AGE STRUCTURED POPULATION GROWTH

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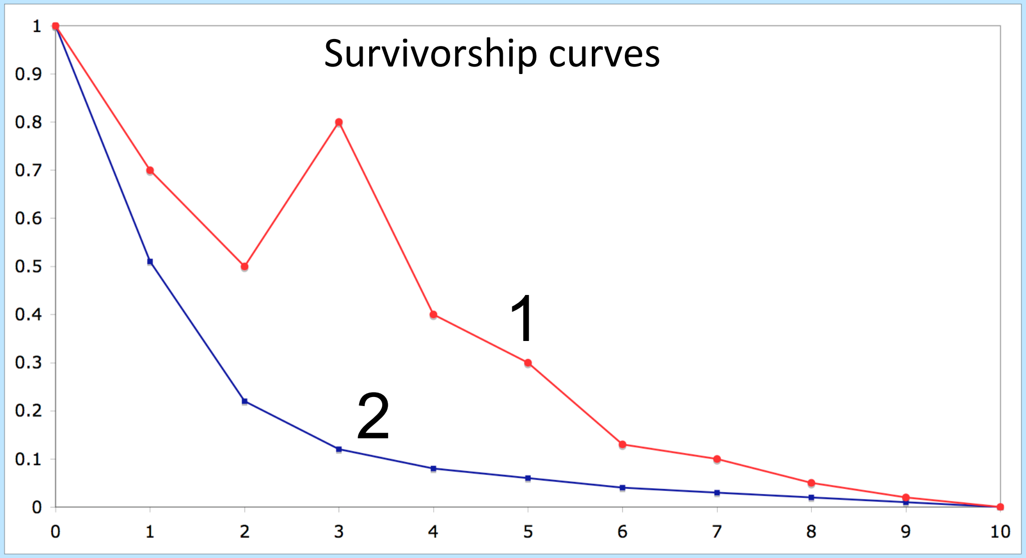
Quiz

Proportion alive at beginning of age interval (l_x)



Age class

A: line 1 represents a possible scenario where young adults (age class 3) have a 'better than expected' chance of surviving to the next age class; line 2 resembles a type 1 survivorship curve

B: line 1 is impossible because l_x can't increase with age class; line 2 shows that adults (age 3+) have better chances of making it to the next age class than juveniles

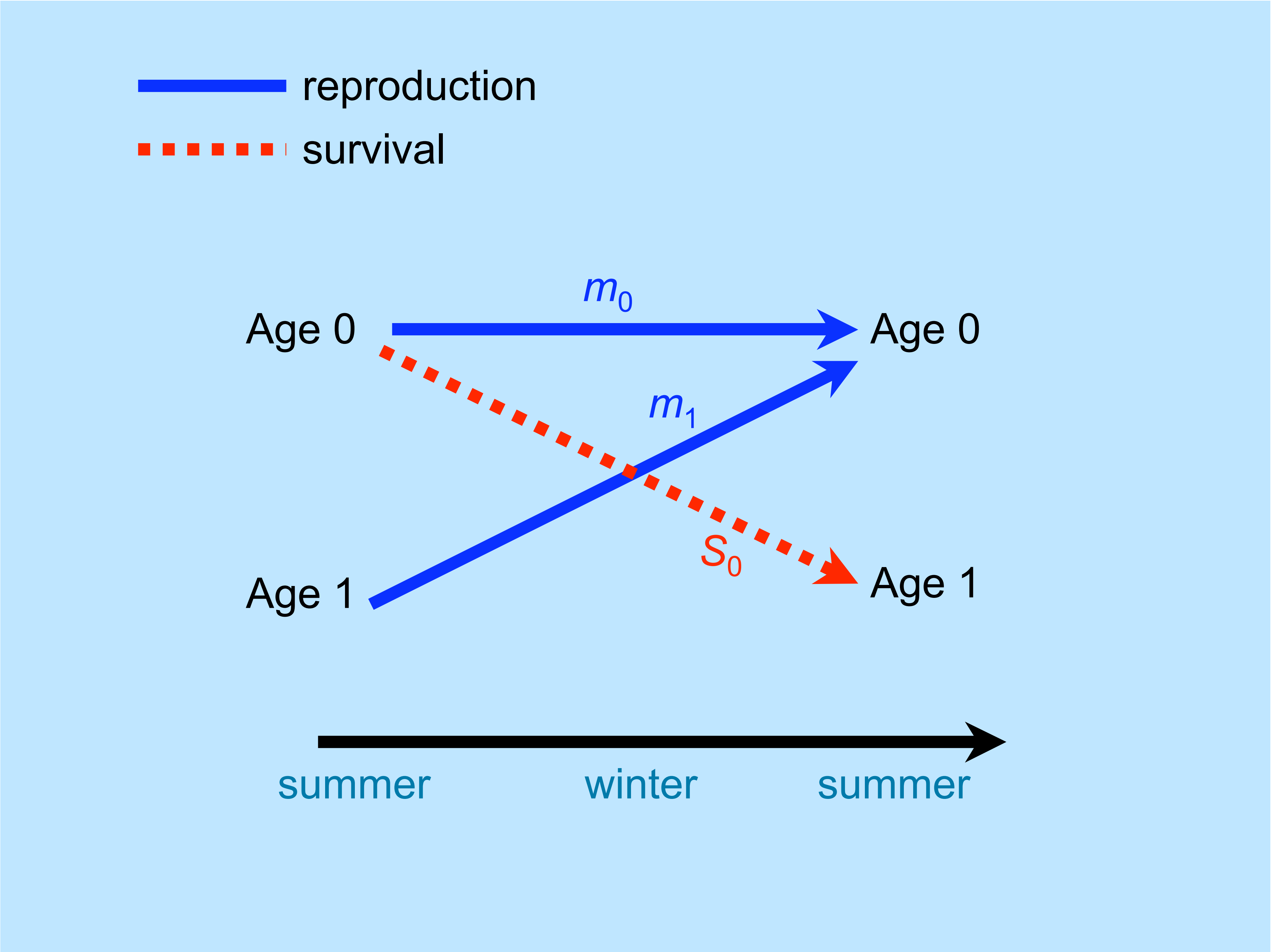
C: line 1 represents a possible scenario with a peak at age 3 due to high fecundity of young adults; line 2 resembles a type 3 survivorship curve

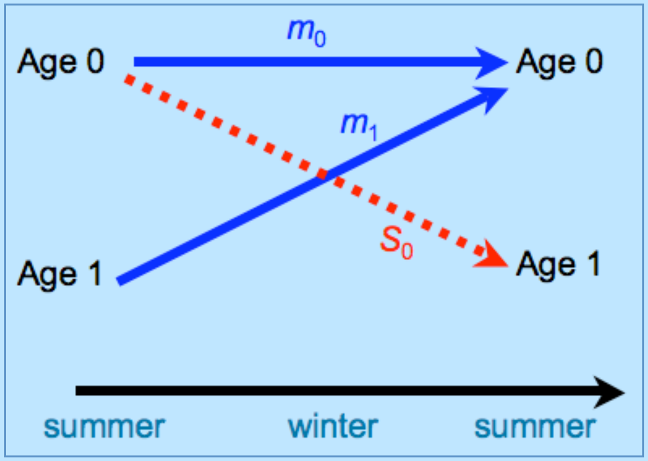
Assumptions of models studied so far...

