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| **Math 235: Mathematics in Population Biology** | **(Due: 03/27/2020)** |

# Problem Set 1

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1. Find the unique solution of the following difference equations satisfying the given initial condition and graph the solutions

**(a)** $x_{t+1} - 5x_t + 4x_{t-1} = 0; \quad x_1 = 9, \quad x_2 = 33$

Let us first assume that the solution $x[t]$ takes the form, $x[t] = \lambda^t$ such that we can recast the difference equation into

$$\begin{aligned} \lambda^{t+1} - 5\lambda^t + 4\lambda^{t-1} &= 0 \\ \lambda^2 - 5\lambda + 4 &= 0 \\ (\lambda - 4)(\lambda - 1) &= 0 \end{aligned}$$

which yields two eigenvalues, $\lambda_1 = 4$, $\lambda_2 = 1$, implying that there are two solutions to this difference equation

$$\begin{aligned} x_1[t] &= 1 \\ x_2[t] &= 4^t \end{aligned}$$

This yields a general solution that is a linear superposition of $x_1$ and $x_2$,

$$x[t] = C_1 + C_2(4^t)$$

To completely solve this problem, we shall impose initial conditions provided:

$$\begin{aligned} 9 &= C_1 + 4C_2 \\ 33 &= C_1 + 16C_2 \end{aligned}$$

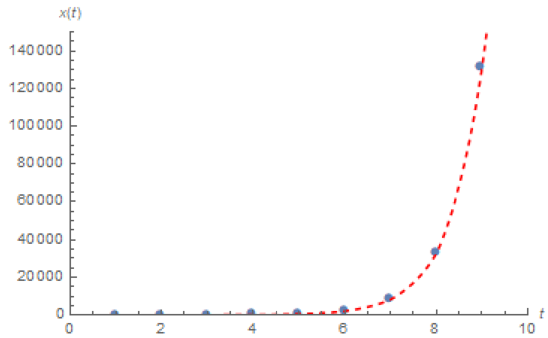
from which we can obtain what $C_1$ and $C_2$ are. From the first equation, $C_1 = 9 - 4C_2$ which, when substituted to the second equation, yields,

$$33 = 9 - 4C_2 + 16C_2 \longrightarrow C_2 = 2$$

$$C_1 = 9 - 4(2) = 1$$

which gives us a final answer,

$$\boxed{x[t] = 1 + 2^{1+2t}}$$



**(b)** $x_{t+2} + x_{t+1} - 2x_t = 0; \quad x_0 = 6, \quad x_1 = 3$

In the same way as we did in the last item, we assume that the solution $x[t]$ takes the form, $x[t] = \lambda^t$. This gives us a characteristic equation of the form,

$$\begin{aligned} \lambda^{t+2} + \lambda^{t+1} - 2\lambda^t &= 0 \\ \lambda^2 + \lambda - 2 &= 0 \\ (\lambda + 2)(\lambda - 1) &= 0 \end{aligned}$$

which yields two eigenvalues of the form, $\lambda_1 = -2$, $\lambda_2 = 1$, implying that there are two solutions to this difference equation

$$\begin{aligned} x_1[t] &= 1 \\ x_2[t] &= (-2)^t \end{aligned}$$

Hence, the general solution is a linear superposition of $x_1$ and $x_2$,

$$x[t] = C_1 + C_2(-2)^t$$

Imposing the boundary values provided gives us values for $C_1$ and $C_2$,

$$\begin{aligned} 6 &= C_1 + C_2 \\ 3 &= C_1 - 2C_2 \end{aligned}$$

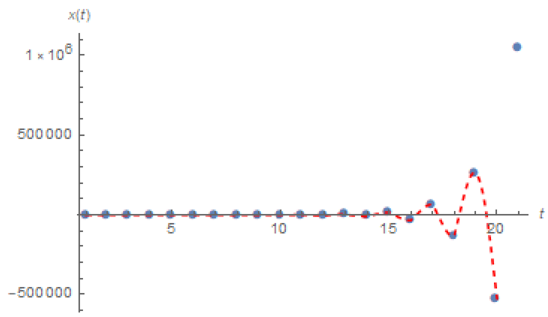
From the first equation, $C_1 = 6 - C_2$. Substituting this to the second equation, we obtain

$$3 = 6 - C_2 - 2C_2 \longrightarrow C_2 = 1$$

$$C_1 = 6 - 1 = 5$$

which gives us a final answer,

$$\boxed{x[t] = 5 + (-2)^t}$$




2. Find the general solutions to the following nonhomogeneous, linear difference equations.

**(a)** $x_{t+2} + x_{t+1} - 6x_t = 5$

The solution to this difference equation can be written as a sum of the homogeneous solution $x_H$ and the particular solution $x_P$. Hence, the first step is for us to solve the homogeneous case,

