Life table methods

Reproduction and survival rate are related

- To be stable, a population has to balance mortality with reproduction
- On average, each individual has to replace itself during its lifetime
- There are different strategies
  - Semelparous/iteroparous
  - K-selected/r-selected

Why not live forever and produce large numbers of large offspring?

- If the Darwinian goal is to maximize fitness, why not:
  - Live a long time
  - Make lots of big offspring every year
- Answer is: trade-offs
  - Somatic/reproductive
  - More large/fewer small offspring

Survival vs. reproduction

- Somatic growth and maintenance = growing and maintaining one’s own body
  - Development
  - Metabolism
  - Storage

- Reproduction = making offspring
- Resources devoted to somatic maintenance aren’t available for reproduction, and vice versa
- For a fixed intake of resources, these two components of fitness trade off

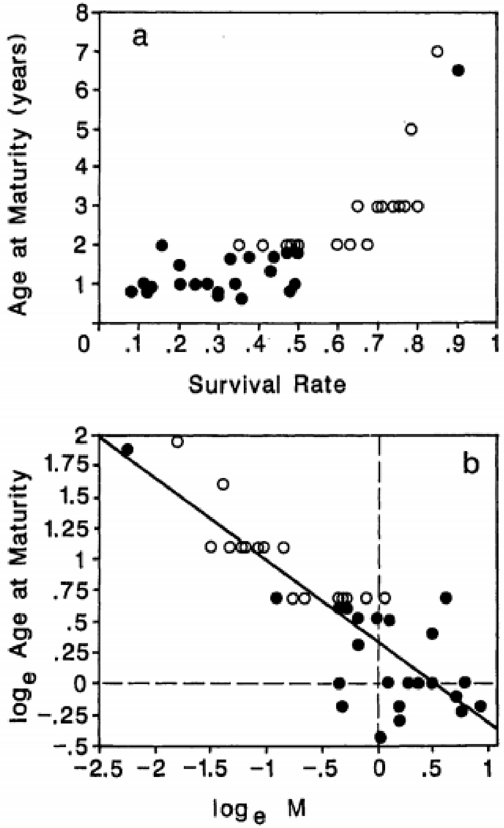
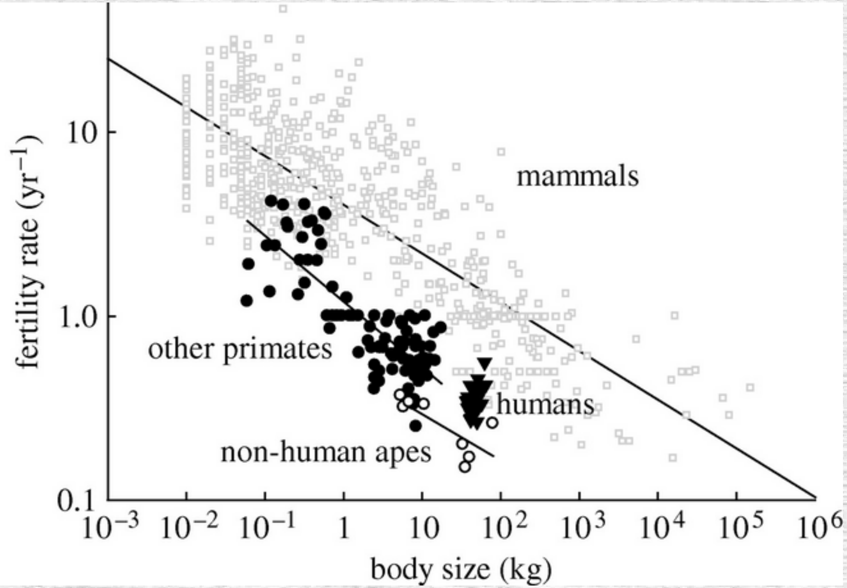


FIG. 2.—*a*, Relationship between annual adult survival rate and age at female maturation for 17 populations of snakes (16 species) and 28 populations of lizards (20 species). *Solid circles*, data points for lizards; *open circles*, data points for snakes. *b*, Regressions of $\log_e M$ (instantaneous adult mortality rate) against $\log_e \alpha$ (age at maturity, in years), for snakes (*open circles*) and lizards (*solid circles*). See text for statistical results and methods of calculation.



