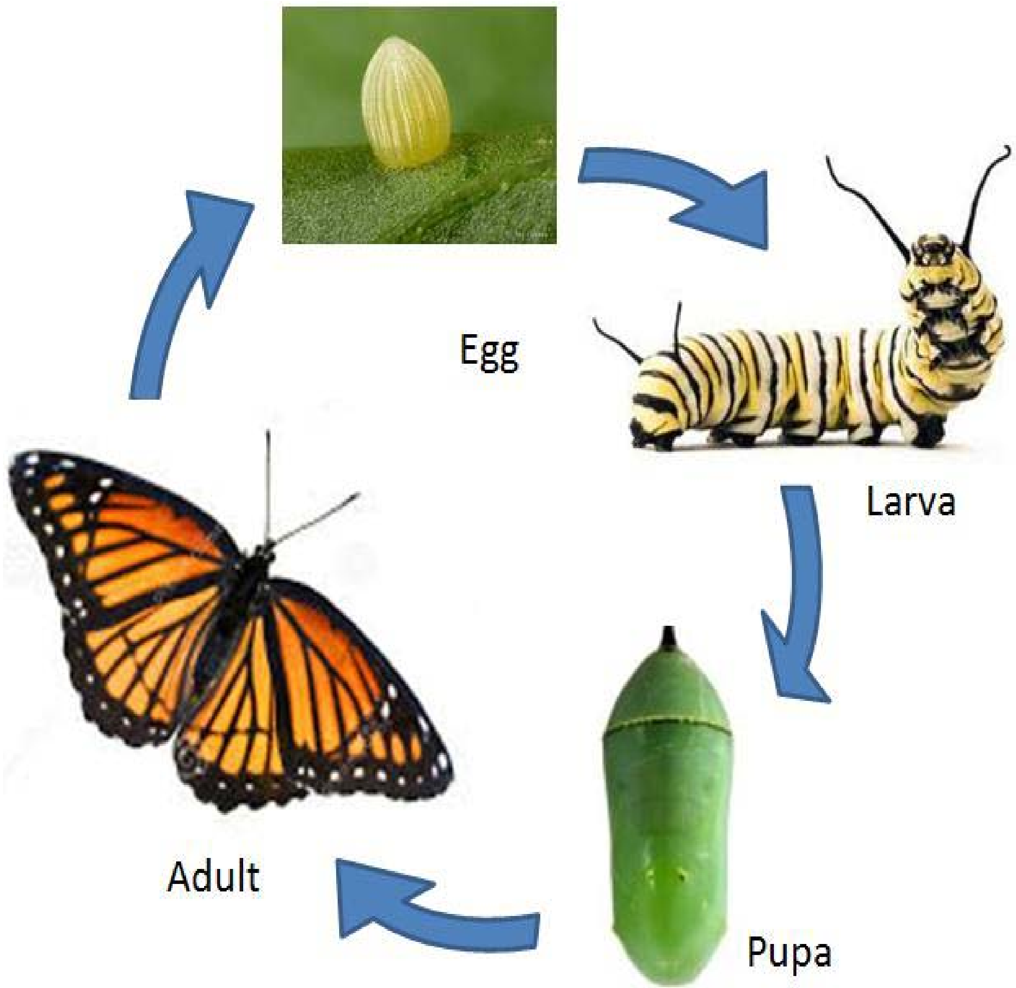
Linear Models of Structured Populations

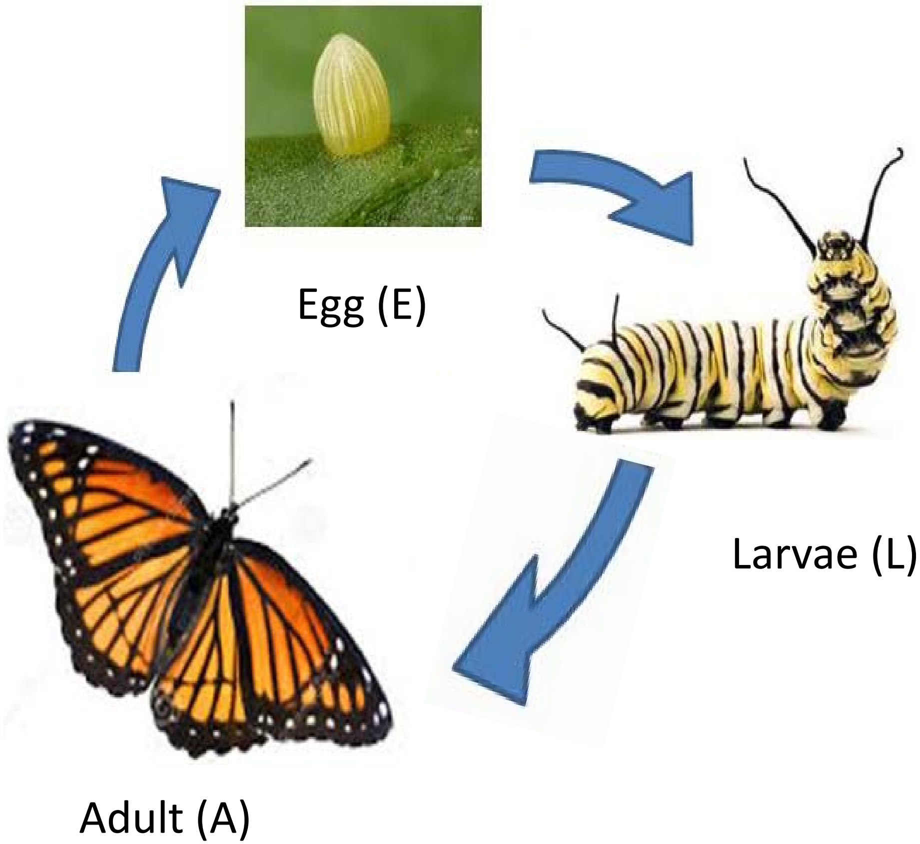
Coupled difference equations and Matrix methods

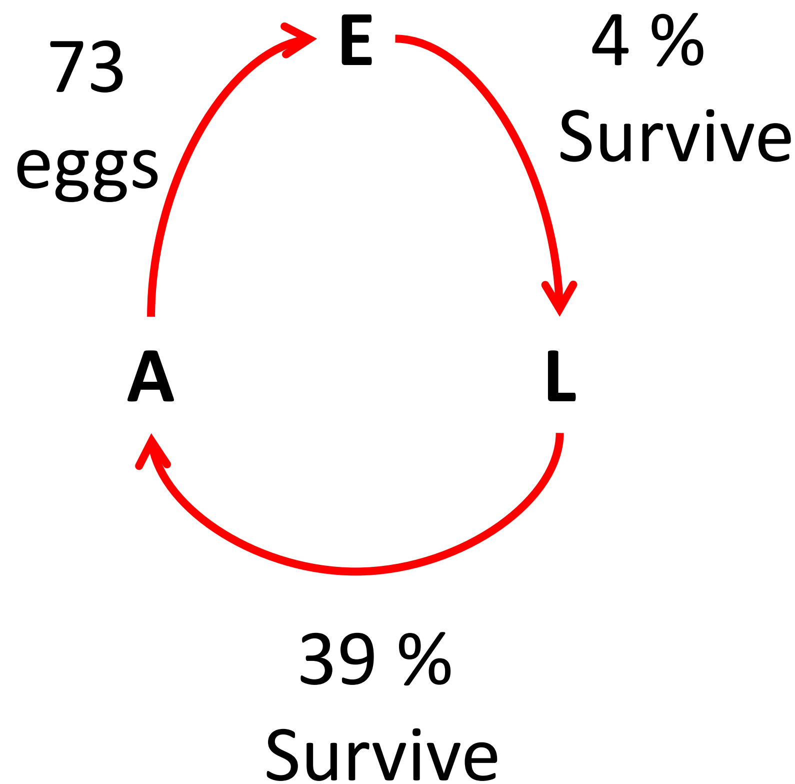
Coupled difference equations: Developmental cycle of butterfly



http://cpsteamwork6.weebly.com/animal-life-cycles.html

Small Network of developmental cycle: Abstraction





Formalization

Let

- E_t = *the number of eggs at time t,*
- L_t = *the number of larvae at time t,*
- A_t = *the number of adults at time t.*

- This can be expressed by the three coupled difference equations

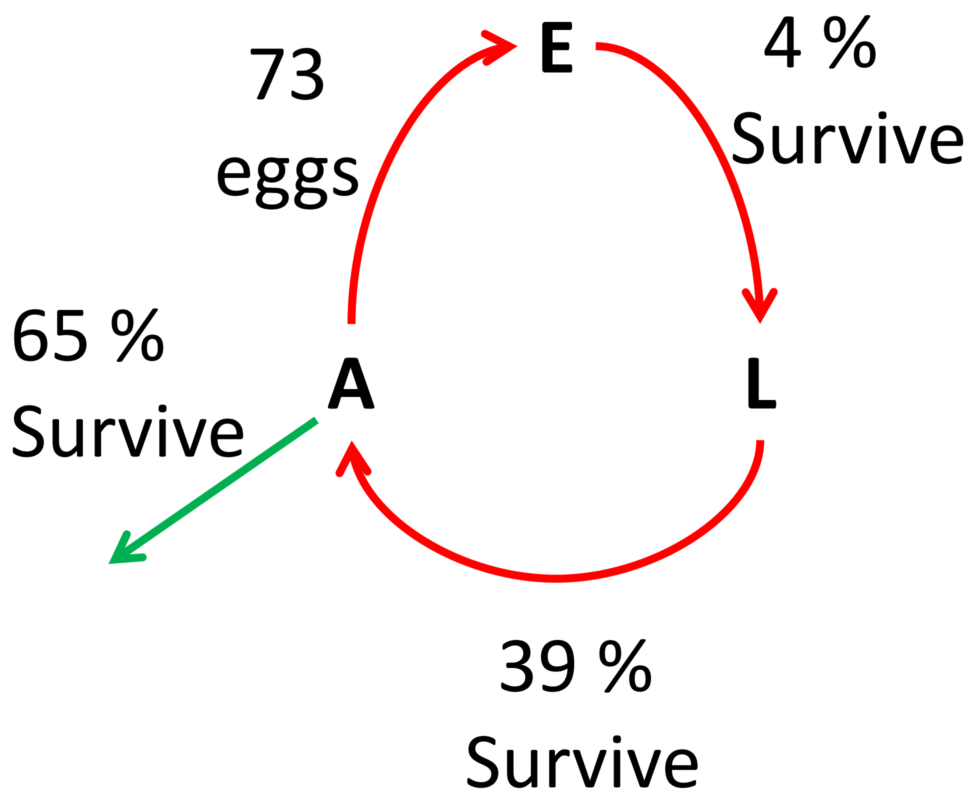
$$E_{t+1} = 73A_t,\ (73\ \text{eggs laid by Adult})$$
$$L_{t+1} = .04E_t,\ (4\%\ \text{egg converted to larva})$$
$$A_{t+1} = .39L_t.\ (39\%\ \text{larva converted to Adult})$$

Three initial values, E_0, L_0, *and* A_0, *one for* each stage class are required.

