Lecture 3: Age & Stage structured population growth

Population: a set of individuals of the same species co-occurring in space and time.

Characteristics of populations

Total number of individuals or population 'density'
Age/Stage/Size structure
Sex ratio
Spatial distribution

$$dN/dt = rN$$

$$N_t = N_0 e^{rt}$$

$$\ln(2)/r = t_{double}$$

$$dN/dt = rN\left(1 - \frac{N}{K}\right)$$

$$dN/dt = rN\left(\frac{K - N}{K}\right)$$

$$N_t = N_0 \frac{K}{(K - N_0)e^{-rt} + N_0}$$

Four important assumptions

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1. Per capita growth rate is a linear function of *N*.
2. Population growth rate responds instantly to changes in N (no time lags).
3. The external environment has no influence on population growth.
4. All individuals are equal (i.e., no age or size effects).

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These models work for ‘simple’ organisms like single-celled bacteria or protozoa.

But for most plants and animals, birth and death rates depe
on age.

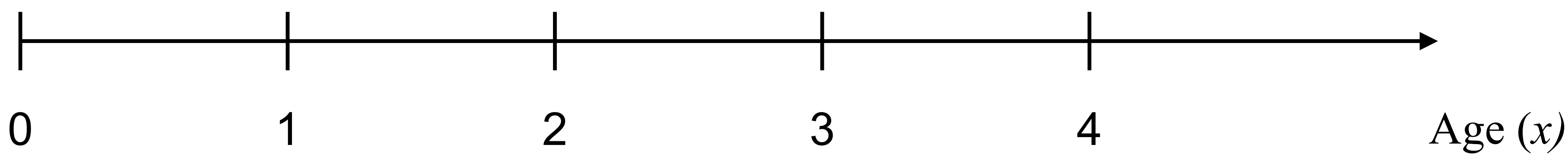
Northern leopard frog, *Rana pipiens*

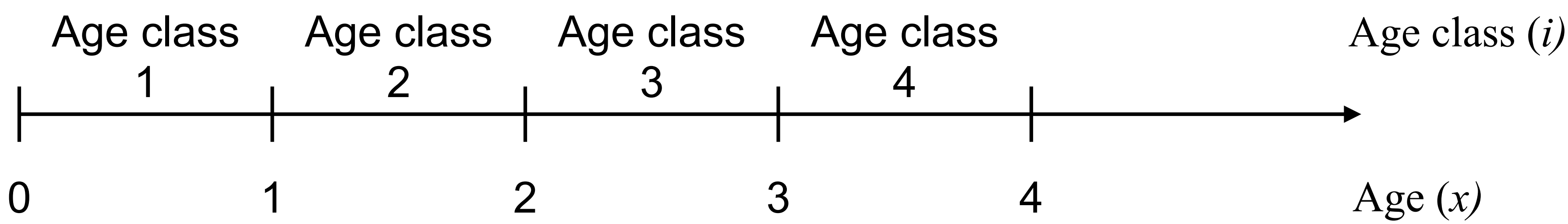
A newborn elephant cannot reproduce immediately, but instead must wait ~10 years.

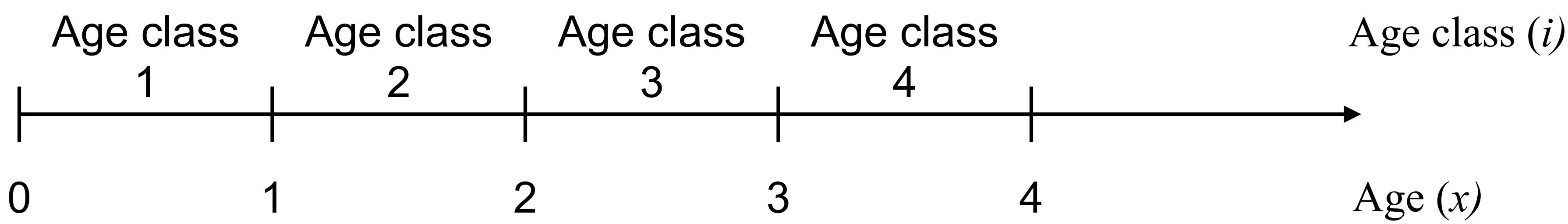
Hatchlings and seedlings often have higher mortality rates than adults.

A population that consisted of only old, post-reproductive chimpanzees will soon go extinct.

