leq 3$, by Perron-Frobenius theorem, there is a positive real number r, called the Perron root or the Perron-Frobenius eigenvalue, such that r is an eigenvalue of $\widetilde{M}$ and any other eigenvalue λ in absolute value is strictly smaller than r, $|\lambda| < r$. Write your own code to implement the Power Method to find the dominant eigenvalue, r, and the corresponding eigenvector $\boldsymbol{v}_r$. Explain how you initialized the Power Method and how many iterations you used. Use software (for example, in MATLAB `eig`) to check your answer. Describe the differences in these matrices, and interpret those differences in terms of annual variations in the butterfly population.*

Solution. The idea behind the *Power Iteration Method* is that the sequence

$$\frac{\boldsymbol{x}}{\|\boldsymbol{x}\|}, \frac{A\boldsymbol{x}}{\|A\boldsymbol{x}\|}, \frac{A^2\boldsymbol{x}}{\|A^2\boldsymbol{x}\|}, \frac{A^3\boldsymbol{x}}{\|A^3\boldsymbol{x}\|}, \dots$$

converges, under certain assumptions, to the *dominant eigenvector* of A, i.e., to the eigenvector that corresponds to the eigenvalue of A whose absolute value is the largest (such eigenvalue is known as the *dominant eigenvalue*; if it is postive it coincides with the *spectral radius* of A).

In the following code we apply the Power Iteration Method to $\widetilde{M}$ (starting with initial guess $\boldsymbol{x}^{(0)} = [5000\ 5000\ 5000]^\top$) [1] to find its dominant eigenvector, and use the *Rayleight quotient*

$$\lambda = \frac{\boldsymbol{x}^\top A \boldsymbol{x}}{\boldsymbol{x}^\top \boldsymbol{x}} \tag{5}$$

to find the corresponding (dominant) eigenvalue:

```
%Import parameters
A1 = 0.125;
A2 = 0.2458;
A3 = 0.586;
A4 = 0.85;
F = 45;
L = 0.03426;
C = 0.85;

%Initialize matrices
M1 = zeros(3);
M2 = zeros(3);
```

[1]Actually, the starting guess is not relevant because in the code I am normalizing, so the method will converge regardless of how absurd the initial guess may be.

```
M3 = zeros(3);
M4 = zeros(3);

%Complete matrices
M1(1,3) = F;
M1(2,1) = L;
M1(3,2) = C;
M1(3,3) = A1;

M2(1,3) = F;
M2(2,1) = L;
M2(3,2) = C;
M2(3,3) = A2;

M3(3,3) = A3;
M4(3,3) = A4;

%Build matrix M  (for Problem 1)
M = M4 * M3 * (M2^6) * (M1^6);

%Build matrix \tilde{M} (for Problem 2)
Mt =  (M1^6) * M4 * M3 * (M2^6);

%Power Iteration code
x0 = [5000; 5000; 5000];        %initial guess
x0 = x0/norm(x0, Inf);          %normalize
x   = zeros(3,1);               %initialize vector
tol = 1e-6;                     %accepted tolerance
it = 0;                         %initialize number of iterations
it_max = 100;                   %max number of iterations allowed

for i = 1:it_max

    it = it + 1;
    x = Mt * x0;
    x = x/norm(x, Inf);    %Normalize

    if norm(x-x0) <= tol
        lmb = (x' * Mt * x)/(x' * x);        %Rayleigh quotient
        disp(['The dominant eigenvalue is ', num2str(lmb),
              '. It took ', num2str(it), ' iterations to converge.'])
        disp('The dominant eigenvector is ')
        disp(x)
        break
    end

    x0 = x;  %update x0 value for next iteration

    if it == it_max
        disp('No convergence; max number of iterations reached.')
    end
end
```

Listing 1: Power Iteration applied to population matrix $\widetilde{M}$. Written in MATLAB.

The output

```
The dominant eigenvalue is 1.6218. It took 2 iterations to converge.
The dominant eigenvector is
    1.0000
    0.1828
    0.6246
```

shows that we get exactly the same dominant eigenvalue as we did with the matrix M in Problem 1. I did validate the code with MATLAB's `eig` and I get the same answer. The dominant eigenvector that we get by using `[V,D] = eig(Mt)` looks different, but that's only due to the scaling; MATLAB uses the 2-norm to scale, while I am using the ∞-norm. The upshot of using the ∞-norm on the dominant eigenvector is that we can easily interpret

$$P_{t_{\text{final}}} = \begin{bmatrix} p_\ell \\ p_c \\ p_a \end{bmatrix} = \begin{bmatrix} 1 \\ 0.1828 \\ 0.6246 \end{bmatrix}$$

as $p_c = 0.1828 p_\ell$ and $p_a = 0.6246 p_\ell$. It makes sense that, unlike in Problem 1, we now have a more varied population, since the form of $\tilde{M}$ indicates that now the end-stage is week 12 of the Spring stage (given by M_1^6). It also makes sense that the population is predominantly composed of eggs/larvae since the female monarchs lay a large number of eggs during this stage, according to Hunt and Tongen's paper. □