- The above example could actually be studied by the model

$$A_{t+3} = (.39)(.04)(73)\ A_t = 1.1388\ A_t \quad \text{(Show !)}$$

Extension of the model



Suppose that rather than dying, 65% of the adults are alive at any time survive for an additional time step.

The extended model is

$$E_{t+1} = 73A_t,$$

$$L_{t+1} = .04E_t$$

$$A_{t+1} = .39L_t + .65A_t.$$

Another example

- Two species of trees, with A_t *and* B_t *denoting the number of each species in the* forest in year *t.*

- When a tree dies, a new tree grows in its place, but the new tree might be of either species; i.e., A or B.

- *A trees are dying* 1% , While B trees die 5 % in any given year.

- 75% of all vacant spots go to species *B trees, and only 25% go to* species *A trees.*

- *How to model this as difference equation?*

Model and solution

- $$A_{t+1} = (.99 + (.25)(.01))A_t + (.25)(.05)B_t \,,$$
  $$B_{t+1} = (.75)(.01)A_t + (.95 + (.75)(.05))B_t \,.$$

- *How to get the above equation?*

Solution

- 1% of A tree dies, so 99% survives. So,
  $$A_{t+1} = .99\, A_t$$

- *5 % of B tree dies, so 95 % survives. So*
  $$B_{t+1} =.95\, B_t$$

Solution

- *Similarly, 75% of 5% B trees grow in the vacant spot, So its* $(0.75)(0.05)B_t$
- $$B_{t+1} = .95\,B_t + (0.75)(0.05)B_t$$
- *Rest 25% of 5% B tree grows as A trees in the vacant spot; i.e.,* $(0.25)(0.05)B_t$ *. So B tree increases A trees.*
- *So it will be* $A_{t+1} = .99\,A_t + (0.25)(0.05)B_t$
- *Similarly, 25% of 1% go to species A; i,e.,* $(0.25)(0.01)\,A_t$*.*
- $$A_{t+1} = .99\,A_t + (0.25)(0.05)B_t + (0.25)(0.01)A_t.$$
- Rest 75% of 1% A tree grows as B tree in the vacant spot; It increases i.e., $(0.75)\,(0.01)\,A_t$.
- $$B_{t+1} = .95\,B_t + (0.75)(0.05)B_t + (0.75)\,(0.01)\,A_t$$

Simplification to Matrix form

$$A_{t+1} = (.99 + (.25)(.01))A_t + (.25)(.05)B_t,$$
$$B_{t+1} = (.75)(.01)A_t + (.95 + (.75)(.05))B_t.$$

$$\downarrow$$

$$A_{t+1} = .9925A_t + .0125B_t,$$
$$B_{t+1} = .0075A_t + .9875B_t.$$

$$\downarrow$$

$$\begin{pmatrix} A_{t+1} \\ B_{t+1} \end{pmatrix} = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix} \begin{pmatrix} A_t \\ B_t \end{pmatrix}$$

Numerical solution

Table 2.1. *Forest Model Simulation*

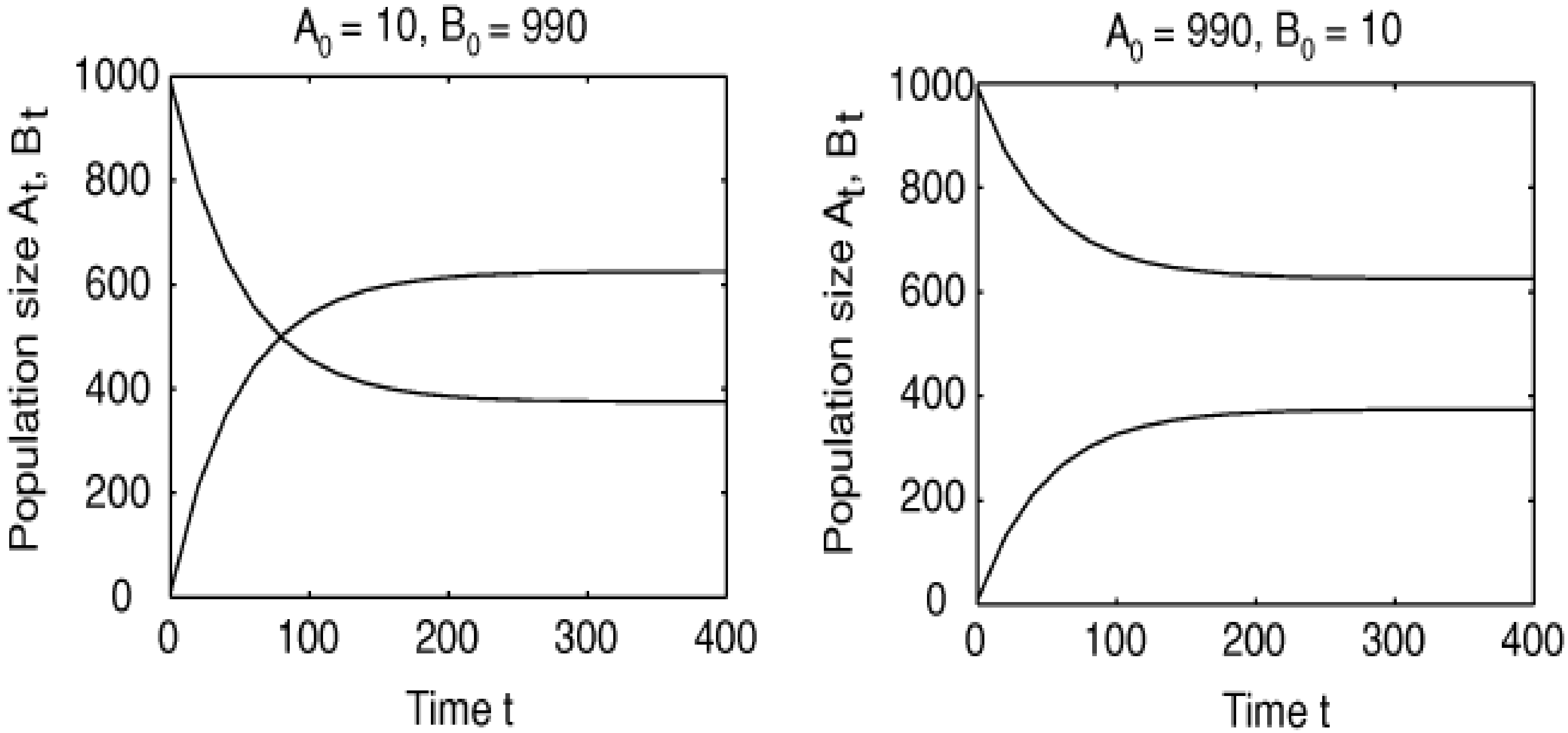
Year	A_t	B_t
0	10	990
1	22.30	977.70
2	34.35	965.65
3	46.17	953.83
4	57.74	942.26
5	69.09	930.91
⋮	⋮	⋮
10	122.50	877.50
⋮	⋮	⋮
50	401.04	598.96
⋮	⋮	⋮
100	543.44	456.56
⋮	⋮	⋮
500	624.97	375.03
⋮	⋮	⋮
1000	625	375
⋮	⋮	⋮

Initial conditions

Converges

The forest approaches an equilibrium, with 625 trees of species *A and 375 of species B.*

Different initial conditions



Projection Matrix

- We rewrite the forest model as

$$A_{t+1} = .9925A_t + .0125B_t$$

$$B_{t+1} = .0075A_t + .9875B_t$$

in matrix notation as

$$\begin{pmatrix} A_{t+1} \\ B_{t+1} \end{pmatrix} = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix} \begin{pmatrix} A_t \\ B_t \end{pmatrix}$$

$$\mathbf{X_{t+1} \quad = \quad P \quad X_t}$$

- P = projection, or transition, matrix for our forest model

- Its projection matrix because the entries in it are the numbers used to project future tree populations.

What to know in matrix operations?

- Matrix multiplication is not commutative;

$$AB \neq BA$$

- Matrix multiplication is associative:

$$(AB)C = A(BC)$$

- To multiply a vector or a matrix by a scalar, multiply every entry by that scalar.

- Vectors and matrices also obey several distributive laws of multiplication over addition

  $A(B + C) = AB + AC$, $(B + C)A = BA + CA$, *and*

  $A(\mathbf{x} + \mathbf{y}) = A\mathbf{x} + A\mathbf{y}$.

- If *P and Q are both* $n \times n$ *square matrices with* $QP = I$ *, then* we say that *Q is the inverse of P. We then use the notation* $Q = P^{-1}$.