- **All individuals are identical**
- **Births and deaths independent of age**

Tells us nothing about the age distribution of individuals in the population

Does this matter?


reproduction
survival
m_0
Age 0
Age 0
m_1
S_0
Age 1
Age 1
summer
winter
summer



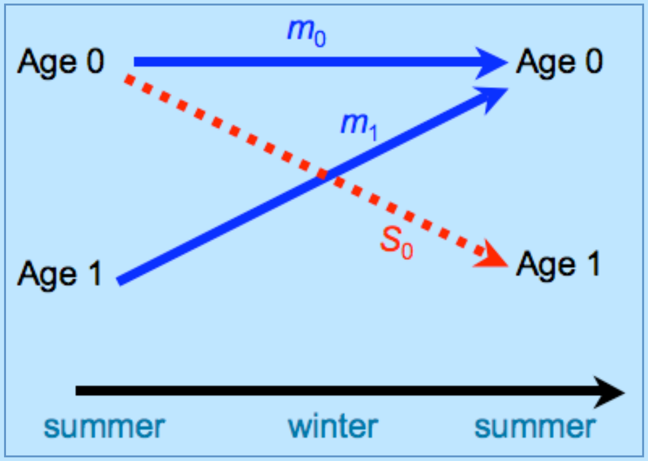
$n_0(t)$ number of individuals of age 0 at time t

$n_1(t)$ number of individuals of age 1 at time t

$$N(t)=n_0(t)+n_1(t)$$

$n_0(t+1)$ = # offspring from age 0 individuals in year t + # offspring from age 1 individuals in year t

$n_1(t+1)$ = # individuals of age 0 in year t x probability of survival from age 0 to age 1

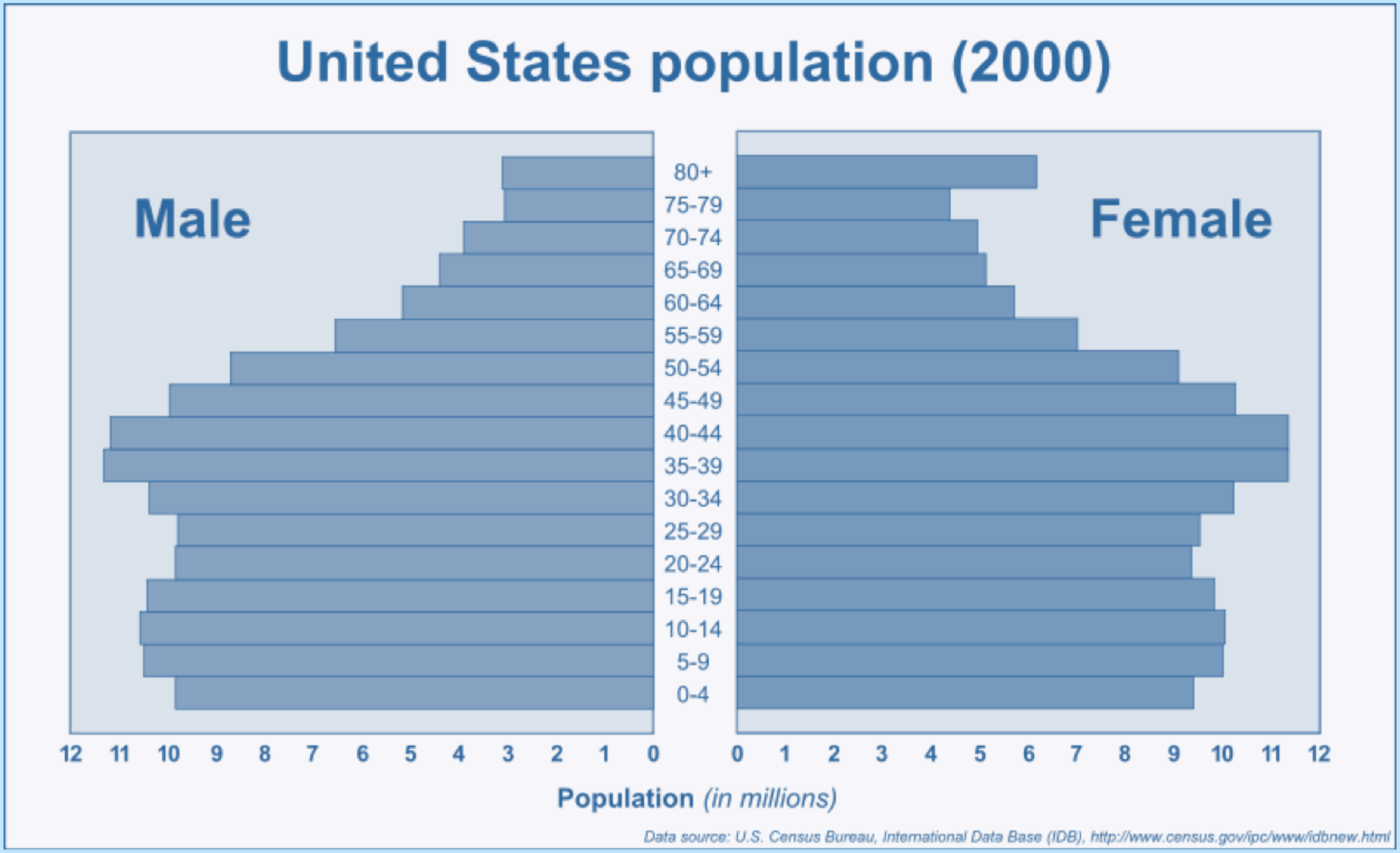


$$n_0(t+1) = n_0(t)m_0 + n_1(t)m_1$$

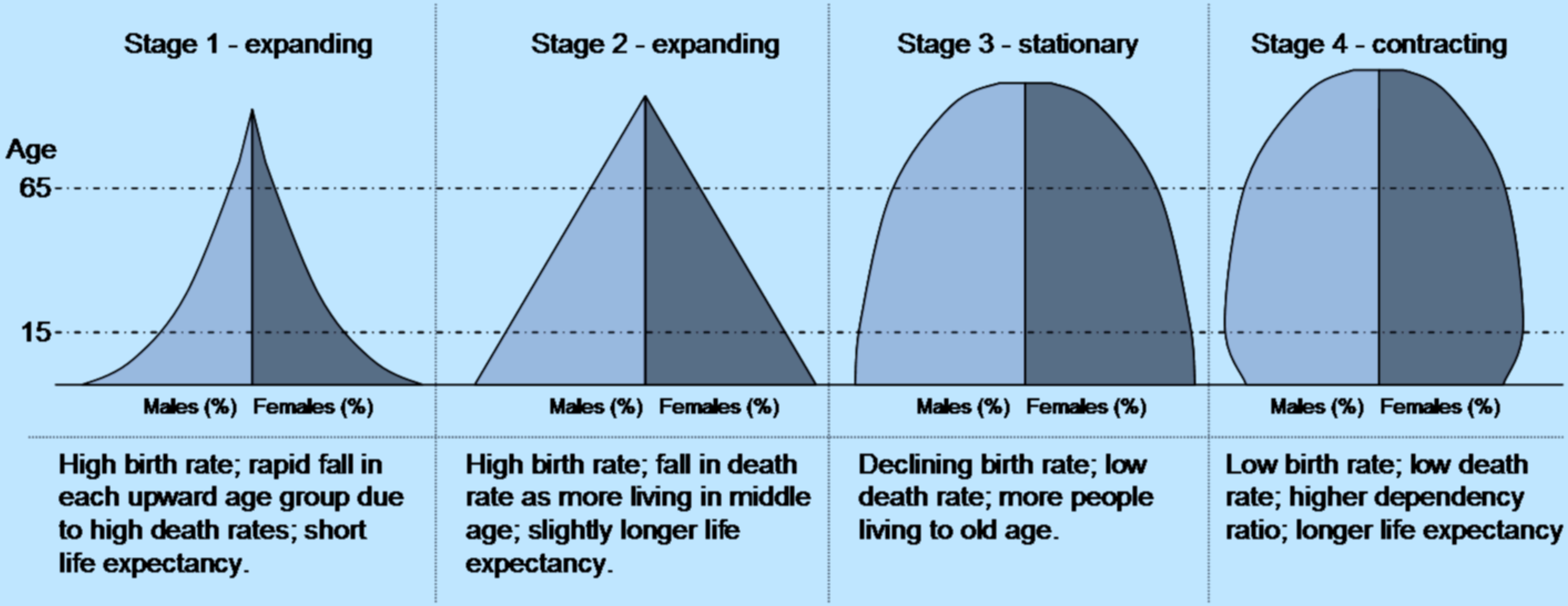
$$n_1(t+1) = n_0(t)S_0$$

	Scenario 1:	Scenario 2:
Initial year	n_0: 10 n_1: 0	n_0: 0 n_1: 10
Next year	n_0: $10m_0$ n_1: $10S_0$	n_0: $10m_1$ n_1: 0

Visualizing age structure: the population pyramid



Age structure is transient



Transient population dynamics is an active area of research
In population ecology

Conservation & management ecology

- All species threatened or endangered
- Accidentally caught in fishing nets
- Hunted for shell (decorative & medical)
- Trapped in marine debris
- Lay eggs on beach
- Hatchlings use light to find horizon (back to sea)
- Fibropapillomatosis disease worst in older animals
- Illegal poaching for meat / eggs