A population of only tadpoles cannot begin to grow until tadpoles become adults and can reproduce.


0
1
2
3
4
Age (x)


Age class 1
Age class 2
Age class 3
Age class 4
Age class (i)
0
1
2
3
4
Age (x)



When using age classes, we treat all individuals in the same class as equivalents.

The fecundity schedule: the average number of female offspring born per unit time to an individual female of a particular age.

$b(x)$ or $m(x)$ $\longrightarrow$ *b*irths or *m*aternity

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$b(6) = 3$ $\longrightarrow$ A female of age 6 has, on average, 3 female offspring

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$
0	500	0					
1	400	2					
2	200	3					
3	50	1					
4	0	0					

The survivorship schedule

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$
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The proportion of the original cohort that survives to the start of that age class

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0	500	0	1				
1	400	2	0.8				
2	200	3	0.4				
3	50	1	0.1				
4	0	0	0				

The proportion of the original cohort that survives to the start of that age class
The probability of surviving to that age class

The survival probability

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$
0	500	0	1				
1	400	2	0.8				
2	200	3	0.4				
3	50	1	0.1				
4	0	0	0				

The probability that an individual of age x survives to age x +1

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0	500	0	1	0.80			
1	400	2	0.8	0.50			
2	200	3	0.4	0.25			
3	50	1	0.1	0			
4	0	0	0				

The probability that an individual of age x survives to age x +1

The net reproductive rate, R_0

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$
0	500	0	1	0.80			
1	400	2	0.8	0.50			
2	200	3	0.4	0.25			
3	50	1	0.1	0			
4	0	0	0				

The mean number of female offspring produced per female over her lifetime.

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0	500	0	1	0.80	0		
1	400	2	0.8	0.50	1.6		
2	200	3	0.4	0.25	1.2		
3	50	1	0.1	0	0.1		
4	0	0	0				

The mean number of female offspring produced per female over her lifetime.
The reproductive potential adjusted by the mortality schedule.

The net reproductive rate, R_0

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1	400	2	0.8	0.50	1.6		
2	200	3	0.4	0.25	1.2		
3	50	1	0.1	0	0.1		
4	0	0	0				

$R_0 = \sum l(x)b(x) =$ 2.9 offspring

If $R_0 > 1$, there is a net surplus of offspring produced each generation, and the population increases exponentially.

The net reproductive rate, R_0

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$R_0 = \sum l(x)b(x) = 2.9$ offspring

If $R_0 < 1$, the population declines

The net reproductive rate, R_0

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1	400	2	0.8	0.50	1.6		
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3	50	1	0.1	0	0.1		
4	0	0	0	$R_0 = \sum l(x)b(x) = 2.9$ offspring			

If $R_0 = 1$, the population is stable.

Generation time, G

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$
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Average age of the parents of all the offspring produced by a single cohort

Generation time, G

$$\frac{\sum l(x)b(x)x}{\sum l(x)b(x)}$$

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1	400	2	0.8	0.50	1.6	1.6	
2	200	3	0.4	0.25	1.2	2.4	
3	50	1	0.1	0	0.1	0.3	
4	0	0	0			$\sum = 4.3$	

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3	50	1	0.1	0	0.1	0.3	
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$G = 4.3/2.9 = 1.483$ years

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As generation time increases, rate of increase decreases; as number of offspring per female increases, rate of increase increases.

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This is just an estimate, but a close estimate (usually within ~10%).

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0	500	0	1	0.80	0	0	0
1	400	2	0.8	0.50	1.6	1.6	0.780
2	200	3	0.4	0.25	1.2	2.4	0.285
3	50	1	0.1	0	0.1	0.3	0.012
4	0	0	0				$\sum = 1.077$

The Euler equation (pronounced “Oiler”)

$$1 = \sum e^{-rx} l(x) b(x)$$

Unfortunately, there is no way to solve this equation except to plug in different values of *r.*

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$$r \approx 0.718 \qquad r_{(\text{Euler})} = 0.776$$

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$$\mathbf{n}(t) = \begin{matrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{matrix}$$

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The population from our life table might look like this at $t = 5$.
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Using the mortality and fertility schedules from the life table, we can prediction how the age structure changes from one time period **n**(*t*) to the next, **n**(*t+1*)

Calculating survival probabilities for age classes (Pi)

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$$n_{i+1}(t+1) = P_i n_i(t)$$

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$$n_1(t+1) = \sum_{i=1}^{k} F_i n_i(t)$$

Once the Fi is known for each age class, we multiply these fertilities by the number of individuals in each age class. This product is then summed over all age classes to calculate the number of new offspring.