$$x^H_{t+2} + x^H_{t+1} - 6x^H_t = 0$$

We now assume that the homogeneous solution takes the form $x^H[t] = \lambda^t$, which when we plug in to the difference equation gives a characteristic equation of the form,

$$\lambda^2 + \lambda - 6 = 0$$

the roots of which are $\lambda_1 = -3$ and $\lambda_2 = 2$. Therefore, the general solution to the homogeneous case is given by,

$$x^H[t] = C_1(-3)^t + C_2(2)^t$$

The next step is to find the particular solution $x^P$. For a constant nonhomogeneous term, we assume that the solution to the difference equation takes the form $x^P[t] = \alpha$, such that

$$\alpha + \alpha - 6\alpha = 5 \longrightarrow \alpha = -\frac{5}{4}$$

Hence, the general solution to the difference equation is,

$$\boxed{x[t] = x^H[t] + x^P[t] = C_1(-3)^t + C_2(2)^t - \frac{5}{4}}$$

where $C_1$ and $C_2$ can be obtained by imposing boundary conditions.

**(b)** $x_{t+2} - 4x_t = 6t - 1$

In the same way as we did for the previous item, the first step in solving for the general solution is to solve for the homogeneous solution $x^H$. We assume that $x^H[t] = \lambda^t$ which yields a characteristic equation of the form,

$$\lambda^2 - 4 = 0$$

which has two distinct roots $\lambda_1 = 2$ and $\lambda_2 = -2$. Hence, the homogeneous solution is given by

$$x^H[t] = C_1(2)^t + C_2(-2)^t$$

The next step is to find the particular solution $x^P$ whose form we shall guess as $x^P[t] = \beta t + \gamma$, with $\beta$ and $\gamma$ still to be determined. We substitute this guess solution to the difference equation,

$$\begin{aligned} \beta(t+2) + \gamma - 4(\beta t + \gamma) &= 6t - 1 \\ (-3\beta)t + (2\beta - 3\gamma) &= 6t - 1 \end{aligned}$$

Comparing the coefficients on each side of the equation then gives us two equations to solve,

$$\begin{aligned} -3\beta &= 6 \\ 2\beta - 3\gamma &= -1 \end{aligned}$$

yielding $\beta = -2$ and $\gamma = -1$. Hence, the general solution to this difference equation is given by,

$$\boxed{x[t] = C_1(2)^t + C_2(-2)^t - (2t+1)}$$

3. Convert the following linear difference equations to equivalent first-order systems, Determine the eigenvalues and eigenvectors and express the solution in vector form.

**(a)**$x_{t+2} - 16x_t = 0$

We let $y_1[t] = x[t]$, and $y_2[t] = x[t+1]$ such that

$$\begin{aligned} y_1[t+1] &= y_2[t] \\ y_2[t+1] &= 16y_1[t] \end{aligned}$$

which can be written alternatively as,

$$Y[t+1] = AY[t]$$

where

$$Y[t] = \begin{bmatrix} y_1[t] \\ y_2[t] \end{bmatrix}$$

and

$$A = \begin{bmatrix} 0 & 1 \\ 16 & 0 \end{bmatrix}$$

We can obtain the eigenvalues of the matrix $A$ by first calculating for $\det(A - \mathcal{I}\lambda)$,

$$\lambda^2 - 16 = 0$$

which yields two roots, $\lambda_1 = -4$ and $\lambda_2 = 4$. Say the eigenvectors of this matrix can be written as,

$$\mathbf{x}_1 = \begin{bmatrix} x_1^1 \\ x_1^2 \end{bmatrix} \quad \mathbf{x}_2 = \begin{bmatrix} x_2^1 \\ x_2^2 \end{bmatrix}$$

which correspond to $\lambda_1$ and $\lambda_2$ respectively, such that

$$A\mathbf{x}_1 = \lambda_1 \mathcal{I} \mathbf{x}_1$$
$$\begin{bmatrix} 0 & 1 \\ 16 & 0 \end{bmatrix} \begin{bmatrix} x_1^1 \\ x_1^2 \end{bmatrix} = \begin{bmatrix} -4 & 0 \\ 0 & -4 \end{bmatrix} \begin{bmatrix} x_1^1 \\ x_1^2 \end{bmatrix}$$
$$x_1^2 = -4x_1^1$$