- *A square matrix has an inverse if, and only if, its determinant is nonzero.*

- For matrices usually $(AB)^{-1} \neq A^{-1}B^{-1}$. *Instead, as* long as the inverses exist, $(AB)^{-1} = B^{-1}A^{-1}$.

Projection Matrices for Structured Models: Leslie's model

- In some species, the amount of reproduction varies greatly with the age of individuals.
- Two different human populations that have the same total size.
- However, If one is comprised primarily of those over 50 in age, & the other has mostly individuals in their 20s, quite different population growth is expected.
- Clearly, the age structure of the population matters.
- Partitioning the population into age classes. Such a model is called an 'age'- structured model.

How to build age structure model?

- Age and Age class are different concepts.
- Age is a continuous variable; for example, you can be 19 years, 11 months, and 29 days old.
- Age class is discrete; until you are 20 years old, you are in the age class of 19-year olds.
- There are two basic demographic parameters, survival and fecundity to describe the growth of a population.

Simple example

- Consider the case where number of birds in a population is counted on.
- 26 fledgling last year (i.e, 26 birds are less than 1 year old),
- 16 are between 1 and 2 years old,
- 12 are between 2 and 3 years old, and so on.
- Instead of representing the population with its abundance, N, we represent it by the abundances of different age classes.

$$N(\text{this year}) = \begin{bmatrix} 26 \\ 16 \\ 12 \\ \vdots \\ \vdots \\ \vdots \end{bmatrix}, \text{ or more generally as: } N(t) = \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ \\ \vdots \\ N_\omega(t) \end{bmatrix}$$

N(t) denotes the number of individuals of age class *x* at time *t*.

Leslie model assumptions

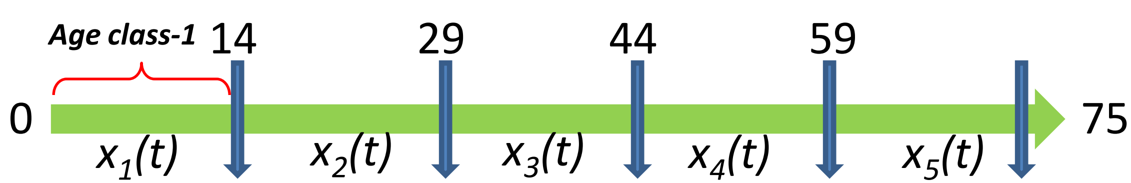
- Only females in the model is considered
- The maximum age attained by the individual is ‘n’ years.
- The population is grouped into n 1-year age class.
- An individual’s chance of surviving from one year to the next is a function of its age.
- The survival rate τ_i is known.
- The reproduction rate or birth rate or fecundity rate F_i is known.
- The initial age distribution is known.

Creating the age-class matrix

- To capture the effects on population growth, we might begin modeling a human population by creating five age classes with:

- $x_1(t)$ = *no. of individuals age 0 through 14 at time t,*
- $x_2(t)$ = *no. of individuals age 15 through 29 at time t,*
- $x_3(t)$ = *no. of individuals age 30 through 44 at time t,*
- $x_4(t)$ = *no. of individuals age 45 through 59 at time t,*
- $x_5(t)$ = *no. of individuals age 60 through 75 at time t.*

- Assumption that no one survives past age 75, and the time step is 15 years



Creating population matrix in terms of fecundity and survival rates

- Using a time step of 15 years, we can describe the population through equations like:

$$
\begin{aligned}
x_1(t+1) &= f_1 x_1(t) + f_2 x_2(t) + f_3 x_3(t) + f_4 x_4(t) + f_5 x_5(t)\\
x_2(t+1) &= \tau_{1,2} x_1(t)\\
x_3(t+1) &= \tau_{2,3} x_2(t)\\
x_4(t+1) &= \tau_{3,4} x_3(t)\\
x_5(t+1) &= \tau_{4,5} x_4(t).
\end{aligned}
$$

- Here, f_i denotes a birth rate (over a 15-year period) for parents in the i^{th} age class.

- $\tau_{i,i+1}$ denotes a survival rate for those in the i^{th} age class passing into the (i + 1)th.

Matrix notation

In matrix notation, the model is simply $\mathbf{x}_{t+1} = P\mathbf{x}_t$, where

$$\mathbf{x}_t = (x_1(t), x_2(t), x_3(t), x_4(t), x_5(t))$$

is the column vector of subpopulation sizes at time t and

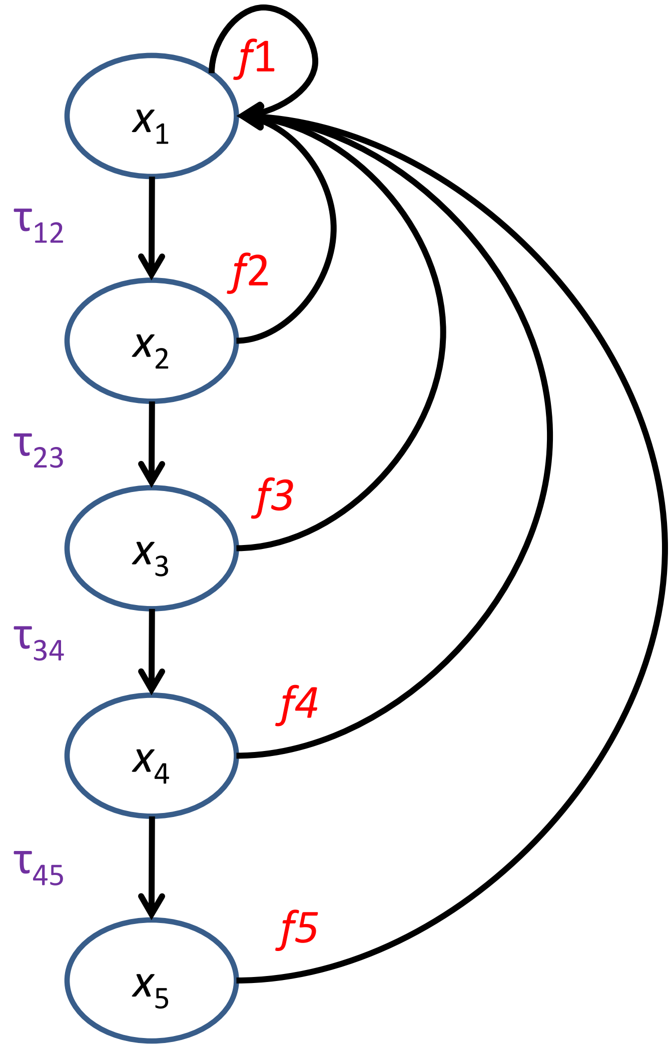
$$P = \begin{pmatrix} f_1 & f_2 & f_3 & f_4 & f_5 \\ \tau_{1,2} & 0 & 0 & 0 & 0 \\ 0 & \tau_{2,3} & 0 & 0 & 0 \\ 0 & 0 & \tau_{3,4} & 0 & 0 \\ 0 & 0 & 0 & \tau_{4,5} & 0 \end{pmatrix}$$

Fecundity and fertility

- Difference between fertility and fecundity:
- Fertility gives the number of offspring (e.g., seeds) produced by an individual in a given breeding season.
- Fecundity is the average number, per individual of age x alive at a given time step, of offspring censused at the next time step.
- This is also important to build Leslie's matrix from life-table

Graphical representation- Leslie Model

$$P = \begin{pmatrix} f_1 & f_2 & f_3 & f_4 & f_5 \\ \tau_{1,2} & 0 & 0 & 0 & 0 \\ 0 & \tau_{2,3} & 0 & 0 & 0 \\ 0 & 0 & \tau_{3,4} & 0 & 0 \\ 0 & 0 & 0 & \tau_{4,5} & 0 \end{pmatrix}$$

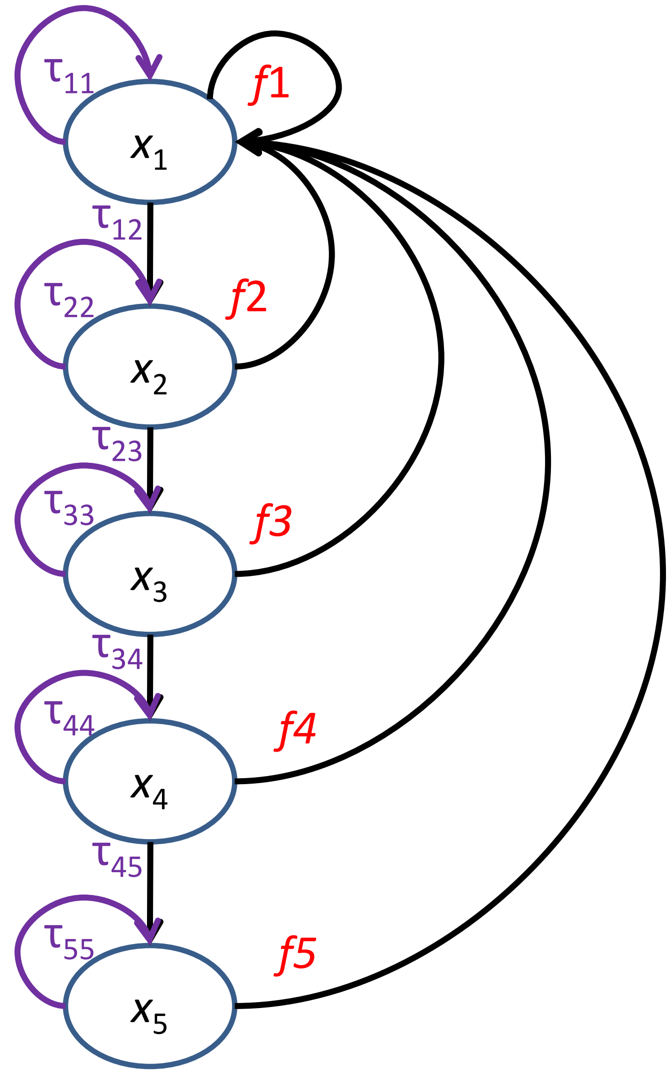


Graphical representation-Usher model

$$\begin{pmatrix} f_1+\tau_{1,1} & f_2 & f_3 & f_4 & f_5 \\ \tau_{1,2} & \tau_{2,2} & 0 & 0 & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} & 0 & 0 \\ 0 & 0 & \tau_{3,4} & \tau_{4,4} & 0 \\ 0 & 0 & 0 & \tau_{4,5} & \tau_{5,5} \end{pmatrix}$$

Diagonal elements are also present

Parameters $\tau_{i,i}$ describes the fraction of the i^{th} age class that remains in that class in passage to the next time step.