Age structured population growth

Survival and fecundity depend on age

Life tables

Calculating useful info: R_0, G, r

Projecting population growth

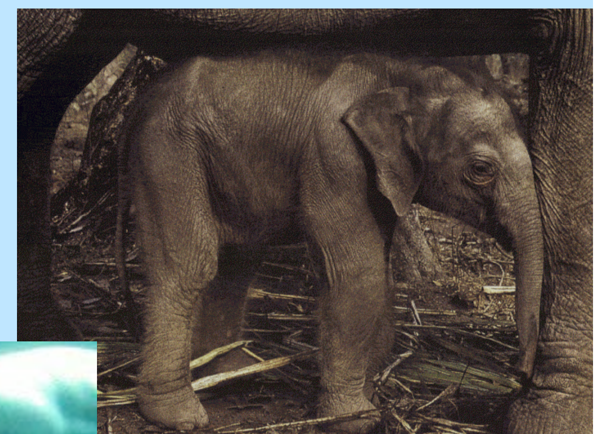
Leslie matrices

Rockwood Ch 4

Age structured population growth

- Birth and death rates often depend on age
  - Fecundity increases with age and experience
  - Mortality may be higher for young or very old ages



Age-specific fecundity

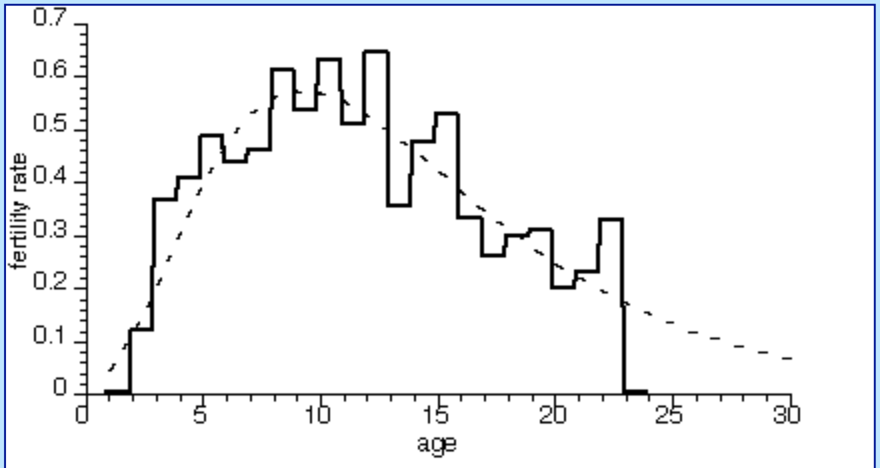


Figure 2b. presents the Hadwiger function (dashed line) fit to the observed Prizwalski's horse fecundity distribution (solid line).

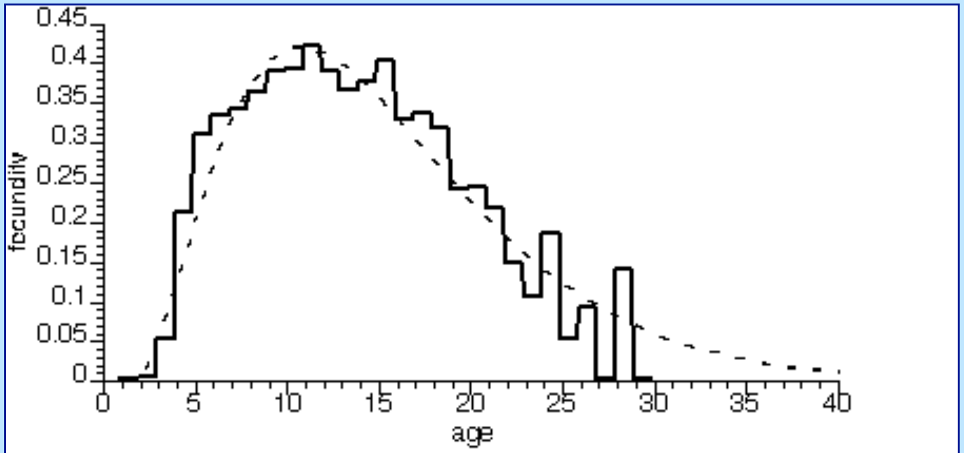
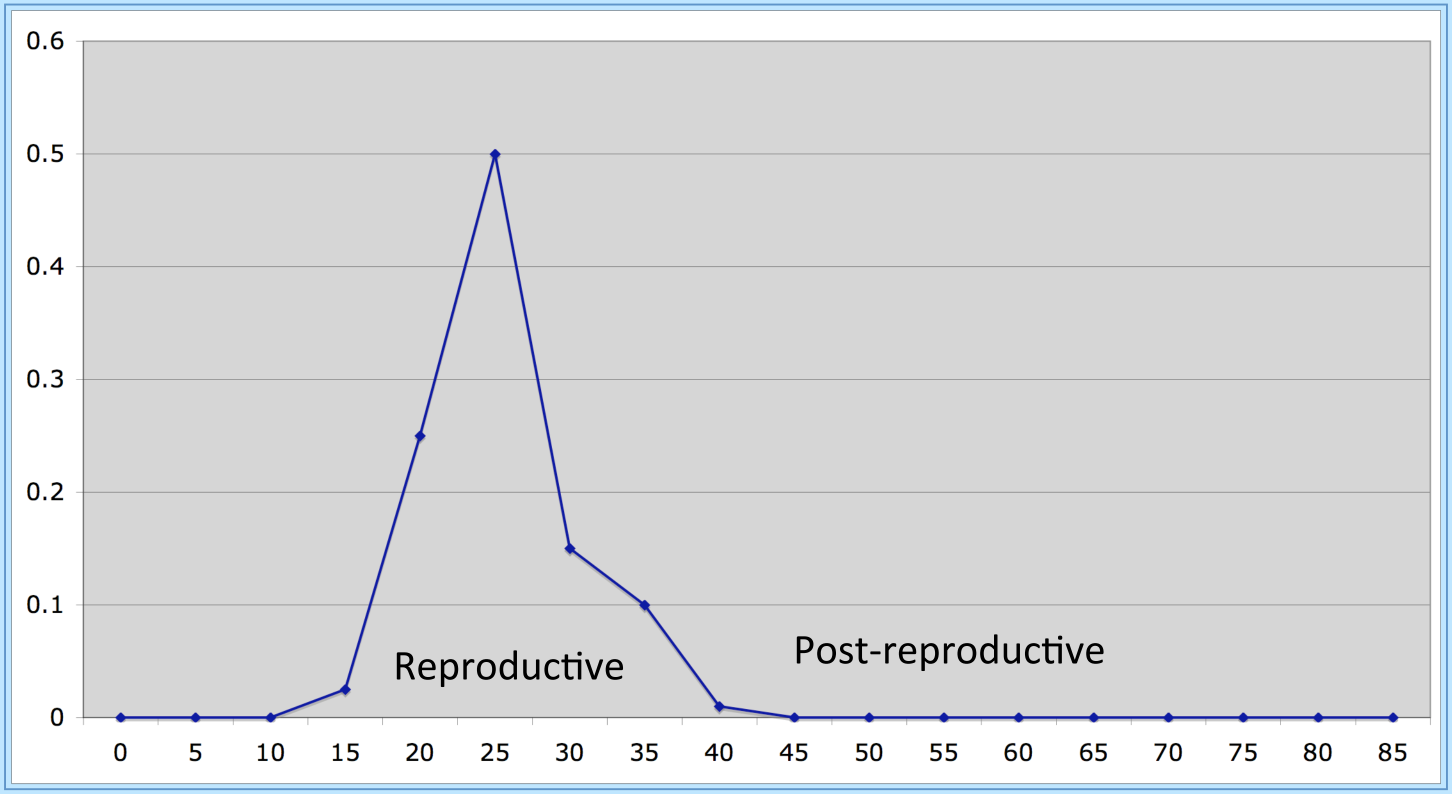


Figure 3a. presents the Gamma distribution (dashed line) fit to the observed Rhesus fecundity distribution (solid line).