Mammals – Walker et al. 2008

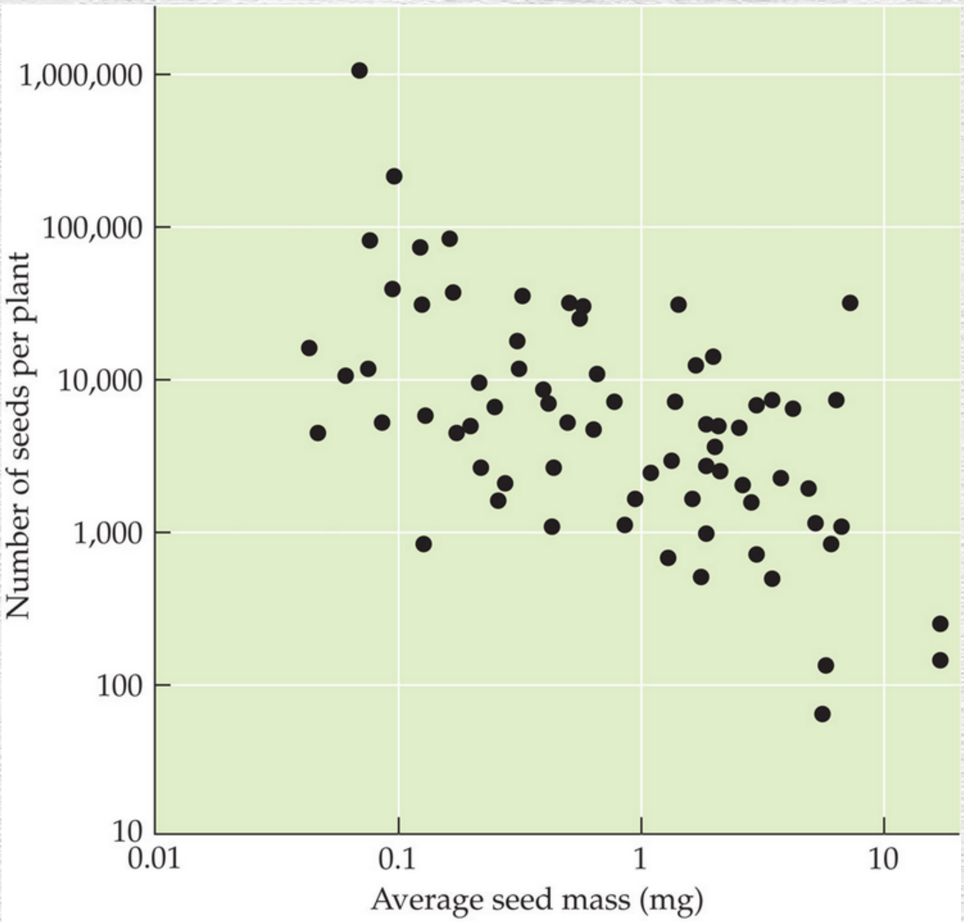
Snakes and lizards – Shine and Charnov 1992

Reproductive trade offs – two common strategies...

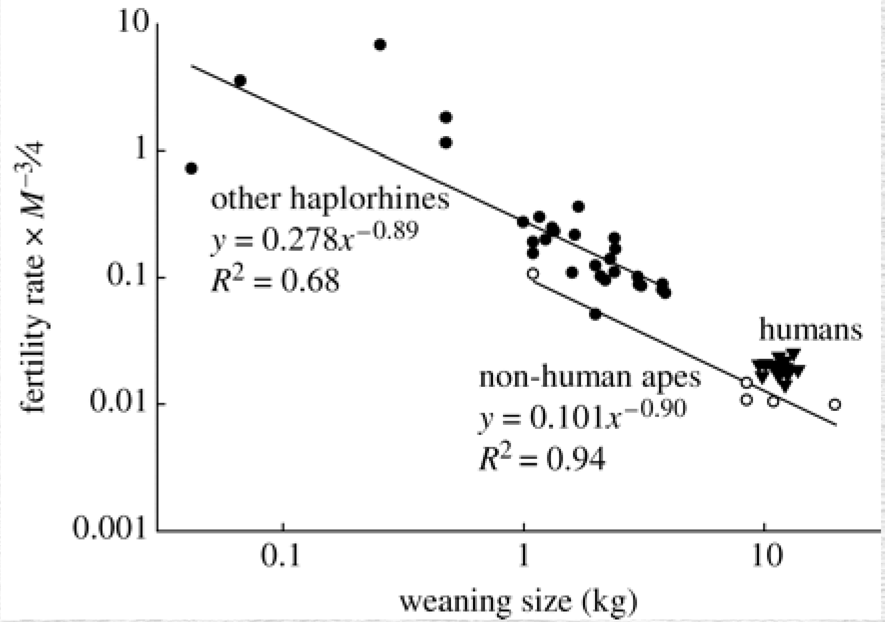
- Large investment in terms of:
  - Egg formation, gestation (mother's bodily resources)
  - Parental care during an extended juvenile period
- Small investment in terms of:
  - Small offspring
  - Lack of parental care
- Large investment per offspring is incompatible with large number of offspring