Example-Usher matrix for Whale breeding

$$\begin{pmatrix} \tau_{1,1} & f_2 & 0 \\ \tau_{1,2} & \tau_{2,2} & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} \end{pmatrix}$$

Problem: For the mammal whale takes several years to reach sexual maturity, and may also live past an age where it breeds. It can be immature, breeding, and post breeding classes. The Usher matrix is given on the left.

Q1. How many age class are there?

Q2. Why is there only one nonzero f_i in this matrix?

Q3. How do you represent this graphically?

Another case -- flowering stage of the plant

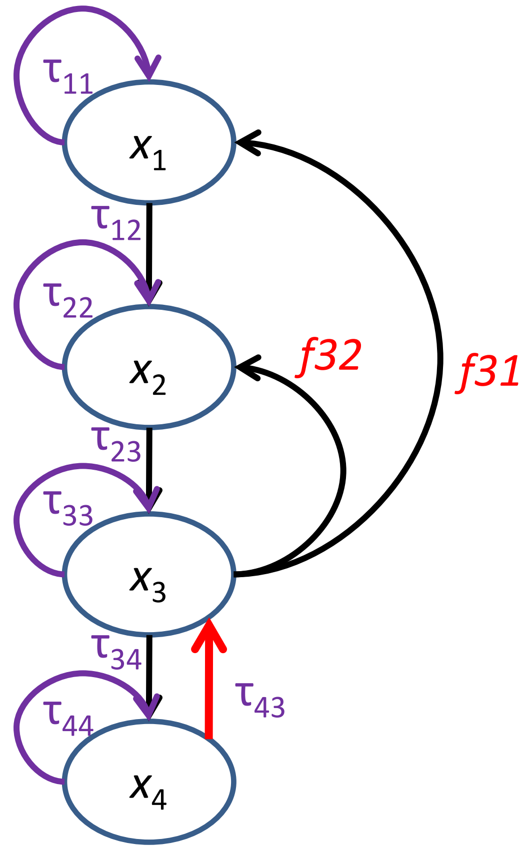
- Consider a plant that takes several years to mature to a flowering stage and that does not flower every year after reaching maturity. In addition, seeds may lie dormant for several years before germinating.

- The life cycle of this plant could be modeled using time steps of a year and the classes

- $x_1(t)$ = no. of ungerminated seeds at time t ,
- $x_2(t)$ = no. of sexually immature plants at time t ,
- $x_3(t)$ = no. of mature plants flowering at time t ,
- $x_4(t)$ = no. of mature plants not flowering at time t .

Graphical representation

$x_1(t)$ = no. of ungerminated seeds at time t ,
$x_2(t)$ = no. of sexually immature plants at time t ,
$x_3(t)$ = no. of mature plants flowering at time t ,
$x_4(t)$ = no. of mature plants not flowering at time t .



Can you build the matrix model from the graph?

Can you interpret the parameter $\tau_{4,3}$? What it describes?

Matrix model for plant and graph

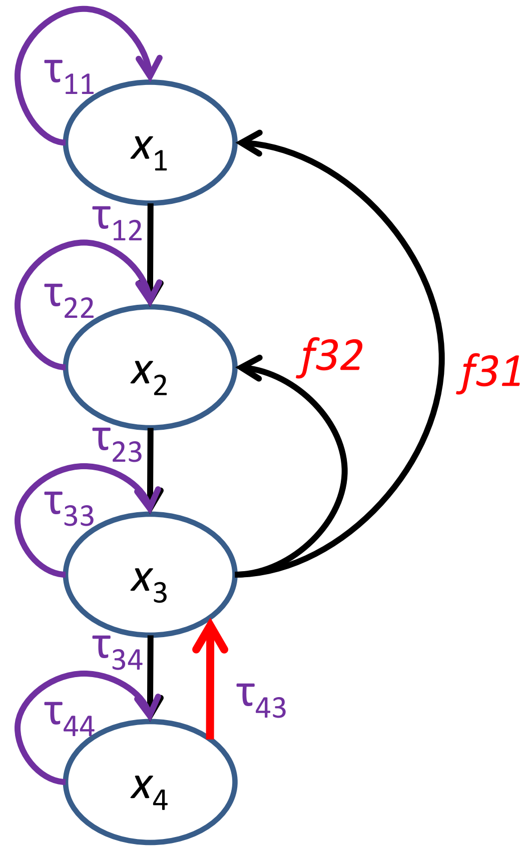
$$\begin{pmatrix} \tau_{1,1} & 0 & f_{3,1} & 0 \\ \tau_{1,2} & \tau_{2,2} & f_{3,2} & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} & \tau_{4,3} \\ 0 & 0 & \tau_{3,4} & \tau_{4,4} \end{pmatrix}$$

Here, the parameter $\tau_{4,3}$ describes mature plants that did not flower in one season passing into the flowering class for the next.

In addition, there are two parameters describing fertility –

f_{31} describes the production of seeds that do not germinate immediately.

f_{32} describes the production of seedlings through new seeds that germinate by the next time step.



Problem-1 (use of matrix inverse)

- For the forest model of Section 2.1, suppose at time 1 the populations were x_1 = (500, 500). What must they have been at time 0?

- The projection matrix is provided below.

$$\begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$$

Solution

To answer this, because $\mathbf{x}_1 = P\mathbf{x}_0$, we multiple by P^{-1} to find

$$\begin{aligned}
\mathbf{x}_0 &= P^{-1}\mathbf{x}_1 \\
&= \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}^{-1} \begin{pmatrix} 500 \\ 500 \end{pmatrix} \\
&= \frac{1}{(.9925)(.9875) - (.0075)(.0125)} \begin{pmatrix} .9875 & -.0125 \\ -.0075 & .9925 \end{pmatrix} \begin{pmatrix} 500 \\ 500 \end{pmatrix} \\
&= \frac{1}{.98} \begin{pmatrix} 487.5 \\ 492.5 \end{pmatrix} \approx \begin{pmatrix} 497.449 \\ 502.551 \end{pmatrix}.
\end{aligned}$$

Problem-2.2.5

2.2.5. A simple Usher model of a certain organism tracks immature and mature classes, and is given by the matrix $P = \begin{pmatrix} .2 & 3 \\ .3 & .5 \end{pmatrix}$.

a. On average, how many births are attributed to each adult in a time step?

b. What percentage of adults die in each time step?

c. Assuming no immature individuals are able to reproduce in a time step, what is the meaning of the upper left entry in P?

d. What is the meaning of the lower left entry in P?

2.2.6. For the model of the last problem,

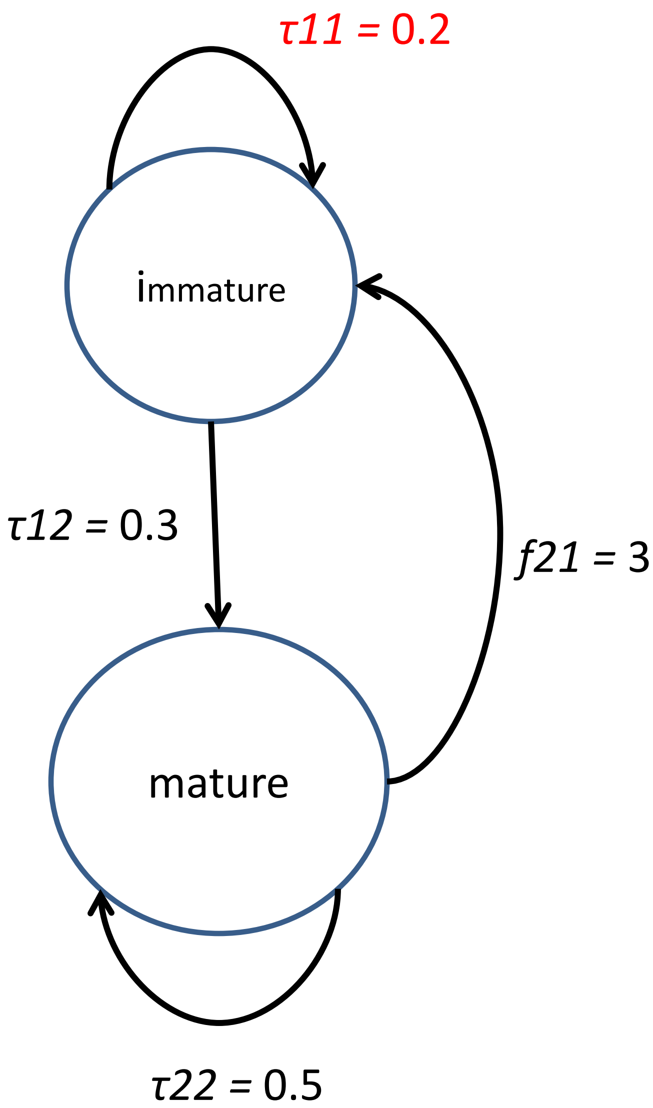
a. Find P^{-1}.

b. If $\mathbf{x}_1 = (1100, 450)$, find $\mathbf{x}_0$ and $\mathbf{x}_2$.

Solution

$$P = \begin{pmatrix} .2 & 3 \\ .3 & .5 \end{pmatrix}$$

(a) = 3
(b) = 50%
(c) Survival rate of the number of immature species
(d) 30% of the immature species transitioned to mature adult.