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The Leslie matrix

$$n_1(t+1) = F_1 n_1(\mathrm{t}) + F_2 n_2(\mathrm{t}) + F_3 n_3(\mathrm{t}) + F_4 n_4(\mathrm{t})$$

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A Leslie matrix describes the changes in population size due to mortality and reproduction.

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A Leslie matrix describes the changes in population size due to mortality and reproduction.

If there are k age classes, the Leslie matrix is a $k \times k$ square matrix.

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$

The Leslie matrix

$$n_1(t+1) = F_1 n_1(\mathrm{t}) + F_2 n_2(\mathrm{t}) + F_3 n_3(\mathrm{t}) + F_4 n_4(\mathrm{t})$$

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Each **column is the age at time** t
Each **row is the age at time** t **+1**
The first row are the fertilities - contributions to newborn of each age class.

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$

The Leslie matrix

$$n_1(t+1) = F_1 n_1(\mathrm{t}) + F_2 n_2(\mathrm{t}) + F_3 n_3(\mathrm{t}) + F_4 n_4(\mathrm{t})$$

$$n_2(t+1) = P_1 n_1(\mathrm{t})$$

$$n_3(t+1) = P_2 n_2(\mathrm{t})$$

$$n_4(t+1) = P_3 n_3(\mathrm{t})$$

A Leslie matrix describes the changes in population size due to mortality and reproduction.

If there are k age classes, the Leslie matrix is a $k \times k$ square matrix.

Each **column is the age at time** t
Each **row is the age at time** t **+1**
The first row are the fertilities - contributions to newborn of each age class.
The survival probabilities are always in the subdiagonal.
They represent transitions from one age class to the next.

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$

The Leslie matrix

$$n_1(t+1) = F_1 n_1(\mathrm{t}) + F_2 n_2(\mathrm{t}) + F_3 n_3(\mathrm{t}) + F_4 n_4(\mathrm{t})$$

$$n_2(t+1) = P_1 n_1(\mathrm{t})$$

$$n_3(t+1) = P_2 n_2(\mathrm{t})$$

$$n_4(t+1) = P_3 n_3(\mathrm{t})$$

$$\boxed{\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)}$$

A Leslie matrix describes the changes in population size due to mortality and reproduction.

If there are k age classes, the Leslie matrix is a $k \times k$ square matrix.

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$

Each **column is the age at time t**
Each **row is the age at time t +1**
The first row are the fertilities - contributions to newborn of each age class.
The survival probabilities are always in the subdiagonal.
They represent transitions from one age class to the next.
0's: those transitions aren't possible.

The Leslie matrix

x	i (age class)	$S(x)$	$b(x)$	$l(x)$	$Pi = l(i)/l(i-1)$	$Fi = b(i)Pi$
0		500	0	1		
1	1	400	2	0.8	0.80	1.6
2	2	200	3	0.4	0.50	1.5
3	3	50	1	0.1	0.25	0.25
4	4	0	0	0	0	0

The Leslie matrix

x	*i* (age class)	*S(x)*	*b(x)*	*l(x)*	*Pi* = *l(i)/l(i-1)*	*Fi* = *b(i)Pi*
0		500	0	1		
1	1	400	2	0.8	0.80	1.6
2	2	200	3	0.4	0.50	1.5
3	3	50	1	0.1	0.25	0.25
4	4	0	0	0	0	0

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

The Leslie matrix

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

The Leslie matrix

Let’s compare two populations.

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} \qquad \mathbf{n}_0 = \begin{pmatrix} 200 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} \qquad \mathbf{n}_0 = \begin{pmatrix} 50 \\ 50 \\ 50 \\ 50 \end{pmatrix}$$