Joey failure to launch

Spider egg sack hatching



ECOLOGY 3e, Figure 7.16

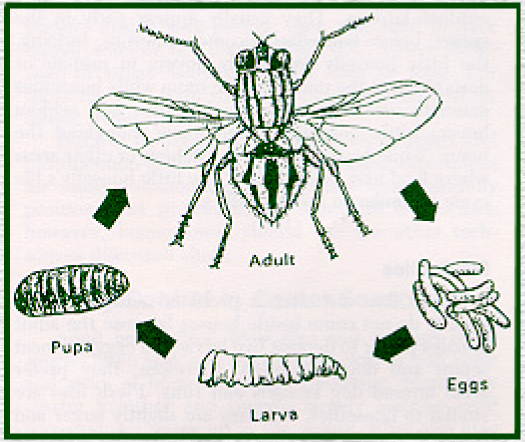


Plants

Primates

Long life, short life

- Some species have very short individual lifespans
  - Annual plants germinate, grow to maturity, breed, and die in one year
  - House flies only need 2-3 weeks from egg deposition to adult breeding (10-12 generations in a summer)



- Some species live a very long time
  - Individual bristlecone pines can live for thousands of years (oldest known 5066 yrs)
  - Orange roughy fish can live over 150 yrs
  - Tortoises can live over 100 yrs

Many possible combinations of survival and reproduction work

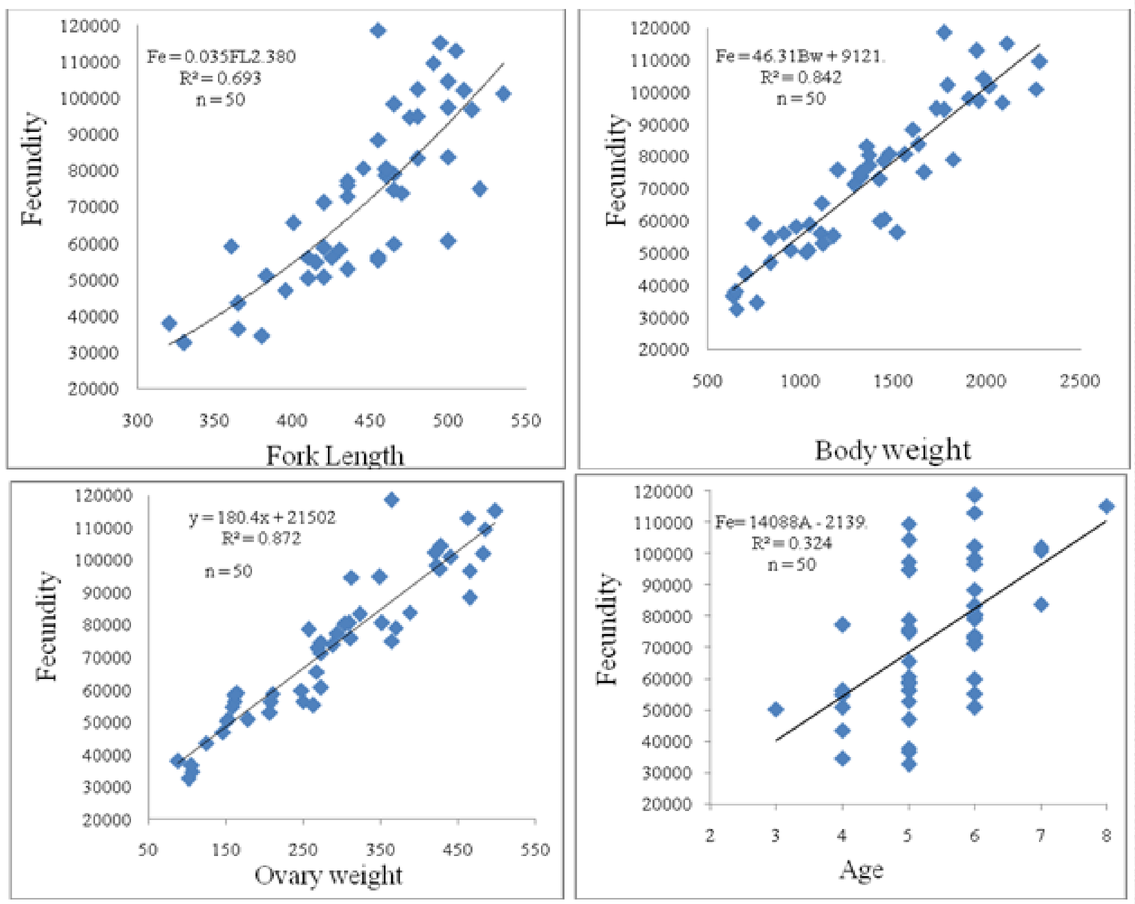
- Long lifespan can be found in combination with:
  - High output of small offspring with high neonate/juvenile mortality (coral)
  - Low output of large offspring, with high juvenile survival (elephants)
- Short lifespan can be found in combination with:
  - High output of offspring with high neonate/juvenile mortality (mayflies)