Problem-2.2.8

2.2.8. A model given in (Cullen, 1985), based on data collected in (Nellis and Keith, 1976), describes a certain coyote population. Three stage classes – pup, yearling, and adult – are used while the matrix

$$P = \begin{pmatrix} .11 & .15 & .15 \\ .3 & 0 & 0 \\ 0 & .6 & .6 \end{pmatrix}$$

describes changes over a time step of 1 year. Explain what each entry in this matrix is saying about the population. Be careful in trying to explain the meaning of the .11 in the upper left corner.

Solution-2.2.8

$$P = \begin{pmatrix} .11 & .15 & .15 \\ .3 & 0 & 0 \\ 0 & .6 & .6 \end{pmatrix}$$

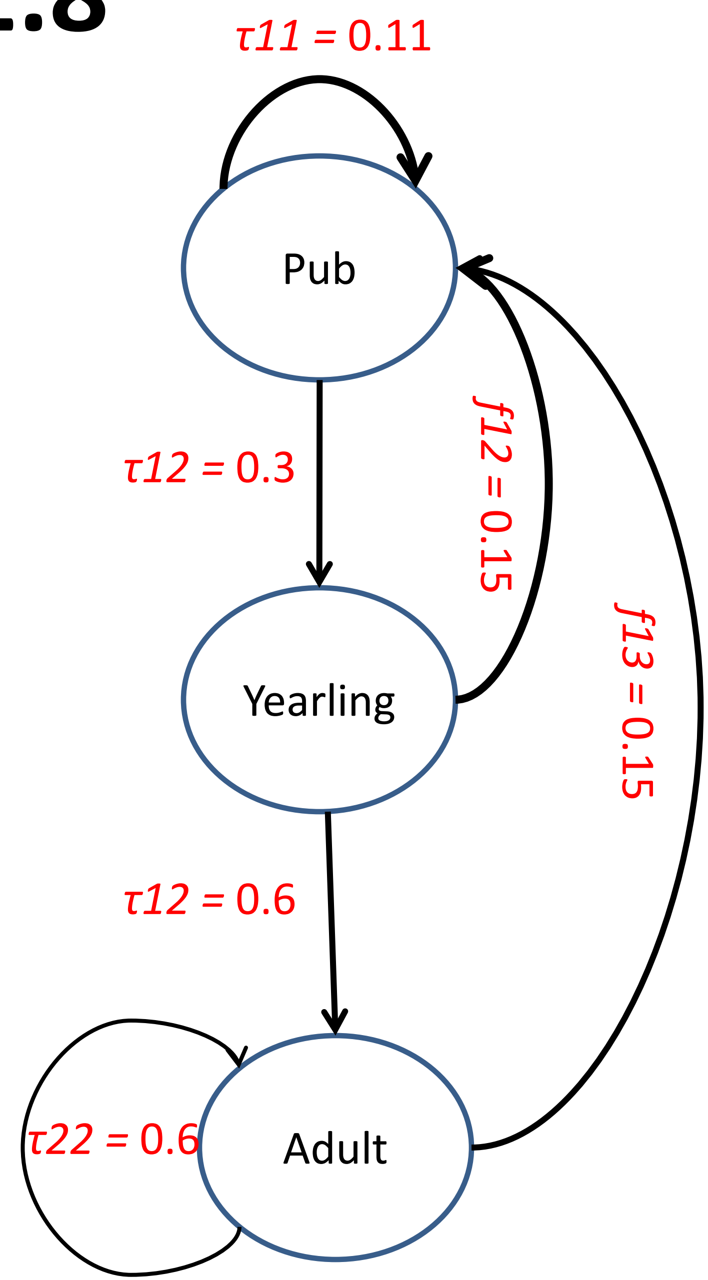
.11 represents the percentage of pups that remain pups after one year.

The *.15 entries indicate that on average* each yearling and adult gives birth to *.15 pups each year.*

The percentage of pups that progress into the yearling stage is 30% each year, so 1−*.11*−*.30 = 59%* of pups die.

60% of the yearlings progress into the adult stage, the remaining 40% die.

Finally, each year 40% of the adult coyotes die, but 60% live on into the next time step.



Problem-2.2.11

2.2.11. The formula $(AB)^{-1} = B^{-1}A^{-1}$ can be explained several ways.

a. Explain why $(B^{-1}A^{-1})(AB) = I$. Why does this show $(AB)^{-1} = B^{-1}A^{-1}$?

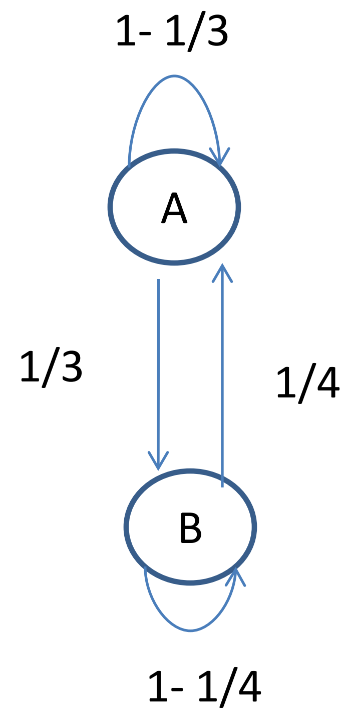
b. Suppose, as in the first section of this chapter, that D is a projection matrix for a forest population in a dry year, and W is a projection matrix for a wet year. Then, if the first year is dry and the second wet, $\mathbf{x}_2 = WD\mathbf{x}_0$. How could you find $\mathbf{x}_1$ from $\mathbf{x}_2$? How could you find $\mathbf{x}_0$ from $\mathbf{x}_1$? Combine these to explain how you could find $\mathbf{x}_0$ from $\mathbf{x}_2$. How does this show $(WD)^{-1} = D^{-1}W^{-1}$?

Problem-2.2.12

2.2.12. A forest is composed of two species of trees, A and B. Each year $\frac{1}{3}$ of the trees of species A are replaced by trees of species B, while $\frac{1}{4}$ of the trees of species B are replaced by trees of species A. The remaining trees either survive or are replaced by trees of their own species.

a. Letting A_t and B_t denote the number of trees of each type in year t, give equations for A_{t+1} and B_{t+1} in terms of A_t and B_t.
b. Write the equations of part (a) as a single matrix equation.
c. Use part (b) to get a formula for A_{t+2} and B_{t+2} in terms of A_t and B_t.
d. Use part (b) to get a formula for A_{t-1} and B_{t-1} in terms of A_t and B_t.

Solution



A(t+1) = ¼ Bt + (1-1/3) At
B(t+1) = 1/3 At + (1-1/4) Bt

A(t+1) = 1/4Bt + 2/3 At
B(t+1) = 1/3 At + ¾ Bt

Solution

a. $A_{t+1} = 2/3A_t + 1/4B_t$, $B_{t+1} = 1/3A_t + 3/4B_t$

b. $P = \begin{pmatrix} 2/3 & 1/4 \\ 1/3 & 3/4 \end{pmatrix}$, with $\mathrm{x}_t = (A_t, B_t)$.

c. $P^2 = \begin{pmatrix} 19/36 & 17/48 \\ 17/36 & 31/48 \end{pmatrix}$ so using decimal approximations $A_{t+1} = .5278A_t + .3542B_t$, $B_{t+1} = .4722A_t + .6458B_t$.

d. $P^{-1} = \begin{pmatrix} 9/5 & -3/5 \\ -4/5 & 8/5 \end{pmatrix}$ so $A_{t-1} = 1.8A_t - .6B_t$, $B_{t+1} = -.8A_t + 1.6B_t$.

Consensus table for Leslie matrix

	Census year			
Age	1991	1992	1993	1994
0	26	28	27	29
1	16	17	20	20
2	12	11	13	14
3	9	8	9	10
4	7	6	6	8
5	5	4	5	5
6	4	3	3	4
7	3	3	2	3
8	2	2	2	2
9	1	1	1	2
Total	85	83	88	97

- Data set consists of Four annual censuses conducted at the same time of the year.

- We assume that these census are made right after the breeding season.
- We assume that species starts breeding at age 1 and the fertility rate does not vary with age among breeding individuals.
- We also adopt the convention that individuals within their first year of life are called zero-year olds.
- Thus the first age class consists of zero-year-old individuals.

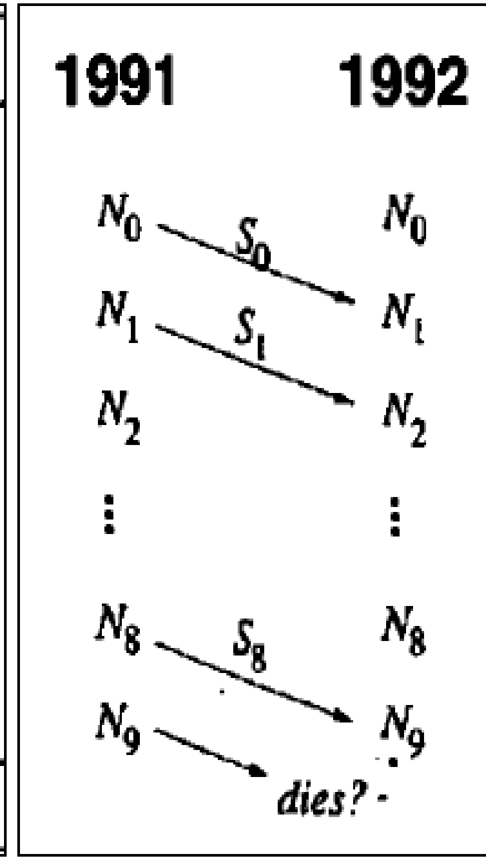
Survival rates

- According to the table, in 1991, we censused a total of 85 individuals.26 zero-year olds, 16 one-year olds, etc.