APPENDIX: BASIC MATRIX MANIPULATIONS

Matrix Multiplication

A matrix is a table of numbers, and the mathematical manipulation of matrices derives from analysis of systems of linear equations. Thus, for example, if we have the system

$$Y_1 = a_1X_1 + b_1X_2 + c_1X_3, \tag{A1a}$$

$$Y_2 = a_2X_1 + b_2X_2 + c_2X_3, \tag{A1b}$$

and

$$Y_3 = a_3X_1 + b_3X_2 + c_3X_3, \tag{A1c}$$

simply as a matter of convenience we can group the X_is to the right and more easily visualize the structure of the system as follows:

$$\begin{vmatrix} Y_1 \\ Y_2 \\ Y_3 \end{vmatrix} = \begin{vmatrix} a_1 & b_1 & c_1 \\ a_2 & b_2 & c_2 \\ a_3 & b_3 & c_3 \end{vmatrix} \begin{vmatrix} X_1 \\ X_2 \\ X_3 \end{vmatrix}.$$

Here we have three matrices: first a matrix with a single column (the *Y*s), second a square matrix with three columns (sometimes referred to as the detached coefficient matrix), and third a matrix with a single column (the *X*s). Sometimes the various matrices are simply referred to using a single letter, but it is customary when speaking of matrices to put them in boldface type, so the above equation could be

$$\mathbf{Y} = \mathbf{AX}. \tag{A2}$$

The Leslie matrix

Let's compare two populations.

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} \qquad \mathbf{n}_0 = \begin{pmatrix} 200 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

1.6*200 + 1.5*0 + 0.25*0 + 0*0 = 320

0.8*200 + 0*0 + 0*0 + 0*0 = 160

0*200 + 0.5*0 + 0*0 + 0*0 = 0

0*200 + 0*0 + 0.25*0 + 0*0 = 0

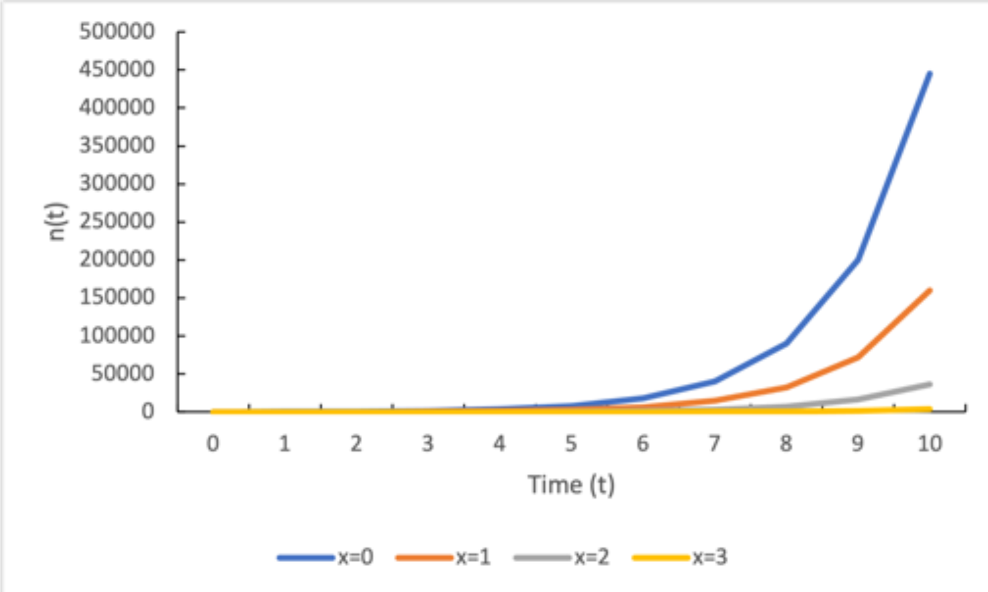
$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} \qquad \mathbf{n}_0 = \begin{pmatrix} 50 \\ 50 \\ 50 \\ 50 \end{pmatrix}$$