such that $\mathbf{x}_1$ can be written as

$$\mathbf{x}_1 = \begin{bmatrix} x_1^1 \\ -4x_1^1 \end{bmatrix}$$

with a non-trivial form when we set $x_1^1 = 1$,

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ -4 \end{bmatrix}$$

$$A\mathbf{x}_2 = \lambda_2 \mathcal{I} \mathbf{x}_2$$
$$\begin{bmatrix} 0 & 1 \\ 16 & 0 \end{bmatrix} \begin{bmatrix} x_2^1 \\ x_2^2 \end{bmatrix} = \begin{bmatrix} 4 & 0 \\ 0 & 4 \end{bmatrix} \begin{bmatrix} x_2^1 \\ x_2^2 \end{bmatrix}$$
$$x_2^2 = 4x_2^1$$

such that $\mathbf{x}_1$ can be written as

$$\mathbf{x}_2 = \begin{bmatrix} x_2^1 \\ 4x_2^1 \end{bmatrix}$$

with a non-trivial form when we set $x_1^1 = 1$,

$$\mathbf{x}_2 = \begin{bmatrix} 1 \\ 4 \end{bmatrix}$$

Therefore, the eigenvalues of matrix $A$ and their corresponding eigenvectors are given by,

$$\boxed{\lambda_1 = -4, \quad \mathbf{x}_1 = \begin{bmatrix} 1 \\ -4 \end{bmatrix}, \quad \lambda_2 = 4, \quad \mathbf{x}_2 = \begin{bmatrix} 1 \\ 4 \end{bmatrix}}$$

**(b)**$x_{t+3} + 5x_{t+2} - x_{t+1} - 5x_t = 0$
We let $y_1[t] = x[t]$, $y_2[t] = x[t+1]$, $y_3[t] = x[t+2]$, such that

$$y_1[t+1] = y_2[t]$$
$$y_2[t+1] = y_3[t]$$
$$y_3[t+1] = -5y_3[t] + y_2[t] + 5y_1[t]$$

which can be alternatively written as,

$$Y[t+1] = AY[t]$$

where

$$Y[t] = \begin{bmatrix} y_1[t] \\ y_2[t] \\ y_3[t] \end{bmatrix}$$

and

$$A = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 5 & 1 & -5 \end{bmatrix}$$

We can obtain the eigenvalues of the matrix $A$ by first calculating for $\det(A - \mathcal{I}\lambda)$,

$$\begin{aligned} -\lambda^2(\lambda+5) + (\lambda+5) &= 0 \\ (\lambda+5)(\lambda^2-1) &= 0 \end{aligned}$$

the roots of which are $\lambda_1 = -5$, $\lambda_2 = 1$, and $\lambda_3 = -1$. Say the eigenvectors of this matrix can be written as,

$$\mathbf{x}_1 = \begin{bmatrix} x_1^1 \\ x_1^2 \\ x_1^3 \end{bmatrix} \quad \mathbf{x}_2 = \begin{bmatrix} x_2^1 \\ x_2^2 \\ x_2^3 \end{bmatrix} \quad \mathbf{x}_3 = \begin{bmatrix} x_3^1 \\ x_3^2 \\ x_3^3 \end{bmatrix}$$

which correspond to $\lambda_1$, $\lambda_2$, and $\lambda_3$ respectively, such that

$$\begin{aligned} A\mathbf{x}_1 &= \lambda_1 \mathcal{I}\mathbf{x}_1 \\ \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 5 & 1 & -5 \end{bmatrix} \begin{bmatrix} x_1^1 \\ x_1^2 \\ x_1^3 \end{bmatrix} &= \begin{bmatrix} -5 & 0 & 0 \\ 0 & -5 & 0 \\ 0 & 0 & -5 \end{bmatrix} \begin{bmatrix} x_1^1 \\ x_1^2 \\ x_1^3 \end{bmatrix} \\ x_1^2 &= -5x_1^1 \\ x_1^3 &= -5x_1^2 \end{aligned}$$

Hence, $\mathbf{x}_1$ can be written as,

$$\mathbf{x}_1 = \begin{bmatrix} x_1^1 \\ -5x_1^1 \\ 25x_1^1 \end{bmatrix}$$

with a non-trivial form when we set $x_1^1 = 1$,

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ -5 \\ 25 \end{bmatrix}$$

$$\begin{aligned} A\mathbf{x}_2 &= \lambda_2 \mathcal{I}\mathbf{x}_2 \\ \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 5 & 1 & -5 \end{bmatrix} \begin{bmatrix} x_2^1 \\ x_2^2 \\ x_2^3 \end{bmatrix} &= \begin{bmatrix} -1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & -1 \end{bmatrix} \begin{bmatrix} x_2^1 \\ x_2^2 \\ x_2^3 \end{bmatrix} \\ x_2^2 &= -x_2^1 \\ x_2^3 &= -x_2^2 \\ 5x_2^1 + x_2^2 &= 4x_2^3 \end{aligned}$$