- Of the 26 zero-year olds we counted in 1991, 17 became one-year olds in year 1992,.and the others died.

- The number that survived to be one-year olds (N_1) is the munber we counted as zero-year olds (N_o) times the survival rate of zero-year olds (N_o)

Age	1991	1992
0	26	28
1	16	17
2	12	11
3	9	8
4	7	6
5	5	4
6	4	3
7	3	3
8	2	2
9	1	1
Total	85	83



$$N_1(1992) = N_0(1991) \cdot S_0$$

$$S_0 = N_1(1992) / N_0(1991)$$

17 / 26 = 0. 654.

Survival rates

- For the other age classes, the calculations are similar. We can write the above equation in a more general form:

$$S_x(t) = N_{x+1}(t+1) / N_x(t)$$

- for x = 1,2,...,9,

- Note that we did not count any 10-year olds, so we cannot estimate S_9, which is survival rate from age 9 to age 10.

	Census year			
Age	1991	1992	1993	1994
0	26	28	27	29
1	16	17	20	20

$N_1(1992)/N_0(1991) = 17/26 = 0.654$
$N_1(1993)/N_0(1992) = 20/28 = 0.714$
$N_1(1994)/N_0(1991) = 20/27 = 0.741$
Average = (2.109/3) = 0.703

Age-specific survival rates based on the data in

Age (x)	Survival rate (S_x)
0	0.703
1	0.717
2	0.751
3	0.769
4	0.746
5	0.717
6	0.806
7	0.778
8	0.667

Fecundities

- The fecundity, F“ is the average number of offspring (per individual of age x alive at a given time step) censused at the next time step.

- For example, the fecundity in year 1991 is the number of offspring produced in 1991 that are still alive in 1992, divided by the number of parents in 1991:

$$F(1991) = \frac{\text{Offspring alive in 1992}}{\text{Parents in 1991}}$$

Fecundity diagram

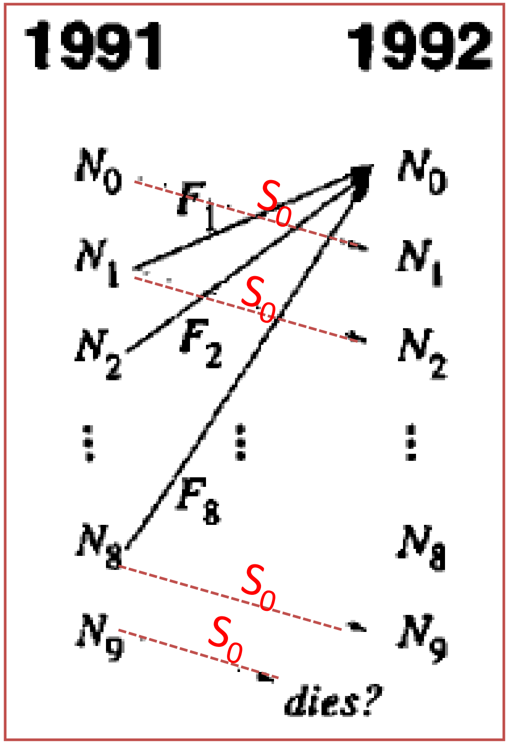
- **Assumption-1:** As stated above, we assume that this species starts breeding at age 1.

- **Assumption-2:** The fertility rate does not vary with age among breeding individuals.

- In other words, we assumed that F0 = 0 , and F1: F2 = F3 = = 1,.

- To calculate fecundity for the reproductive age classes, We divide the number of zero- year olds in the next year's census with the total number of individuals aged1 and older (potential parents) in this year's census.

	Census year			
Age	1991	1992	1993	1994
0	26	28	27	29
1	16	17	20	20
2	12	11	13	14
3	9	8	9	10
4	7	6	6	8
5	5	4	5	5
6	4	3	3	4
7	3	3	2	3
8	2	2	2	2
9	1	1	1	2
Total	85	83	88	97



$$F(1991) = \frac{\text{Offspring alive in 1992}}{\text{Parents in 1991}}$$

$$F(1991) = \frac{28}{59} = 0.4746 \quad F(1992) = \frac{27}{55} = 0.4909 \quad F(1993) = \frac{29}{61} = 0.4754$$

The **average of these three numbers** is about 0.48, which we will use as the mean fecundity.

Leslie Model

- Given a set-of age -specific fecundities, the number of zero-year olds in calculated by the formula

$$N_0(t+1) = F_0(t)\,N_0(t) + F_1(t)\,N_1(t) + F_2(t)\,N_2(t) + \ldots + F_\omega(t)\,N_\omega(t)$$

- The number of offspring produced by each age class is equivalent to

$$N_0(t+1) = \sum_{x=0}^{\omega} F_x(t)\,N_x(t)$$

$\sum_{x=0}^{\omega}$ means we add for all values of x from 0 to the maximum age.

- we can now predict the abundance in each age class from time step t to 1+1.

- Below, we consider the specific case of predicting abundances for four age classes.

Leslie Matrix

$$N_0(t+1) = F_0(t)\cdot N_0(t) + F_1(t)\cdot N_1(t) + F_2(t)\cdot N_2(t) + F_3(t)\cdot N_3(t)$$

$$N_1(t+1) = N_0(t)\cdot S_0$$

$$N_2(t+1) = N_1(t)\cdot S_1$$

$$N_3(t+1) = N_2(t)\cdot S_2$$

Fecundities

Survival rates

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+t) \\ N_2(t+1) \\ N_3(t+1) \end{bmatrix} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix}$$

Projection Matrix

$$P = \begin{pmatrix} f_1 & f_2 & f_3 & f_4 & f_5 \\ \tau_{1,2} & 0 & 0 & 0 & 0 \\ 0 & \tau_{2,3} & 0 & 0 & 0 \\ 0 & 0 & \tau_{3,4} & 0 & 0 \\ 0 & 0 & 0 & \tau_{4,5} & 0 \end{pmatrix}$$

Leslie matrix of the data considered

	Census year			
Age	1991	1992	1993	1994
0	26	28	27	29
1	16	17	20	20
2	12	11	13	14
3	9	8	9	10
4	7	6	6	8
5	5	4	5	5
6	4	3	3	4
7	3	3	2	3
8	2	2	2	2
9	1	1	1	2
Total	85	83	88	97

$$\begin{bmatrix} 0 & 0.48 & 0.48 & 0.48 & 0.48 & 0.48 & 0.48 & 0.48 & 0.48 & 0.48 \\ 0.703 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.717 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.751 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.769 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.746 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.717 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.806 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.778 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.667 & 0 \end{bmatrix}$$

Check whether the elements in the matrix is correct!

Eigen value and eigen vector

Definition. If A is an $n \times n$ matrix, $\mathbf{v}$ a nonzero vector in $\mathbb{R}^n$, and λ a scalar such that $A\mathbf{v} = \lambda\mathbf{v}$, then we say that $\mathbf{v}$ is an *eigenvector* of A with *eigenvalue* λ.

Theorem. *If $\mathbf{v}$ is an eigenvector of A with eigenvalue λ, then for any scalar c, $c\mathbf{v}$ is also an eigenvector of A with the same eigenvalue λ.*

Proof. If $A\mathbf{v} = \lambda\mathbf{v}$, then $A(c\mathbf{v}) = c(A\mathbf{v}) = c(\lambda\mathbf{v}) = \lambda(c\mathbf{v})$.

- Understanding eigenvectors is crucial to understanding linear models.
- Consider when the initial values of a linear model are given by an eigenvector.
- Consider a model $x_{t+1} = Ax_t$, where we know that $Av = \lambda v$.
- if $x_0 = v$, we produce the table 2.2, which finally gives

$$x_t = \lambda^t v$$

Table 2.2. *Linear Model Simulation with Eigenvector as Initial Values*

t	$\mathbf{x}_t$
0	$\mathbf{v}$
1	$A\mathbf{v} = \lambda\mathbf{v}$
2	$A\lambda\mathbf{v} = \lambda^2\mathbf{v}$
3	$A\lambda^2\mathbf{v} = \lambda^3\mathbf{v}$
⋮	⋮

How to solve for eigen values and eigen vectors?

- First consider the matrix A
- Solve the secular equation $|A-\lambda I|=0$ (it doesn't have inverse)
- Get the eigen values λ's; i.e., $\lambda_{1,2,3,\ldots}$
- For each eigen value, get corresponding eigen vector V_1 by solving $(A-_{\lambda 1}I)\ V_1= 0$.
- Repeat for all eigen values to get corresponding eigen vectors.
- Then the solution will be $x_t = C_1\lambda_1^{\ t} v_1 + C_2\, \lambda_2^{\ t} v_2 + C_3\, \lambda_3^{\ t}\ v_3\ + \ldots$

Eigen values and eigen vectors

- Let us take an example of 2 X 2 matrix

$$\mathbf{A} = \begin{pmatrix} 3 & -1 \\ 6 & -4 \end{pmatrix}$$

$$\begin{aligned}
0 &= \det(\mathbf{A} - \lambda\mathbf{I}) \\
&= \det\left[\begin{pmatrix} 3 & -1 \\ 6 & -4 \end{pmatrix} - \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix}\right] \\
&= \det\begin{pmatrix} 3-\lambda & -1 \\ 6 & -4-\lambda \end{pmatrix} \\
&= (3-\lambda)(-4-\lambda) - (-1)(6) \\
&= \lambda^2 + \lambda - 12 + 6 = \lambda^2 + \lambda - 6 \\
&= (\lambda - 2)(\lambda + 3)
\end{aligned}$$