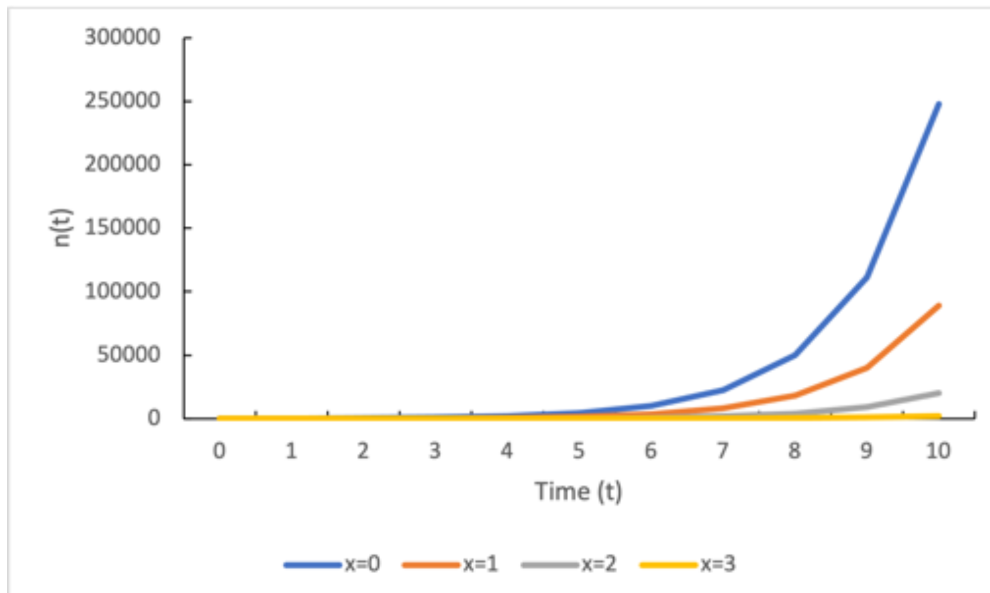
1.6*50 + 1.5*50 + 0.25*50 + 0*50 = 205

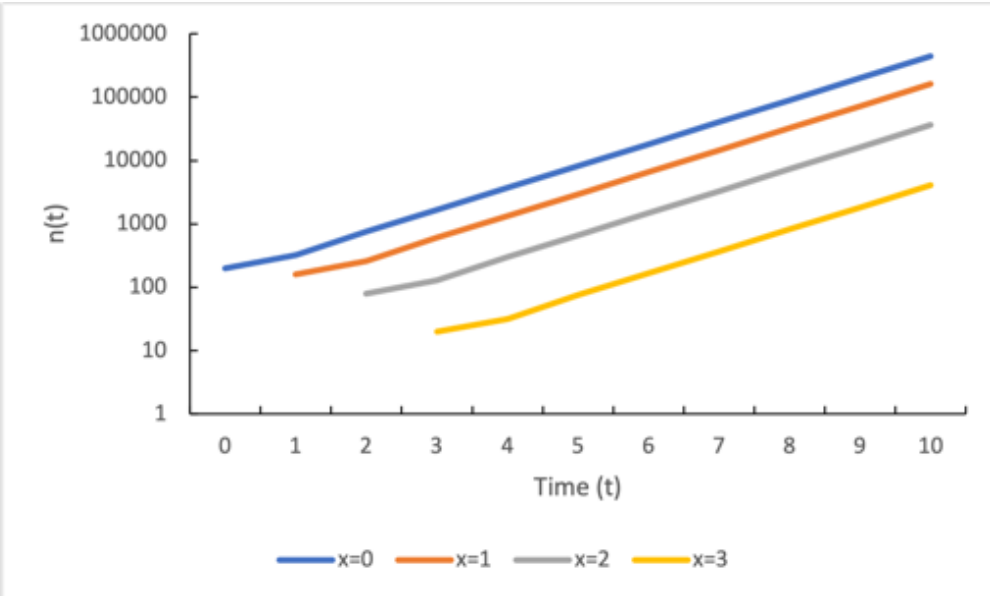
0.8*50 + 0*50 + 0*50 + 0*50 = 40

0*50 + 0.5*50 + 0*50 + 0*50 = 25

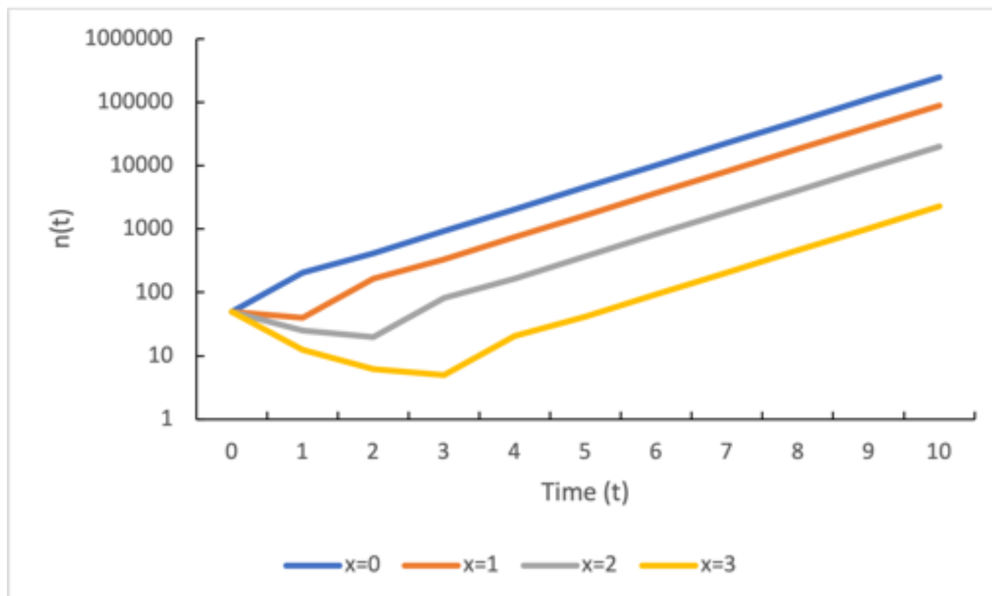
0*50 + 0*50 + 0.25*5 + 0*50 = 12.5


500000
450000
400000
350000
300000
250000
200000
150000
100000
50000
0
n(t)
0 1 2 3 4 5 6 7 8 9 10
Time (t)
x=0
x=1
x=2
x=3


300000
250000
200000
150000
100000
50000
0
n(t)
0 1 2 3 4 5 6 7 8 9 10
Time (t)
x=0
x=1
x=2
x=3



If a population is growing with constant birth and death rates, it will quickly converge on a stable age distribution, with relative numbers in each age class staying about the same.



Stage- and size-structured population growth

Sometimes size or life stage is more important than age.

Remember each column represents the stage at time *t* and each row represents the stage at time *t* + 1.