Human fertility for the population of the US (1985)

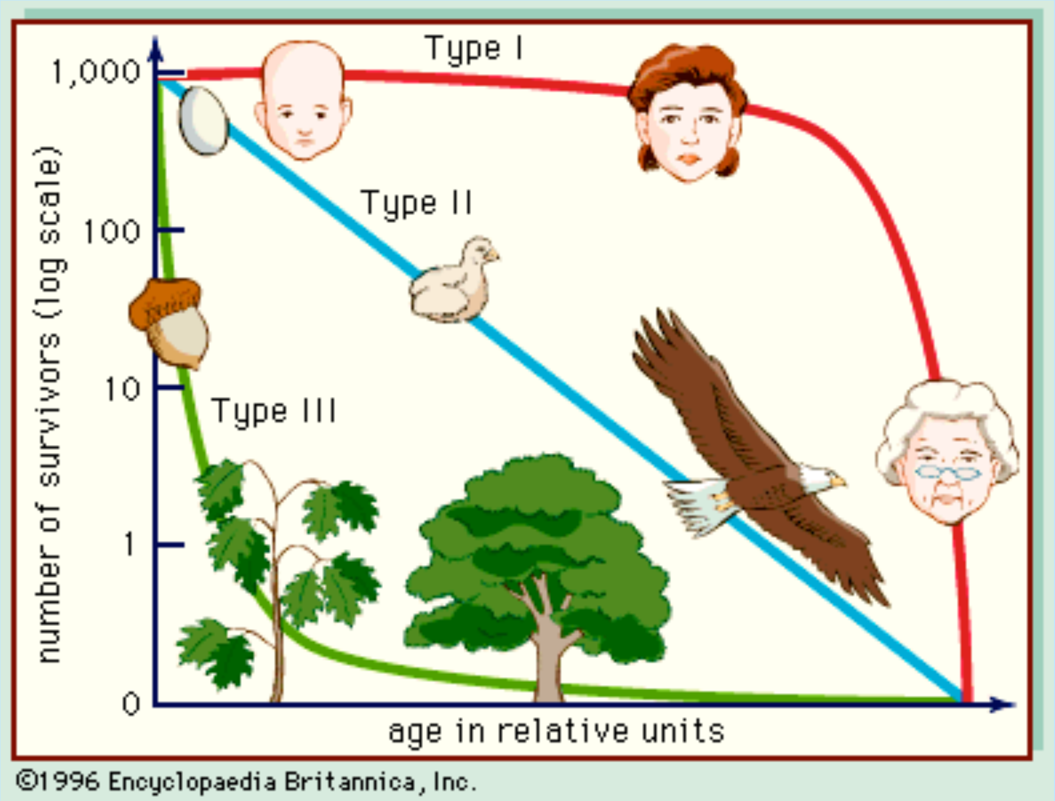


Mean number of daughters per female

Pre-reproductive

Age class

Survivorship Curves



Variability in shape – broadly classified into types 1,2,3

Type 2: straight line on survivorship vs age -> constant number survive to next age class

Straight line on $\log_e$(survivorship) -> constant probability survive to next age class

Data for survivorship curves

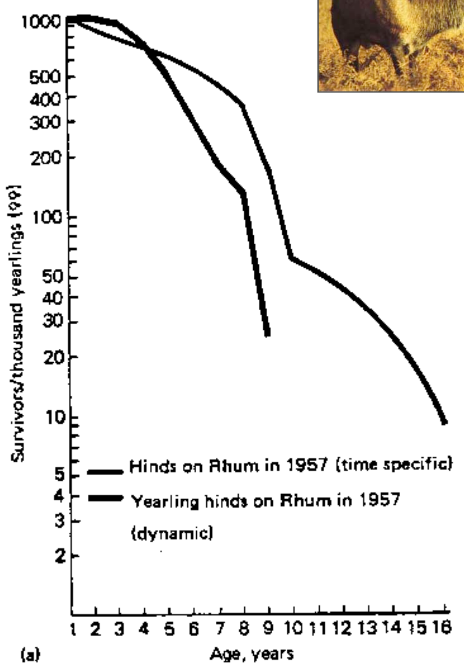


Figure 14.17 Type I survivorship curves for hinds (females) and stags (males) of red deer on Isle of Rhum. The green curve is derived from the time-specific life table; the black curve from the 1957 cohort life table. (From Lowe 1969: 436, 437.)

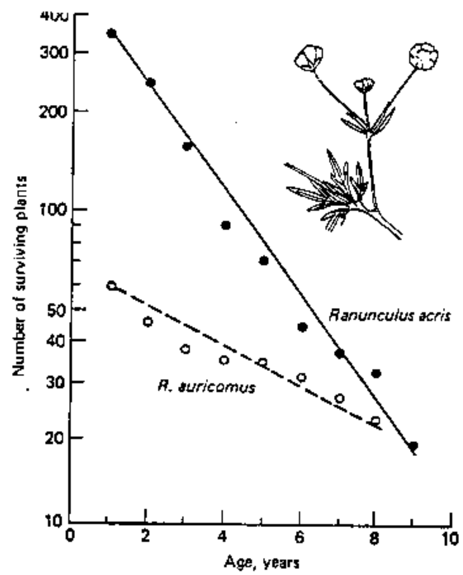
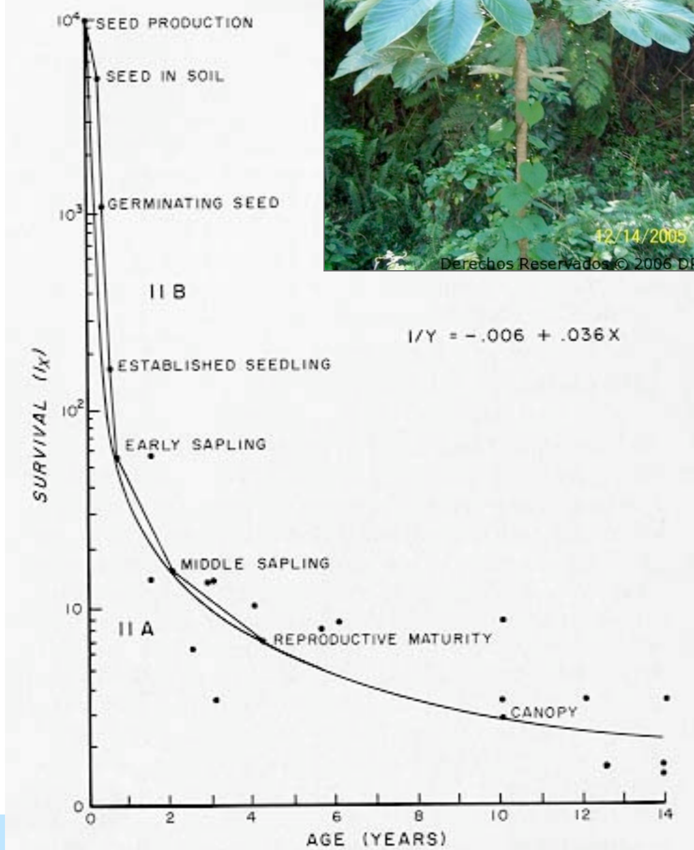


Figure 14.19 Survivorship curves of the buttercups *Ranunculus acris* and *Ranunculus auricomus*. These curves are linear or Type II. (From Sarukhan and Harper 1974.)



How to get these data?

It’s difficult

Fecundity: e.g. estimate age at pregnancy

How to get these data?

Survivorship

Fixed cohort, dynamic, horizontal

How to get these data?

Survivorship

Estimate age of dead individuals

Notation for age classes

x = age class of individual

- Defines age INTERVAL (e.g. age class "0" denotes 0-1 interval)
- Choice of interval depends on organism

  (could be 1 yr, 1 mth, 1 wk)
- Within an age class individuals behave similarly in terms of births and deaths