This quadratic equation has the two solutions

$$\lambda_1 = 2 \qquad \text{and} \qquad \lambda_2 = -3.$$

Eigen vectors-1 for eigen value-1

We now find eigenvectors associated with each eigenvalue by solving $(\mathbf{A} - \lambda\mathbf{I})\mathbf{v} = 0$. Corresponding to λ_1, $\mathbf{v}_1$ must satisfy

$$(\mathbf{A} - \lambda\mathbf{I})\mathbf{v}_1 = \begin{pmatrix} 3 - \lambda_1 & -1 \\ 6 & -4 - \lambda_1 \end{pmatrix}\begin{pmatrix} v_{11} \\ v_{12} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

Since $\lambda_1 = 2$, the system of equations is

$$\begin{pmatrix} 1 & -1 \\ 6 & -6 \end{pmatrix}\begin{pmatrix} v_{11} \\ v_{12} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

that is,

$$\begin{aligned} v_{11} - v_{12} &= 0, \\ 6v_{11} - 6v_{12} &= 0. \end{aligned}$$

Notice that the equations are redundant. We use one of these, with an arbitrary value for one of the variables (for example, $v_{11} = 1$) to conclude that

$$\mathbf{v}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}.$$

Eigen vector-2 for eigen value-2

To find $\mathbf{v}_2$, repeat the procedure with the second eigenvalue, $\lambda_2 = -3$. The system of equations is then

$$\begin{pmatrix} 6 & -1 \\ 6 & -1 \end{pmatrix} \begin{pmatrix} v_{21} \\ v_{22} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

that is,

$$6v_{21} - v_{22} = 0,$$
$$6v_{21} - v_{22} = 0.$$

Arbitrarily selecting $v_{21} = 1$, we obtain

$$\mathbf{v}_2 = \begin{pmatrix} 1 \\ 6 \end{pmatrix}.$$

Class problem-2

- What are the eigen value and eigen vector for the following matrix A

$$A = \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}.$$

Solution-problem-2

The eigenvalues of $\mathbf{A}$ satisfy the relation

$$0 = \det(\mathbf{A} - \lambda\mathbf{I}) = \det\begin{pmatrix} 1-\lambda & -1 \\ 1 & 1-\lambda \end{pmatrix}$$
$$= (1-\lambda)^2 + 1$$
$$= \lambda^2 - 2\lambda + 2.$$

Thus

$$\lambda_{1,2} = \frac{2 \pm \sqrt{4-8}}{2} = 1 \pm i.$$

The eigenvector of $\mathbf{A}$ corresponding to $\lambda_1 = 1 + i$ satisfies

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} = (\mathbf{A} - \lambda_1\mathbf{I})\mathbf{v}_1$$
$$= \begin{pmatrix} 1-(1+i) & -1 \\ 1 & 1-(1+i) \end{pmatrix}\begin{pmatrix} v_{11} \\ v_{12} \end{pmatrix}$$
$$= \begin{pmatrix} -i & -1 \\ 1 & -i \end{pmatrix}\begin{pmatrix} v_{11} \\ v_{12} \end{pmatrix}.$$

Thus

$$-iv_{11} - v_{12} = 0.$$

Taking arbitrarily $v_{11} = 1$ one obtains $v_{12} = -iv_{11} = -i$. Thus

$$\mathbf{v}_1 = \begin{pmatrix} 1 \\ -i \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} - i\begin{pmatrix} 0 \\ 1 \end{pmatrix} = \mathbf{a} - i\mathbf{b}.$$

It follows that $\mathbf{v}_2$ is the complex conjugate of $\mathbf{v}_1$; that is,

$$\mathbf{v}_2 = \begin{pmatrix} 1 \\ i \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} + i\begin{pmatrix} 0 \\ 1 \end{pmatrix} = \mathbf{a} + i\mathbf{b}.$$

Example: Forest model

Example. If the forest model with $P = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$

Show that the eigen value is 0.98 and corresponding eigen vector is (1,-1), and another eigen value is 1 with corresponding eigen vector (1,0.6) (or) (5,3)

Initial population vector and equilibrium values

The key idea is to try to write our initial population vector in terms of eigenvectors. Specifically, given an initial population vector $\mathbf{x}_0 = (A_0, B_0)$, we look for two scalars, c_1, and c_2, with

$$\begin{pmatrix} A_0 \\ B_0 \end{pmatrix} = c_1 \begin{pmatrix} 5 \\ 3 \end{pmatrix} + c_2 \begin{pmatrix} 1 \\ -1 \end{pmatrix}.$$

Equivalently, we need to solve

$$\begin{pmatrix} A_0 \\ B_0 \end{pmatrix} = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix}.$$

Theorem. *Suppose A is an $n \times n$ matrix with n eigenvectors that form the columns of a matrix S. If S has an inverse, then any vector can be written as a sum of eigenvectors.*

Example to compute C's

Example. When we investigated the forest model numerically, we used the initial population vector $\mathbf{x}_0 = (10, 990)$. The eigenvector matrix is $S = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix}$. To solve $\begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix}$, we compute $S^{-1} =$

Show what is S^{-1} to compute C's.

C's to get Equilibrium values

Example. When we investigated the forest model numerically, we used the initial population vector $\mathbf{x}_0 = (10, 990)$. The eigenvector matrix is $S = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix}$. To solve $\begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix}$, we compute $S^{-1} = \frac{1}{-8} \begin{pmatrix} -1 & -1 \\ -3 & 5 \end{pmatrix}$, so

$$\begin{pmatrix} c_1 \\ c_2 \end{pmatrix} = \frac{1}{-8} \begin{pmatrix} -1 & -1 \\ -3 & 5 \end{pmatrix} \begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} 125 \\ -615 \end{pmatrix}.$$

Thus

eq value <0 ?

$$\begin{pmatrix} 10 \\ 990 \end{pmatrix} = 125 \begin{pmatrix} 5 \\ 3 \end{pmatrix} - 615 \begin{pmatrix} 1 \\ -1 \end{pmatrix}.$$

doubt

Equilibrium values

How to find x_t at any time?

- Now that we understand how to express initial values in terms of eigenvectors, how do we use that expression?
- Let's suppose A is n × n, with n eigenvectors v1, v2,...,vn , whose corresponding eigenvalues are λ1,λ2,...,λn .
- We express our initial vector x_0 as
- $x_0 = c_1v_1 + c_2v_2 +\cdots+c_nv_n$,

so then

$$\begin{aligned}\mathbf{x}_1 = A\mathbf{x}_0 &= A(c_1\mathbf{v}_1 + c_2\mathbf{v}_2 + \cdots + c_n\mathbf{v}_n) \\ &= Ac_1\mathbf{v}_1 + Ac_2\mathbf{v}_2 + \cdots + Ac_n\mathbf{v}_n.\end{aligned}$$

But each term in this last expression is simply A applied to an eigenvector, so we see

$$\mathbf{x}_1 = c_1\lambda_1\mathbf{v}_1 + c_2\lambda_2\mathbf{v}_2 + \cdots + c_n\lambda_n\mathbf{v}_n.$$

But then

$$\begin{aligned}\mathbf{x}_2 = A\mathbf{x}_1 &= A(c_1\lambda_1\mathbf{v}_1 + c_2\lambda_2\mathbf{v}_2 + \cdots + c_n\lambda_n\mathbf{v}_n) \\ &= Ac_1\lambda_1\mathbf{v}_1 + Ac_2\lambda_2\mathbf{v}_2 + \cdots + Ac_n\lambda_n\mathbf{v}_n,\end{aligned}$$

and because each term is again A times an eigenvector,

$$\mathbf{x}_2 = c_1\lambda_1^2\mathbf{v}_1 + c_2\lambda_2^2\mathbf{v}_2 + \cdots + c_n\lambda_n^2\mathbf{v}_n.$$

Continuing to apply A, we obtain the formula

$$\mathbf{x}_t = c_1\lambda_1^t\mathbf{v}_1 + c_2\lambda_2^t\mathbf{v}_2 + \cdots + c_n\lambda_n^t\mathbf{v}_n.$$

Understanding the eigenvectors has allowed us to find a formula for the values of x_t at any time.

Example Problem

Example. For the populations used in the numerical investigation of the forest model, we have already seen $\mathbf{x}_0 = \begin{pmatrix} 10 \\ 990 \end{pmatrix} = 125 \begin{pmatrix} 5 \\ 3 \end{pmatrix} - 615 \begin{pmatrix} 1 \\ -1 \end{pmatrix}$. This means

$$\begin{aligned}
\mathbf{x}_t &= 1^t(125)\begin{pmatrix} 5 \\ 3 \end{pmatrix} + .98^t(-615)\begin{pmatrix} 1 \\ -1 \end{pmatrix} \\
&= \begin{pmatrix} 1^t(125)(5) + .98^t(-615)(1) \\ 1^t(125)(3) + .98^t(-615)(-1) \end{pmatrix} = \begin{pmatrix} 625 - (615).98^t \\ 375 + (615).98^t \end{pmatrix}.
\end{aligned}$$

Asymptotic behavior

- Given a linear model $x_{t+1} = Ax_t$ with initial vector x0.

- To find an explicit formula for x_t , We determine the eigen values $\lambda 1$,$\lambda 2$,...,λn and the corresponding eigenvectors v1, v2,...,vn then writing x_0 in terms of the eigenvectors
- $$x_t = c_1\lambda^t{}_1v_1 + c_2\lambda^t{}_2v_2 + \cdots + c_n\lambda^t{}_nv_n \,.$$

Conditions:

- If $|\lambda_i| < 1$; $x_t \rightarrow 0$ as $t \rightarrow$ infinity.

- If $|\lambda_{i-1}| < 1$ and $\lambda_i > 1$, then x_t will have exponential growth as $t \rightarrow$ infinity.

- The negative value for λ_i should produce some form of oscillatory behavior, because it alternate in sign.

Dominant eigen value and eigen vector

- Definition. An eigenvalue of A that is **largest in absolute value** is called a dominant eigenvalue of A. An eigenvector corresponding to it is called a dominant eigenvector.