Problem 3. *Find the sensitivity and elasticity matrices associated with M and $\tilde{M}$. These matrices indicate how the dominant eigenvalue depend on the elements of M and $\tilde{M}$, but they do not tell us directly how that eigenvalue depends on the parameters A_1, A_2, A_3, A_4, F, L, and C. Why not? What would you have to do to determine how the dominant eigenvalue depends on these parameters? Note, I am not asking you to derive a formula, I'd just like you to outline what you'd have to do.*

Solution. The sensitivity (S) and elasticity (E) matrices associated to a matrix A are given by

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \qquad \text{(Sensitivity)} \qquad (6a)$$

$$E_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}, \qquad \text{(Elasticity)} \qquad (6b)$$

where λ is the dominant eigenvalue of A. However, it is not immediately obvious how to quantify the effect of A's entries on λ (i.e., how to compute $\partial\lambda/\partial a_{ij}$). To do this we will need to use both the right ($\boldsymbol{v}$) and left ($\boldsymbol{w}$) eigenvectors, as given by $A\boldsymbol{v} = \lambda\boldsymbol{v}$ and $\boldsymbol{w}^\top A = \lambda\boldsymbol{w}^\top$, respectively. To see how, consider the (first-order) perturbation on the right eigenvector equation:

$$\begin{aligned}
(A + \delta A)\,(\boldsymbol{v} + \delta\boldsymbol{v}) &= (\lambda + \delta\lambda)\,(\boldsymbol{v} + \delta\boldsymbol{v}) \\
A\boldsymbol{v} + A\delta\boldsymbol{v} + \delta A\boldsymbol{v} + \cancelto{0}{\delta A\delta\boldsymbol{v}} &= \lambda\boldsymbol{v} + \lambda\delta\boldsymbol{v} + \delta\lambda\boldsymbol{v} + \cancelto{0}{\delta\lambda\delta\boldsymbol{v}} \\
A\delta\boldsymbol{v} + \delta A\boldsymbol{v} &= \lambda\delta\boldsymbol{v} + \delta\lambda\boldsymbol{v}.
\end{aligned}$$

Multiplying both sides on the left by $\boldsymbol{w}^\top$, we get

$$\begin{aligned}
\boldsymbol{w}^\top\,(A\delta\boldsymbol{v} + \delta A\boldsymbol{v}) &= \boldsymbol{w}^\top\,(\lambda\delta\boldsymbol{v} + \delta\lambda\boldsymbol{v}) \\
\boldsymbol{w}^\top A\delta\boldsymbol{v} + \boldsymbol{w}^\top\delta A\boldsymbol{v} &= \lambda\boldsymbol{w}^\top\delta\boldsymbol{v} + \delta\lambda\boldsymbol{w}^\top\boldsymbol{v} \\
\boldsymbol{w}^\top\delta A\boldsymbol{v} &= \delta\lambda\boldsymbol{w}^\top\boldsymbol{v}. \qquad (7)
\end{aligned}$$

Hence, if we only consider change on a single entry of A, the expression (7) implies

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{w_i v_j}{\boldsymbol{w}^\top\boldsymbol{v}}. \qquad (8)$$

We are now ready to calculate the matrices (6):

```
n = 3;
%Initialize Sensitivity & Elasticity matrices for M and \tilde{M}
S = zeros(n);
E = zeros(n);
St = zeros(n);
Et = zeros(n);

%eigenvalues and left & right eigenvectors for  M and \tilde{M}
[V,D,W] = eig(M);
[Vt,Dt,Wt] = eig(Mt);

%find index where dominant eigenvalue lies
index = find( diag(D) == max(diag(D)) );
index_t = find( diag(Dt) == max(diag(Dt)) );

%define the dominant eigenvalue
lmb = D(index ,index);
lmb_t = D(index_t, index_t);

%define the dominant right (v) and left (w) eigenvectors
v = V(:,index);
w = W(:,index);
vt = Vt(:,index_t);
wt = Wt(:,index_t);

for i = 1:n
    for j = 1:n
        if M(i,j) ~= 0
            S(i,j) = ( w(i) * v(j) )/( w' * v );
            E(i,j) = ( M(i,j)/lmb ) * S(i,j);
        end
```

```
            if Mt(i,j) ~= 0
                St(i,j) = ( wt(i) * vt(j) )/( wt' * vt );
                Et(i,j) = ( Mt(i,j)/lmb_t ) * St(i,j);
            end
        end
end

disp('The sensitivity matrix for M is ')
S
disp('The elasticity matrix for M is ')
E
disp('The sensitivity matrix for \tilde{M} is ')
St
disp('The elasticity matrix for \tilde{M} is ')
Et
```