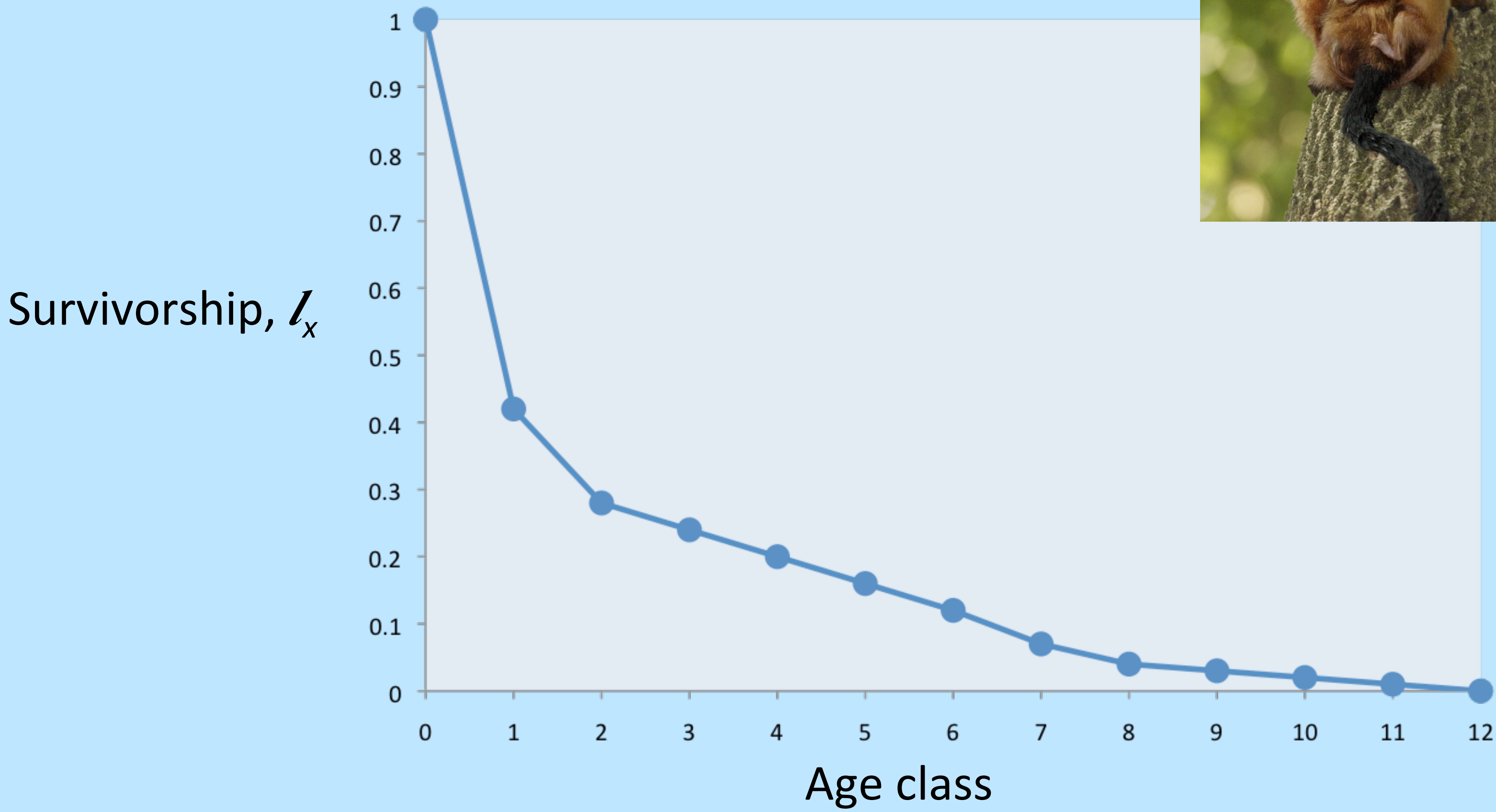
Life tables

- Age-specific survival and reproduction
- Define S_x as the # of survivors from one age class to the next (starting from cohort of size 1000)
- Define l_x as the proportion that survived from age 0 to age "x" (cumulative)
- Define m_x as avg. # offspring per female at age "x"

Age category (x)	# who died in the age category	# alive at start of age category	S_x based on cohort of 1000	Survivorship, l_x (=S_x/1000)
0	0	56	1000	1.0
1-4	3	56	1000	1.0
5-9	7	53	946	0.946
10-14	14	46	821	0.821
15-19	26	32	571	0.571
20-24	4	6	107	0.107
25-29	2	2	36	0.36
30+	0	0	0	0.0