Hence, $\mathbf{x}_2$ can be written as,

$$\mathbf{x}_2 = \begin{bmatrix} x_2^1 \\ -x_2^1 \\ x_2^1 \end{bmatrix}$$

with a non-trivial form when we set $x_2^1 = 1$,

$$\mathbf{x}_2 = \begin{bmatrix} 1 \\ -1 \\ 1 \end{bmatrix}$$

$$A\mathbf{x}_3 = \lambda_3 \mathcal{I}\mathbf{x}_3$$
$$\begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 5 & 1 & -5 \end{bmatrix} \begin{bmatrix} x_3^1 \\ x_3^2 \\ x_3^3 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} x_3^1 \\ x_3^2 \\ x_3^3 \end{bmatrix}$$
$$x_3^2 = x_3^1$$
$$x_3^3 = x_3^2$$
$$5x_3^1 + x_3^2 = 6x_3^3$$

Hence, $\mathbf{x}_3$ can be written as,

$$\mathbf{x}_3 = \begin{bmatrix} x_3^1 \\ x_3^1 \\ x_3^1 \end{bmatrix}$$

with a non-trivial form when we set $x_2^1 = 1$,

$$\mathbf{x}_3 = \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}$$

Therefore, the eigenvalues of matrix $A$ and their corresponding eigenvectors are given by,

$$\boxed{\lambda_1 = -5, \quad \mathbf{x}_1 = \begin{bmatrix} 1 \\ -5 \\ 25 \end{bmatrix}, \quad \lambda_2 = -1, \quad \mathbf{x}_2 = \begin{bmatrix} 1 \\ -1 \\ 1 \end{bmatrix}, \quad \lambda_3 = 1, \mathbf{x}_3 = \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}}$$

which in vector form is given by,

$$\mathbf{x} = c_1(-5)^t \begin{bmatrix} 1 \\ -5 \\ 25 \end{bmatrix} + c_2(-1)^t \begin{bmatrix} 1 \\ -1 \\ 1 \end{bmatrix} + c_3 \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}$$

4. Let $X(t+1) = AX(t)$, where $A = \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix}$. The general solution is $X(t) = A^t X(0)$. Find $A^2$, $A^3$, and $A^4$, then find a general expression for $A^t$ and write the general solution.

We proceed in evaluating the matrix operations required in the problem. $A^2$, $A^3$, and $A^4$, can be easily obtained by performing ordinary matrix multiplication,

$$\begin{aligned}
A^2 &= \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \\
&= \begin{bmatrix} 1+0 & 1+2 \\ 0 & 4+0 \end{bmatrix} = \begin{bmatrix} 1 & 3 \\ 0 & 4 \end{bmatrix} \\
A^3 &= \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \\
&= \begin{bmatrix} 1 & 3 \\ 0 & 4 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \\
&= \begin{bmatrix} 1+0 & 1+6 \\ 0 & 8 \end{bmatrix} = \begin{bmatrix} 1 & 7 \\ 0 & 8 \end{bmatrix} \\
A^4 &= \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \\
&= \begin{bmatrix} 1 & 7 \\ 0 & 8 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \\
&= \begin{bmatrix} 1 & 1+14 \\ 0 & 16+0 \end{bmatrix} = \begin{bmatrix} 1 & 15 \\ 0 & 16 \end{bmatrix}
\end{aligned}$$

We use the previously obtained products as our base case and assume that for some arbitrary $k > 0$,

$$A^k = \begin{bmatrix} 1 & 2^k - 1 \\ 0 & 2^k \end{bmatrix}$$

We then proceed by applying this formula to the $k+1$ case, that is

$$\begin{aligned} A^{k+1} &= A^k(A) \\ &= \begin{bmatrix} 1 & 2^k - 1 \\ 0 & 2^k \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} = \begin{bmatrix} 1 & 1 + 2(2^k - 1) \\ 0 & 2^{k+1} \end{bmatrix} \\ &= \begin{bmatrix} 1 & 2^{k+1} - 1 \\ 0 & 2^{k+1} \end{bmatrix} \end{aligned}$$