The output shows

$$S = E = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix};$$
$$\tilde{S} = \begin{bmatrix} 0.0160 & 0.0029 & 0.0100 \\ 0.1721 & 0.0315 & 0.1075 \\ 1.5249 & 0.2787 & 0.9525 \end{bmatrix};$$
$$\tilde{E} = \begin{bmatrix} 0.0003 & 0.0005 & 0.0153 \\ 0.0005 & 0.0010 & 0.0300 \\ 0.0153 & 0.0300 & 0.9073 \end{bmatrix}.$$

To determine how the dominant eigenvalue depends on the parameters themselves, we would have to see how the entries of the population matrix depend on the latter. We can do this by applying a chain rule; for instance, for the parameter C and population matrix M we would do

$$\frac{\partial \lambda}{\partial C} = \sum_{i,j} \frac{\partial \lambda}{\partial M_{ij}} \frac{\partial M_{ij}}{\partial C}. \tag{9}$$

From Eq. (8) we already know how to compute $\partial\lambda/\partial M_{ij}$, but $\partial M_{ij}/\partial C$ is more involved (we require transition probabilities and other quantities that we discussed in class for the killer whale population model). □

Problem 4. *Eqn. (8) in the paper uses a matrix H to characterize the effect of a late frost in the early spring. Write down the analog of Eqn. (8) for the case in which the frost occurs two weeks* later *than Hunt and Tongen take it to occur. Use this analogous formulation and study how such frosts of different severity affect the growth of the population, that is, the dominant eigenvalue of the relevant matrix.*

Solution. Eqn. (8) in the paper is given by

$$M = M_4 M_3 M_2^6 M_1^5 H M_1,$$

where H is a a diagonal matrix whose nonzero entries are the survival probability of the insects during frost. If all larvae, chrysalis , and adult monarchs have a survival probability $h_{ii} = 1$, then H is the identity matrix and has no effect on M, of course. The analogous matrix that we will be working with is

$$\widehat{M} = M_4 M_3 M_2^6 M_1^4 H M_1^2, \tag{10}$$

since we want the frost to occur two weeks *later* than in Hunt and Tongen's (recall that both M_1 and M_2 represent two-weeks periods). To study the impact of the frost (nonzero entries of H) on the growth of the population (dominant eigenvalue λ), we need to apply an equation analogous to Eq. (9):

$$\frac{\partial \lambda}{\partial h_\gamma} = \sum_{i,j} \frac{\partial \lambda}{\partial \widehat{M}_{ij}} \frac{\partial \widehat{M}_{ij}}{\partial h_\gamma}, \tag{11}$$

where the index $\gamma \in \{\ell, c, a\}$ indicates the frost-survival probability of larvae (h_ℓ), chrysalis (h_c), and adults (h_a). However, while the sensitivity matrix $\partial\lambda/\partial\widehat{M}_{ij}$ is straightforward to compute, the matrix $\partial\widehat{M}_{ij}/\partial h_\gamma$ is much more difficult. Hence, instead of computing Eq. (11) directly, we will infer the impact of frosts of different severity on the population growth by recording some values of λ corresponding to a handful of frost survival rates. We will use the same values of h_γ used on Table 4 from the paper to compare the results and see what differences (if any) a frost happening two weeks later would have on the monarch population.

TABLE 4 The effect of a late frost at the beginning of the spring migration: $M = M_4 M_3 M_2^6 M_1^5 H M_1$

Larva Survival (h_l)	Chrysalis Survival (h_c)	Adult Survival (h_a)	Growth Rate
1	1	1	1.6218
0.9	0.9	0.1	1.4199
0.5	0.5	0.5	0.8109
0.5	0.5	0.1	0.7910
0.5	0.1	0.5	0.8109
0.1	0.5	0.5	0.1821

Here is the corresponding table for population matrix $\widehat{M}$ from Eq. (10):

h_ℓ	h_c	h_a	λ
1	1	1	1.6218
0.9	0.9	0.1	1.449
0.5	0.5	0.5	0.81092
0.5	0.5	0.1	0.8056
0.5	0.1	0.5	0.18208
0.1	0.5	0.5	0.79635

Table 1: The effect of a frost happening two weeks later than in Hunt & Tongen's Table 4.

A comparison of our table with Hunt & Tongen's shows that in most situations the growth rates are nearly identical in the two cases. A glaring exception is the last two rows of both tables, which are flipped. It makes sense that this is the case, since two weeks later into the spring the survival of the chrysalis plays a more important role in the population growth than the larvae. $\square$