Combinations that are very unlikely

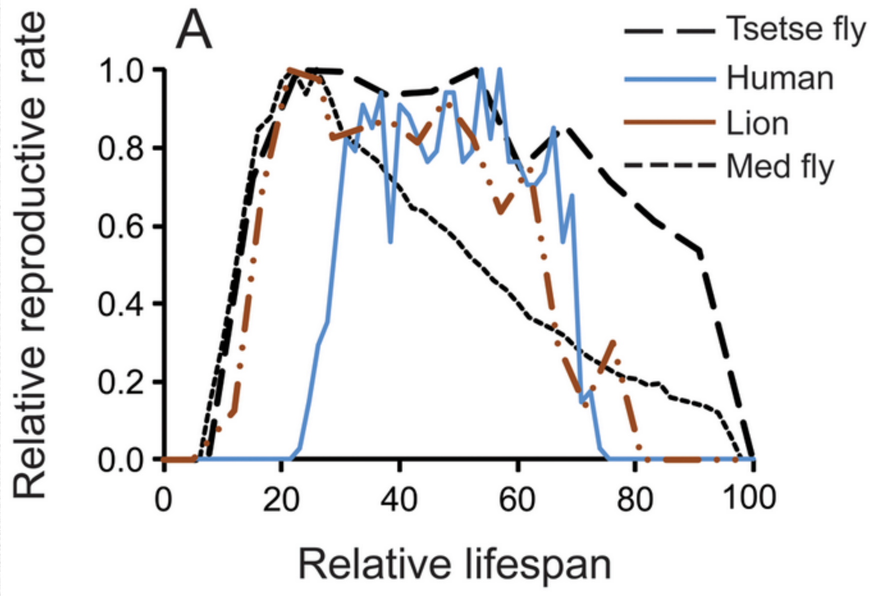
- Combinations that are too good to be true – not possible with a somatic/reproductive tradeoff
  - Production of large numbers of offspring that are large, and have a high probability of surivival
- Combinations in which reproduction doesn’t offset mortality – species go extinct
  - Short lifespan coupled with low production of small offspring with low survival probability

Most demographic rates are age-specific

- Survival probability is associated with size
  - Larger animals are less susceptible to predation
  - Larger individuals are often better able to withstand environmental stress
- Survival probability is associated with age
  - Older individuals are more experienced, better able to exploit their surroundings
  - Older individuals may experience increase mortality due to biological aging
- Reproduction is associated with size
  - Especially in egg-laying species, bigger individuals have higher reproductive output
- Reproduction is associated with age
  - Older individuals may be more experienced parents
  - Some species experience reproductive senescence