Numbering the eigenvalues so that λ_1 is a dominant one, then can be rewritten as

$$\mathbf{x}_t = \lambda_1^t \left(c_1 \mathbf{v}_1 + c_2 \left(\frac{\lambda_2}{\lambda_1} \right)^t \mathbf{v}_2 + \cdots + c_n \left(\frac{\lambda_n}{\lambda_1} \right)^t \mathbf{v}_n \right).$$

- Assuming λ1 is strictly dominant, then $\lambda_i/\lambda_1 < 1$ all the in the parentheses will decay, and this leads to

$$\mathbf{x}_t \approx \lambda_1^t c_1 \mathbf{v}_1.$$

Continued..

- For a population model, the dominant eigenvector is hence often referred to as the stable age distribution or stable stage distribution.

- Dominant eigenvector gives us the proportions of the population that should appear in each age or stage class, once we account for the growth trend.

- **H.W.** Take the example for the Usher model from the book to determine the nature of eigenvalues and show how it behaves asymptotically?

Question-1

1. (a) If every individual produces 4 babies per day, how many individuals will be in the population after 4 days if $N(0) = 4$. Assume that no deaths occur and that a baby produced today does not reproduce until tomorrow.

   (b) The general model for the above equation can be written as $N(t) = N(0)e^{rt}$. What is ‘r’ in this case? Note: $e^{0.693} = 2$

   (c) From the above equation in (b) find the tripling time of the population.

Solution-1 :

(a) $N(0) = 4$; $N(1) = 4(4)=16$; $N(2) = (16)(4)= 64$; $N(3) = (64)(4) = 256$; $N(4) = 1024$.

(b) $r = 1.39$, since the model $N(t) = N(0)e^{rt} = 4\ 4^t = 4\ e^{(1.39)t}$

(c) $N(t) = 3\ N(0)$; so; $t = \log 3/r = 1.094/1.39$.

Solution-2: $N(0) = 4$; $N(1) = 4(4)=16$; $16+4 = 20$ individuals

$N(2) = (20)(4)= 80+ 20 = 100$ individuals

$N(3) = (100)(4) = 400+ 100 = 500$ individuals

$N(4) = (500)(4) = 2000 + 500= 2500$ individuals

(b) = log(5);

(C) = log(3)/log(5);

Question-2

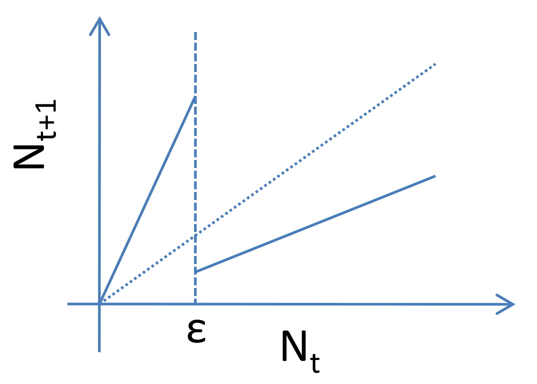
2. Suppose the population increases exponentially when its density is below some value (say $N = \varepsilon$) and decreases exponentially when its density is above that density. Write an equation for this situation and construct its graph of N_{t+1} vs N_t.

Hint: Write two piecewise equation.

Solution:

$$N_{t+1} = a_1 N_t \text{ for } N_t <= \varepsilon \ (a_1 > 1)$$

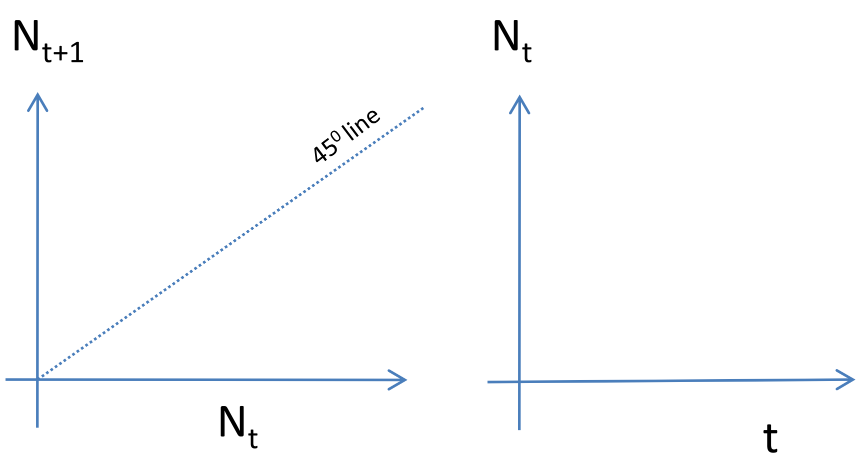
$$N_{t+1} = a_2 N_t \text{ for } N_t >= \varepsilon \ (a_2 < 1)$$



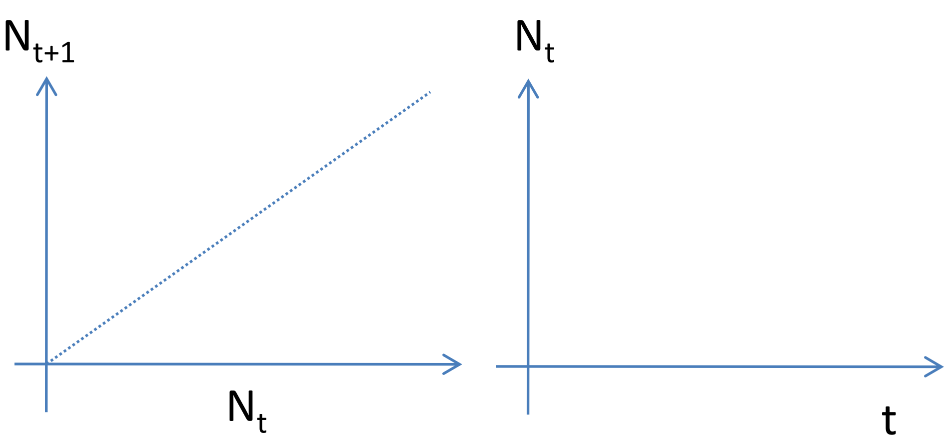
Question-3

- Consider the following two equations;
- (a) $N_{t+1} = N_t e^r$ (b) $N_{t+1} = e^r K N_t/(N_t(e^r - 1) + K)$
- Take r = 0.693 and K = 100.
- Complete the graphs below of N_{t+1} Vs N_t space as well as its corresponding projection N_{t+1} Vs t.

(a)

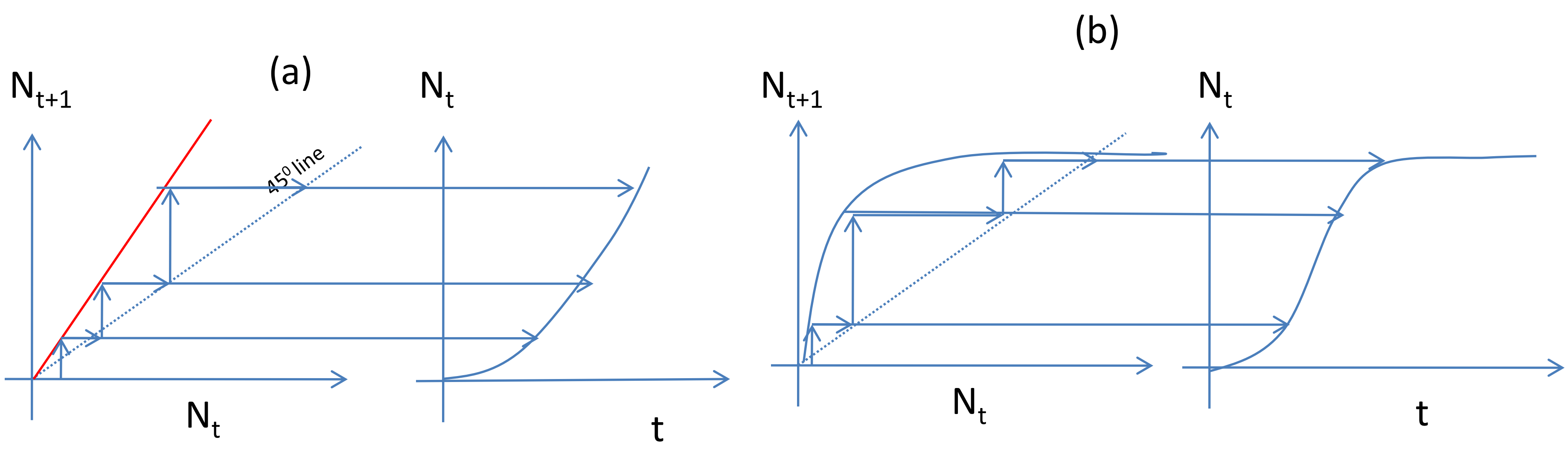


(b)



Solution

- Consider the following two equations;
- (a) $N_{t+1} = N_t e^r$ (b) $N_{t+1} = e^r K N_t / (N_t(e^r - 1) + K)$
- Take $r = 0.693$ and $K = 100$.
- Solution: (a) $N_{t+1} = 2N_t$ (b) $N_{t+1} = 200N_t / (100 + N_t)$



Question-4

- 4. For the following, determine the equilibrium points and use only derivatives to determine the stability of equilibria.
- $$P_{t+1} = P_t + rP_t\,(1 - P_t)$$

Solution:

- If $f(P) = P + rP(1 - P) = (1+r)P - rP^2$, then $f'(P) = (1+r) - 2rP$. So, $f(0) = 1 + r$ and $f(1) = 1 - r$. Thus,
- $P^* = 0$ *is stable if* $|1 + r| < 1$ *and* unstable if $|1+r| > 1$.
- $P^* = 1$ *is stable if* $|1-r| < 1$ *and unstable if* $|1-r| > 1$.

Question -5

5. Mark both the direction field of the plot given below and also the stable (filled circle) /unstable equilibrium (unfilled circle) points. Is there a bifurcation point? If so, show it in the plot.