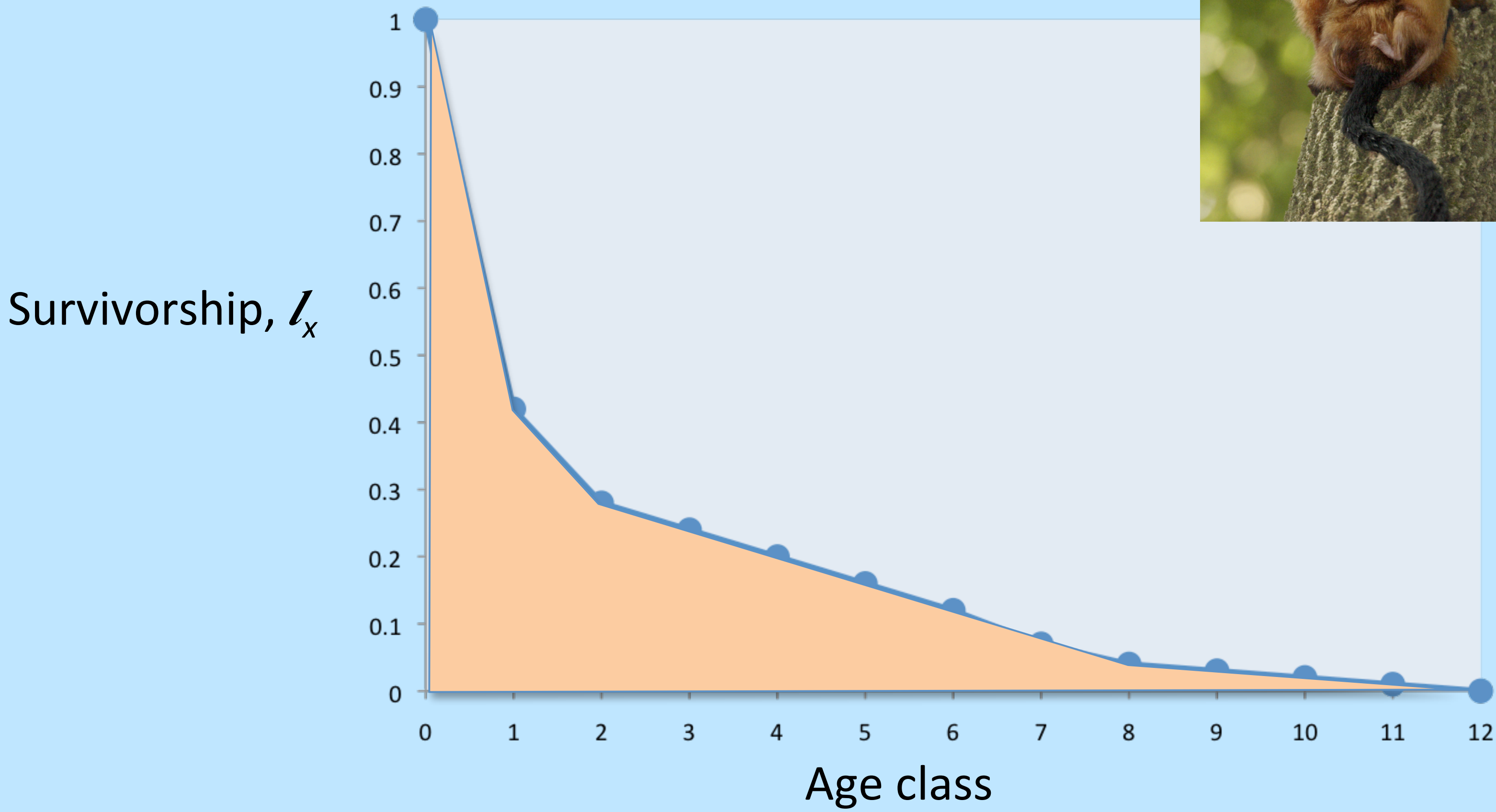
Calculating survivorship

Life expectancy



Life expectancy (at birth) = area under survivorship curve

Life expectancy



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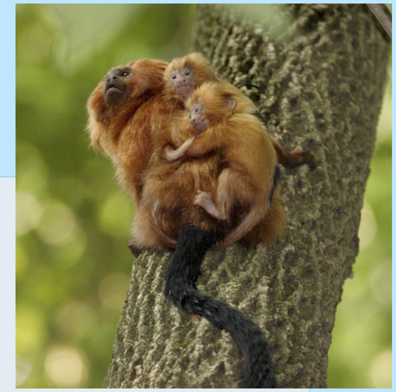
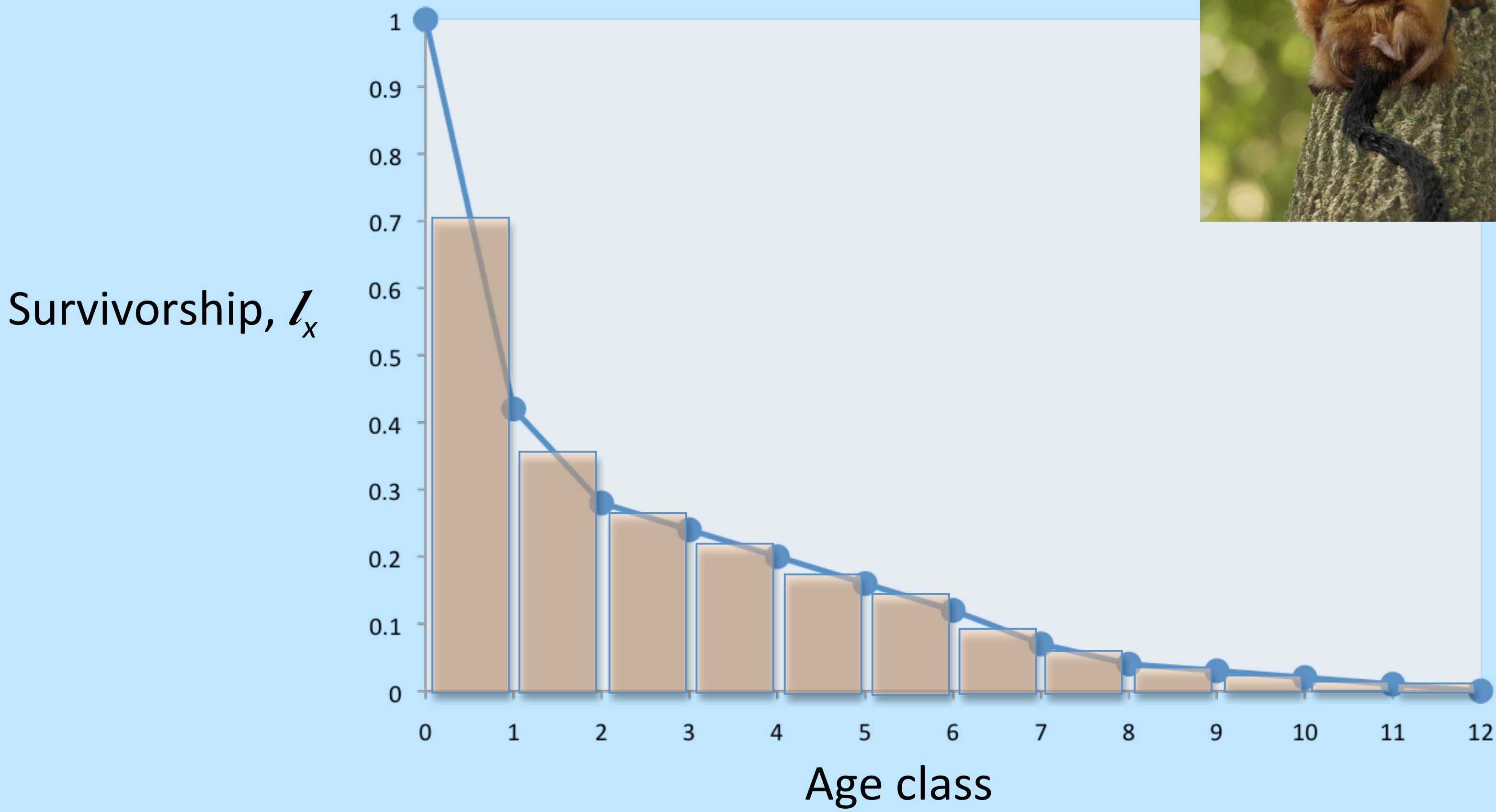
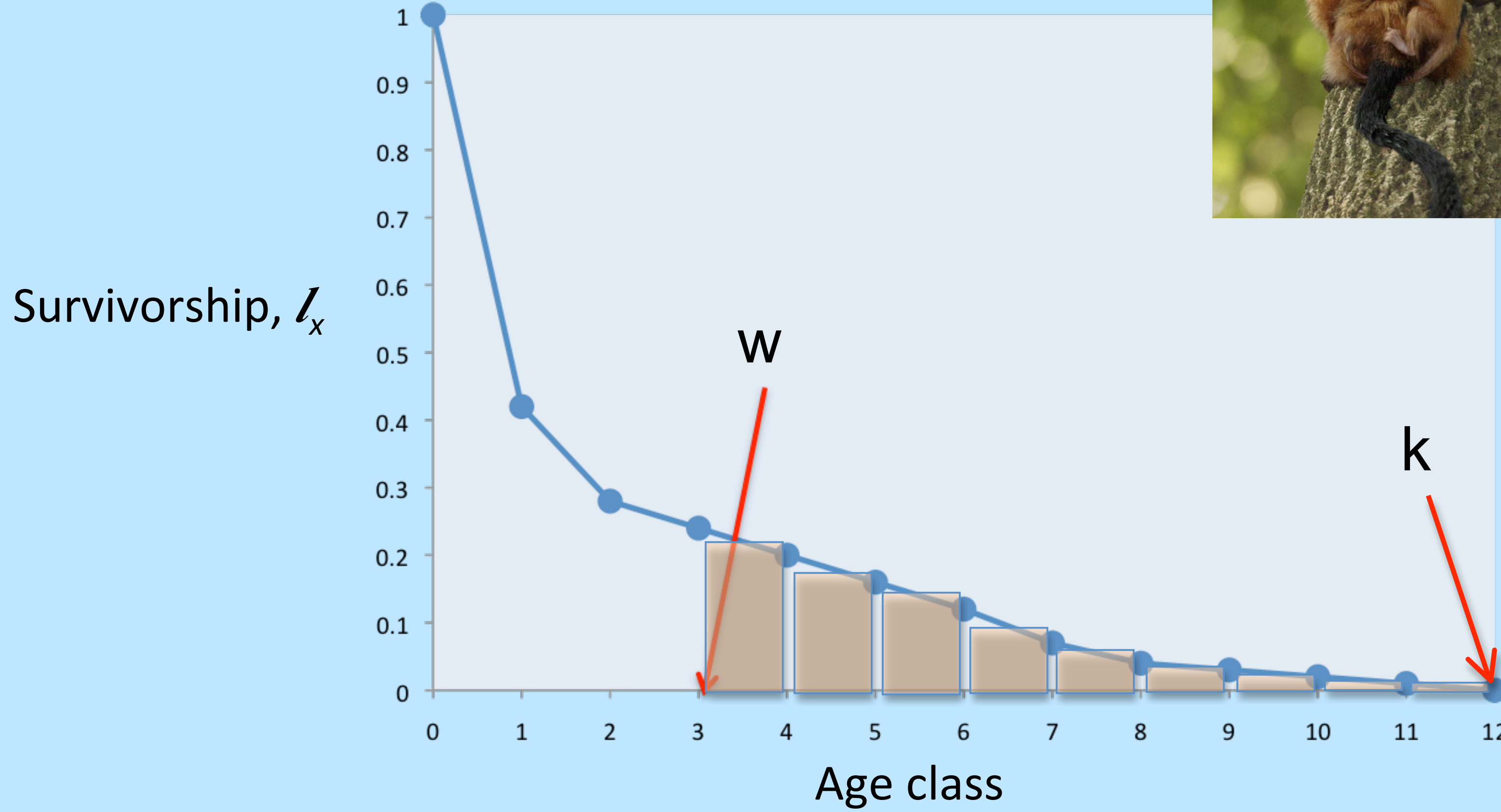




Rectangles have area $L_x = (l_{x+1} + l_x)/2$

Area $\approx \Sigma L_x$

Life expectancy



Life expectancy (from age w) ≈ $$\frac{\sum_{x=w}^{x=k} L_x}{l_w}$$

Age category (x)	Mean # female offspring per female (m_x)
0-9	0
10-19	0.5
20-29	0.6
30-39	0.1
40-49	0.03
50+	0

Fecundity in a life table

$m_{10\text{-}19}$: on average a female in this age category produces 0.5 females (e.g. one offspring, 50% chance female)

Age (x)	l_x	m_x	p_x	q_x	l_xm_x
0	1.0	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
2	0.116	2.28	0.767	0.233	0.264
3	0.089	2.28	0.652	0.348	0.203
4	0.058	2.28	0.672	0.328	0.132
5	0.039	2.28	0.641	0.359	0.089
6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0