$$\begin{array}{cc} & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\ \begin{array}{c} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix} \end{array}$$

Remember each column represents the stage at time t and each row represents the stage at time $t + 1$.

$$\begin{array}{cc} & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\ \begin{array}{c} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix} \end{array}$$

The first row represents the fertilities.

Remember each column represents the stage at time *t* and each row represents the stage at time *t* + 1.

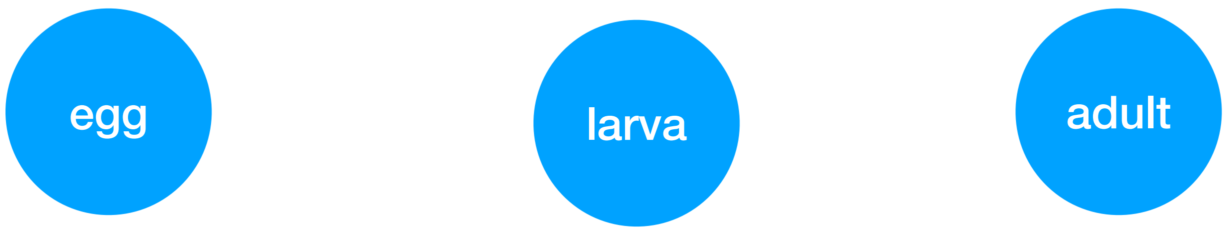
$$\begin{array}{r c} & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\ \begin{array}{r} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix} \end{array}$$

The first row represents the fertilities.

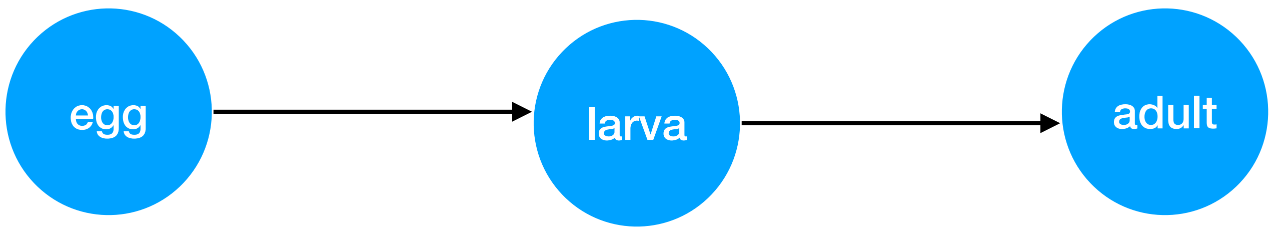
The other entries are *transition probabilities.*