Fish – indeterminate growth, increase in fecundity with age



Senescence in two mammal and two insect species

Population dynamics in species with age-specific demographic rates

- Age structure requires methods of analysis that account for age-specific demographic rates
  - Species that live more than one year
  - Species with overlapping generations (i.e. more than one generation alive at once)
- Two basic approaches are life table analysis and matrix population models
- We'll focus today on life tables

Cohort life tables

- Cohort-based approach to population demography (also called “horizontal” life tables)
  - Start with a number of individuals (females) at birth
  - Count how many are alive each year
  - Record how many offspring they produce each year per capita
  - Known fates – assumed encounter probability is 1 for living animals
- From this you can construct a life table
  - Rows are years
  - Column for number alive each year
  - Column for number of babies born per female each year
- Analysis of the life table can give you growth rate, and other useful statistics

Example: Gray squirrel population

	A	B
1	Age	Number alive (n_x)
2	0	1000
3	1	253
4	2	116
5	3	89
6	4	58
7	5	39
8	6	25
9	7	22
10	8	0

From Barkalow et al. 1970

1000 individuals marked at birth

Followed until all of them die

n_x = number alive at age x

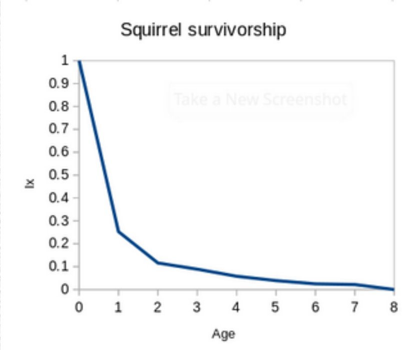
Survivorship (l_x)

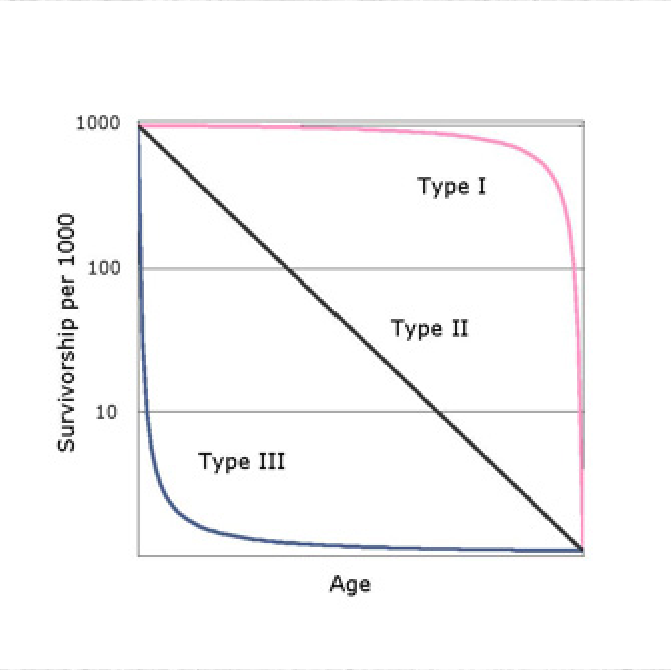
Survivorship is proportion still alive at age x

$l_x = n_x / n_0$

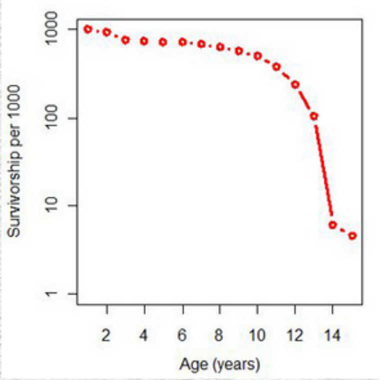
Age	Number alive (n_x)	Survivorship (l_x)
0	1000	1.000
1	253	0.253
2	116	0.116
3	89	0.089
4	58	0.058
5	39	0.039
6	25	0.025
7	22	0.022
8	0	0.000