Age (*x*)	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.0	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
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8	0	0	-	-	0

p_x = probability of surviving to the next age class = l_{x+1}/l_x

Age (x)	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.0	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
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7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0

q_x = probability of not surviving to the next age class = $1-p_x$

Age (x)	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.0	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
2	0.116	2.28	0.767	0.233	0.264
3	0.089	2.28	0.652	0.348	0.203
4	0.058	2.28	0.672	0.328	0.132
5	0.039	2.28	0.641	0.359	0.089
6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0

Gross reproductive rate = $\Sigma\, m_x$

Age (x)	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.0	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
2	0.116	2.28	0.767	0.233	0.264
3	0.089	2.28	0.652	0.348	0.203
4	0.058	2.28	0.672	0.328	0.132
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6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0

Net reproductive rate = $\Sigma\, l_x m_x$

R_0 = Net Reproductive Rate

R_0 = The expected lifetime reproductive output per female

$$R_0 = l_0 m_0 + l_1 m_1 + l_2 m_2 + \ldots . l_k m_k$$

$$R_0 = \sum_{x=0}^{k} l_x m_x$$

$R_0 = 1$ means each female just replaces herself

When $R_0 < 1$ get decline

When $R_0 > 1$ get increase

Mean Generation Time

Average age of a female when offspring are born

$$G = \frac{\sum x l_x m_x}{R_0}$$

G reflects how long it takes population to increase by a factor of R_0

Mean Generation Time

Average age of a female when offspring are born

Probability of making it into age class *x*

$$G = \frac{\sum x l_x m_x}{R_0}$$

G reflects how long it takes population to increase by a factor of R_0

Mean Generation Time

Average age of a female when offspring are born

$$G = \frac{\sum x l_x m_x}{R_0}$$

Probability of having an offspring in this age class

G reflects how long it takes population to increase by a factor of R_0

Mean Generation Time

Average age of a female when offspring are born

Summed over all ages

$$G = \frac{\sum x l_x m_x}{R_0}$$

G reflects how long it takes population to increase by a factor of R_0

Intrinsic growth rate

$$N_{t+\mathrm{G}}=R_0 N_t$$

Tells us by how much a given generation will increase the population size, but says nothing about time

Recall: $N_{t+1}=\lambda N_t$

$N_{t+1}=e^r N_t$

Similarly: $N_{t+\mathrm{G}}=e^{rG} N_t$

For the exact value of the intrinsic rate of increase we could solve the Euler equation

$$r=\ln(R_0)/G$$

Euler Equation:

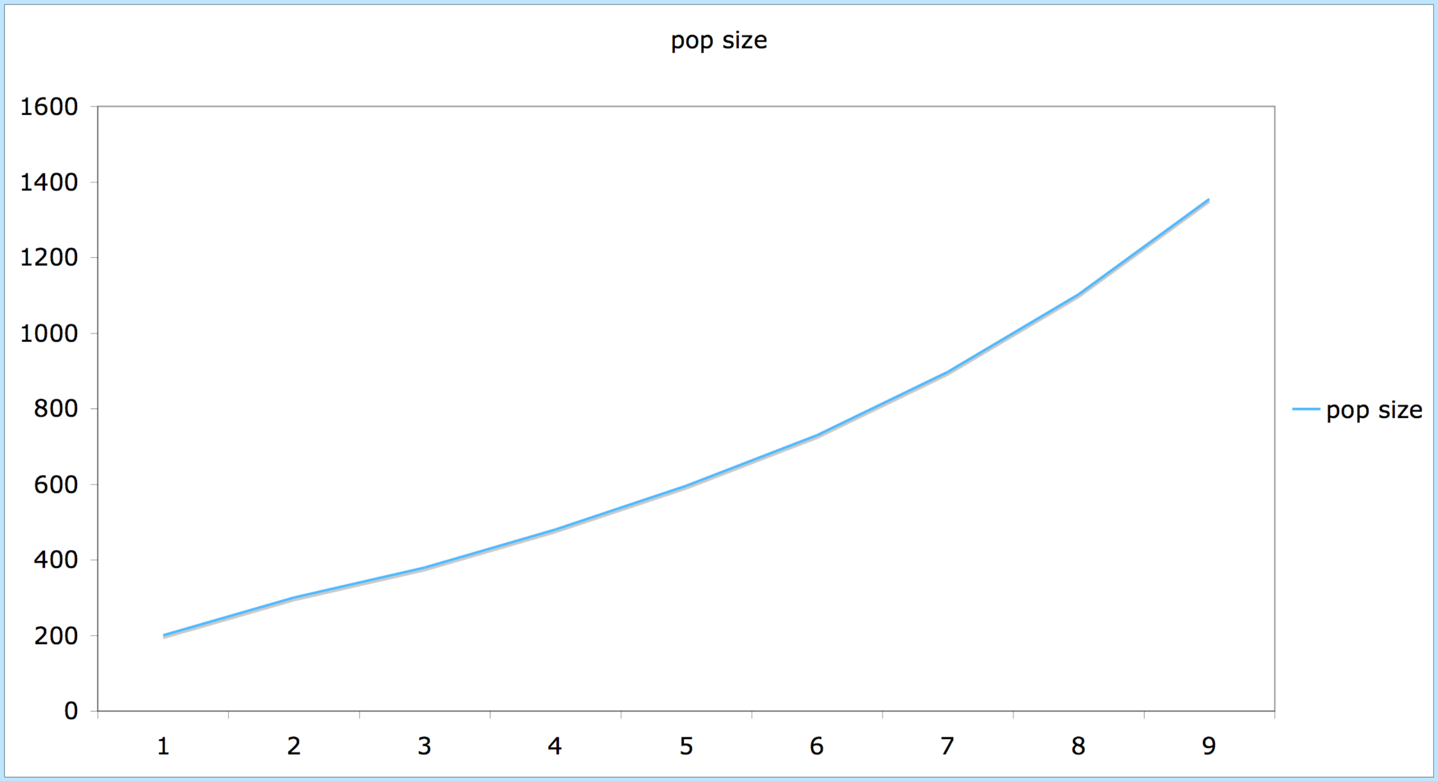
$$1=\sum e^{-rx} l_x b_x$$

Predicting growth and age distribution

Age (x)	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.0	0	0.253	0.747	0
1	0.5	2.0	0.458	0.542	0.324
2	0.2	1.0	0.767	0.233	0.264
3	0.1	1.0	0.652	0.348	0.203
4	0	0	-	-	-
sums		GRR=4.0			R_0=1.3

We'll start with 200 individuals all in age class x=0

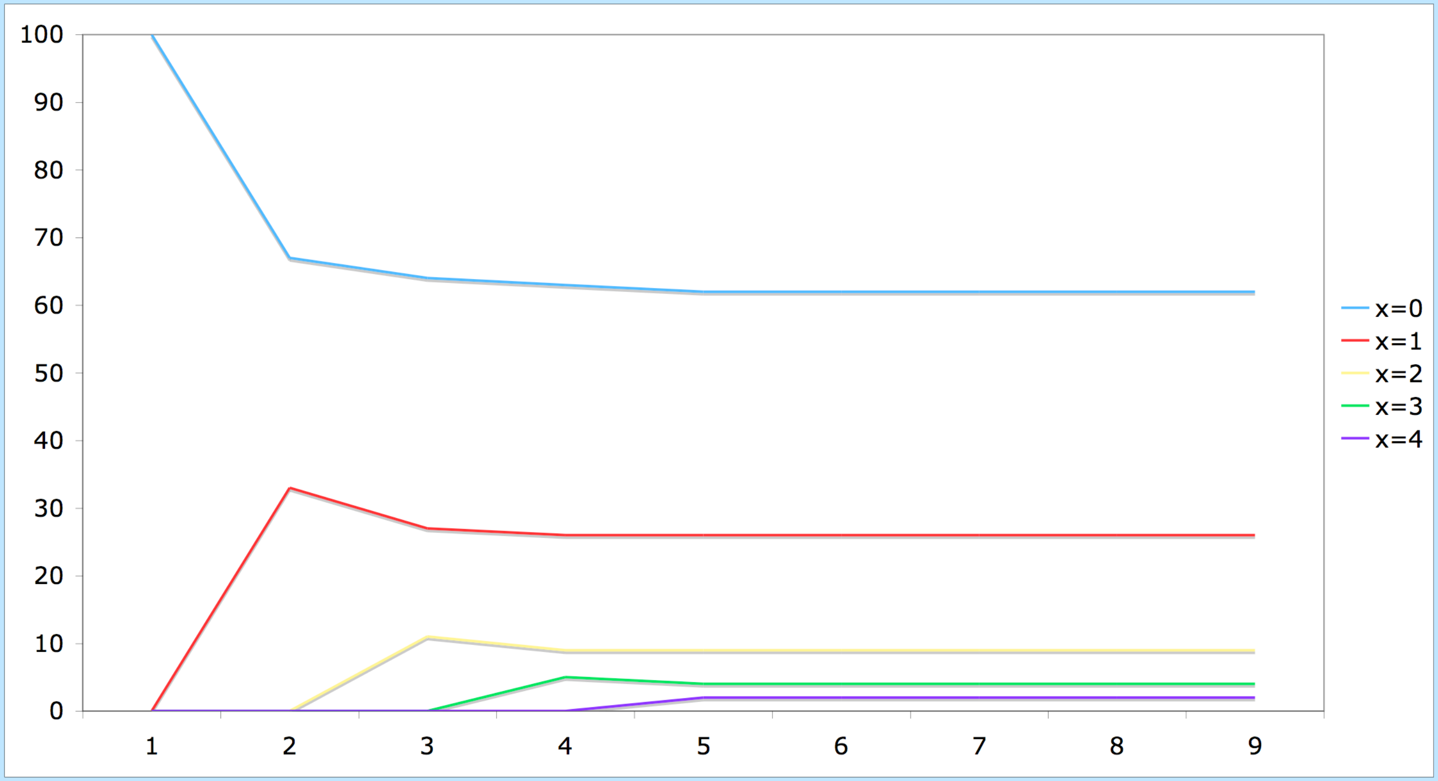
Population size increases by R_0=1.3 every generation