$$
\begin{array}{c|ccccc}
 & \text{size 1} & \text{size 2} & \text{size 3} & \text{size 4} & \text{size 5} \\
\hline
\begin{array}{c}\text{size 1}\\ \text{size 2}\\ \text{size 3}\\ \text{size 4}\\ \text{size 5}\end{array} &
\multicolumn{5}{c}{\begin{bmatrix}
P_{11} & F_{21} & F_{31} & F_{41} & F_{51} \\
P_{12} & P_{22} & 0 & 0 & 0 \\
0 & P_{23} & P_{33} & 0 & 0 \\
0 & 0 & P_{34} & P_{44} & 0 \\
0 & 0 & 0 & P_{45} & P_{55}
\end{bmatrix}}
\end{array}
$$

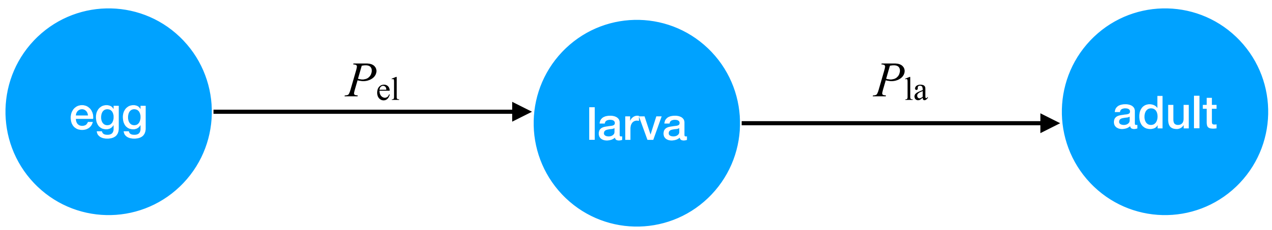
$$
\begin{array}{r c}
 & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\
\begin{array}{r} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix}
\end{array}
$$



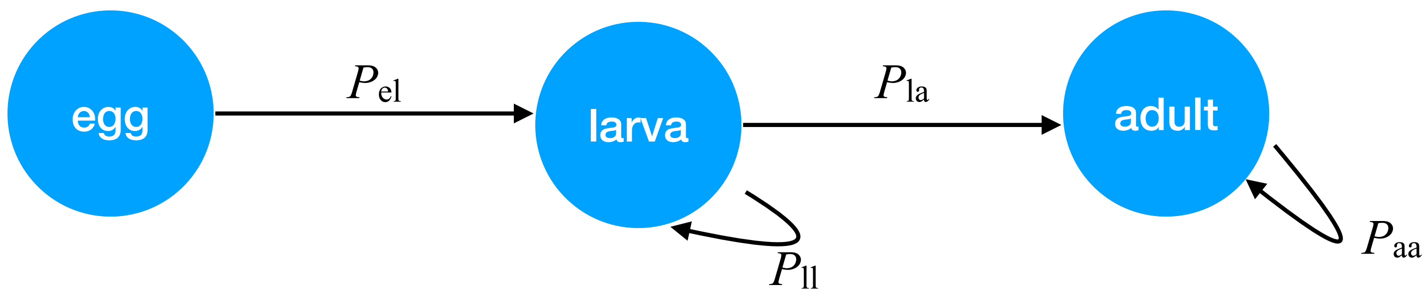
$$
\begin{array}{c c}
 & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\
\begin{array}{c} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix}
\end{array}
$$



$$
\begin{array}{cc}
 & \begin{array}{ccc} \text{egg} & \text{larva} & \text{adult} \end{array} \\
\begin{array}{c} \text{egg} \\ \text{larva} \\ \text{adult} \end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix}
\end{array}
$$



$$
\begin{array}{r c}
 & \begin{array}{ccc} \textbf{egg} & \textbf{larva} & \textbf{adult} \end{array} \\
\begin{array}{r} \textbf{egg} \\ \textbf{larva} \\ \textbf{adult} \end{array} &
\begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix}
\end{array}
$$



$$\begin{array}{cc} & \begin{array}{ccc}\text{egg} & \text{larva} & \text{adult}\end{array} \\ \begin{array}{c}\text{egg}\\ \text{larva}\\ \text{adult}\end{array} & \begin{bmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{bmatrix} \end{array}$$