which shows that $A^{k+1}$ indeed holds. Since both the base step(s) and inductive step hold, by mathematical induction, the $t$-th exponent of $A$ is given by

$$A^t = \begin{bmatrix} 1 & 2^t - 1 \\ 0 & 2^t \end{bmatrix}$$

for all $t \geq 0$, where $A^0$ is the identity matrix. From this result, we can write the general solution $X(t)$ as,

$$\boxed{X(t) = \begin{bmatrix} 1 & 2^t - 1 \\ 0 & 2^t \end{bmatrix} X(0)}$$

5. (Edelstein-Keshet 1998) In the circulatory system, red blood cells are constantly being destroyed and replaced. They carry oxygen throughout the body and they must be maintained at a constant level. The spleen filters out and destroys a fraction of the cells daily and the bone marrow produces a number proportional to the number lost on the previous day. The cell count of day $t$ is modeled as follows:

- $R_t$ is the number of red blood cells in circulation on day $t$,
- $M_t$ is the number of red blood cells produced by marrow on day $t$,
- $f$ is the fraction of red blood cells removed by spleen, $0 < f < 1$, and
- $\gamma$ is the production constant, $\gamma > 0$.

The system of difference equations by $R_t$ and $M_t$ is,

$$\begin{aligned} R_{t+1} &= (1 - f)R_t + M_t \\ M_{t+1} &= \gamma f R_t \end{aligned}$$

a Express the system as a matrix equation $X_{t+1} = AX_t$. Find the eigenvalues of $A$ and determine their signs.

We can write the linear system above as a matrix equation $X_{t+1} = AX_t$, where

$$A = \begin{bmatrix} 1 - f & 1 \\ \gamma f & 0 \end{bmatrix}$$

and,

$$X_t = \begin{bmatrix} R_t \\ M_t \end{bmatrix}$$

We can obtain the eigenvalues of matrix $A$ by obtaining the determinant of $(A - \mathcal{I}\lambda)$ and equating it to zero. Doing so yields,

$$\begin{aligned} -\lambda(1 - (f + \lambda)) - \gamma f &= 0 \\ \lambda^2 - (1 - f)\lambda - \gamma f &= 0 \end{aligned}$$

which has roots,

$$\lambda_{1/2} = \frac{(1 - f) \pm \sqrt{(1 - f)^2 + 4\gamma f}}{2}$$

Since $0 < f < 1$ and $\gamma > 0$,

$$\begin{aligned} \sqrt{(1 - f)^2 + 4\gamma f} &> 1 - f \\ (1 - f) + \sqrt{(1 - f)^2 + 4\gamma f} &> 0 \\ (1 - f) - \sqrt{(1 - f)^2 + 4\gamma f} &< 0 \end{aligned}$$

Hence,

$$\lambda_1 > 0, \quad \lambda_2 < 0$$

b For homeostasis in the red cell count, the total number of red blood cells, $R_t$, should remain roughly constant. Show that one way of achieving this is by letting $\lambda = 1$. What does this imply about $\gamma$?

Say, we assume that the positive eigenvalue is equal to 1. If so,

$$\lambda_1 = 1 = \frac{(1-f) + \sqrt{(1-f)^2 + 4\gamma f}}{2}$$

$$\begin{aligned} 2 - (1-f) &= \sqrt{(1-f)^2 + 4\gamma f} \\ (f+1)^2 &= (f-1)^2 + 4\gamma f \\ &= f^2 + 2(2\gamma - 1)f + 1 \end{aligned}$$

Matching the coefficients of $f^2$, and $f$, we find that

$$2 = 2(2\gamma - 1)$$

Hence, $\gamma = 1$; that is, if there is homeostasis for this value of $\gamma$, it should be the ratio of the number of red blood cells produced per the number that is lost.

c Let $\lambda_1 = 1$. Find $\lambda_2$ and describe the behavior of $R_t$.

Now that we have a value for $\gamma$, we find that the value of the second eigenvalue is given by,

$$\begin{aligned} \lambda_2 &= \frac{(1-f) - \sqrt{(1-f)^2 + 4f}}{2} \\ &= \frac{(1-f) - \sqrt{(f+1)^2}}{2} \\ &= \frac{(1-f) - (f+1)}{2} \\ &= -f \end{aligned}$$

This implies that the behavior of the solution $R_t$ has a damped oscillatory behavior over different values of $t$, the general solution of which is given by,

$$R[t] = C_1 + C_2(-f)^t$$

whose value asymptotically reaches $C_1$ for large values of $t$. As an illustration, we use values $C_1 = 1$, $C_2 = 1$, for different values of $f$,