Generation

After a transient phase, a stable age distribution is reached

% in
age class



Generation

Stable Age Structure

- The proportion of individuals in each age class remains constant over time, even as population size varies
- Stable age structure develops as a population achieves a constant growth rate (positive, negative, or zero)
  - under **constant environmental conditions**

Intrinsic Rate of Increase

- The per capita rate of increase under a given set of environmental conditions when a population has stable age structure
- Observed population growth rate will ‘bounce around’ until population reaches stable age distribution

Census population

- Instead of N(t), record:

$$N_x(t) = \begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ N_4 \end{pmatrix} \qquad N_x(5) = \begin{pmatrix} 600 \\ 270 \\ 100 \\ 50 \\ 15 \end{pmatrix}$$

Each value corresponds to the number of individuals in a particular age class at a particular time

Projecting future populations

- Age class "0":

$$N_0(t+1) = N_1(t)m_1 + N_2(t)m_2 + N_3(t)m_3....$$

- Other age classes:

$$N_1(t+1) = N_0(t)p_0$$
$$N_2(t+1) = N_1(t)p_1$$
$$N_3(t+1) = N_2(t)p_2$$
$$etc.$$

Projecting future populations

- Age class "0":

$$N_0(t+1) = N_1(t)m_1 + N_2(t)m_2 + N_3(t)m_3 \ldots.$$

- Other age classes:

$$N_1(t+1) = N_0(t)p_0$$
$$N_2(t+1) = N_1(t)p_1$$
$$N_3(t+1) = N_2(t)p_2$$
$$etc.$$

Leslie Matrix

- Notation for growth of age-structured population
- If "k" age classes, then a k x k square matrix
- Columns represent ages 1 through k
- Row 1 → fertility values
- Rows 2-k → survival probabilities

Leslie Matrix

$$\mathbf{A} = \begin{pmatrix} p_0 m_1 & p_1 m_2 & p_2 m_3 & p_3 m_4 & 0 \\ p_0 & 0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 \end{pmatrix}$$

Contributions to newborns from each age class

Survival probabilities: transitions from one age class to the next

Rules of matrix algebra

$$\begin{pmatrix} b_1 \\ b_2 \end{pmatrix} * \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} (b_1 * a_{11} + b_2 * a_{12}) \\ (b_1 * a_{21} + b_2 * a_{22}) \end{pmatrix}$$

Projection with Leslie Matrix

$$\mathbf{N}(t+1) = \mathbf{A} * \mathbf{N}(t)$$

Analogous to $N(t+1)=\lambda N(t)$

Just as $N(t)=\lambda^t N(0)$

So $\mathbf{N}(t)=\mathbf{A}^t * \mathbf{N}(0)$

Projection with Leslie Matrix

$$\mathbf{N}(t+1) = \mathbf{A} * \mathbf{N}(t)$$

Analogous to $N(t+1)=\lambda N(t)$

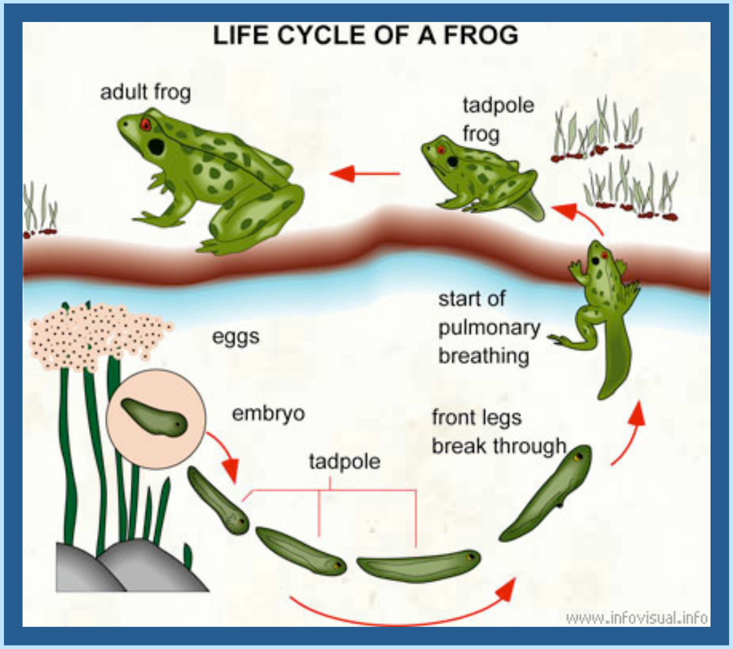
Computers can calculate this very easily

Just as $N(t)=\lambda^t N(0)$

We can easily examine matrix A to work out λ

So $\mathbf{N}(t)=\mathbf{A}^t * \mathbf{N}(0)$

Some species best described by stages rather than age



Lefkovitch modification, still recover λ

Worked example 1

A field ecologist followed a cohort of female chipmunks from birth and recorded the number that survived to each successive year. From the same cohort, they also recorded the total number of newborn females each year resulting from the entire cohort, and obtained the following results:

Age (x, in years)	# surviving to age x	# newborn females from cohort	Cumulative proportion surviving, l_x	Mean number of (female) offspring per female of age x, m_x
0	1000	0	1.0	
1	175	700		
2	120	360		
3	50	500		
4	0	0		

Complete the life table for these chipmunks, providing l_x (cumulative proportion surviving to age x), and m_x (age-specific births). Sketch l_x as a function of age (x). Does this resemble a type 1, 2 or 3 survivorship curve?

Worked example 2

In the following Leslie matrix for population change with age classes 1, 2 & 3, which letters or formulas represent *(i)* fecundity of 2-year-olds *(ii)* probability that a 1-year-old reaches age class 3?

$$\begin{matrix} 0 & W & X \\ Y & 0 & 0 \\ 0 & Z & 0 \end{matrix}$$

A) (i)=W; (ii)=Z
B) (i)=W; (ii)=Y+Z
C) (i)=W; (ii)=Y
D) (i)=W; (ii)=Y*Z
E) (i)=Y; (ii)=X
F) (i)=Y; (ii)=W+X

Summary

- We generalized our simple fundamental equation of population ecology to account for one source of individual variation – namely, age
- We found that there are general patterns in age-specific reproduction and survival
- We introduced tools to study demography (age pyramid, life table)
- We introduced mathematical procedures (matrix algebra) to study the dynamics of age-structured population growth

Summary

- We observed that after a transient phase, a stable age distribution is reached and the population grows / declines according to λ
- We don't have to divide up the population by age, we can instead consider different stages (e.g. eggs, juveniles, adults)
- Valuable skill set for conservation and management (especially when resources $$$ are low)
- As well as preserving threatened species we can also consider the best way to deal with undesirable "invasive" species