Typical survivorship curves

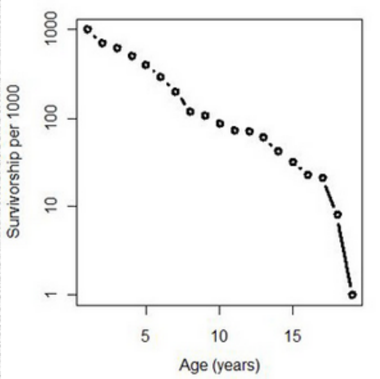




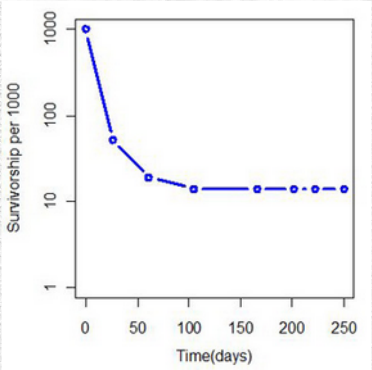
Dall sheep



Slider turtle



Cheatgrass



Which pattern does the squirrel follow?

Annual survival, annual mortality

	A	B	C	D	E
1	Age	Number alive (n_x)	Survivorship (l_x)	Annual survival (p_x)	Annual mortality (q_x)
2	0	1000	1.000	0.253	0.747
3	1	253	0.253	0.458	0.542
4	2	116	0.116	0.767	0.233
5	3	89	0.089	0.652	0.348
6	4	58	0.058	0.672	0.328
7	5	39	0.039	0.641	0.359
8	6	25	0.025	0.880	0.120
9	7	22	0.022	0.000	1.000
10	8	0	0.000		

Annual survival probability (p_x) = l_{x+1} / l_x

Annual mortality rate (q_x) = $1-p_x$

Age-specific fertility (m_x)

Age	Number alive (n_x)	Survivorship (l_x)	Fertility (m_x)
0	1000	1.000	0
1	253	0.253	1.28
2	116	0.116	2.28
3	89	0.089	2.28
4	58	0.058	2.28
5	39	0.039	2.28
6	25	0.025	2.28
7	22	0.022	2.28
8	0	0.000	0

Number of offspring produced per individual at age x

Net reproductive rate (R_0)

	A	B	C	D	E
1	Age	Number alive (n_x)	Survivorship (l_x)	Fertility (m_x)	Offspring per ind. ($l_x m_x$)
2	0	1000	1.000	0	0.000
3	1	253	0.253	1.28	0.324
4	2	116	0.116	2.28	0.264
5	3	89	0.089	2.28	0.203
6	4	58	0.058	2.28	0.132
7	5	39	0.039	2.28	0.089
8	6	25	0.025	2.28	0.057
9	7	22	0.022	2.28	0.050
10	8	0	0.000	0	0.000
11					
				R_0	1.120

Average expected number of offspring – if R0 = 1 population is stable,

R0 > 1 population is increasing,

R0 < 1 population is decreasing

$$R_0 = \sum l_x m_x$$

Population growth rate from a life table

- We can get intrinsic rate of increase, r = b-d, from the Euler equation

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

- Solved iteratively – values or r selected until the equation balances

Growth rate for the squirrel data

	A	B	C	D	E	F
1	Age	Number alive (n_x)	Survivorship (l_x)	Fertility (m_x)	Offspring per ind. ($l_x m_x$)	$l_x m_x e^{-rx}$
2	0	1000	1.000	0	0.000	0.000
3	1	253	0.253	1.28	0.324	0.324
4	2	116	0.116	2.28	0.264	0.264
5	3	89	0.089	2.28	0.203	0.203
6	4	58	0.058	2.28	0.132	0.132
7	5	39	0.039	2.28	0.089	0.089
8	6	25	0.025	2.28	0.057	0.057
9	7	22	0.022	2.28	0.050	0.050
10	8	0	0.000	0	0.000	0.000
11						
12					Euler	1.11956
13						
14				R_0	1.120	
15				r	0	

Change this until this equals 1

Growth rate for the squirrel data

	A	B	C	D	E	F
1	Age	Number alive (n_x)	Survivorship (l_x)	Fertility (m_x)	Offspring per ind. ($l_x m_x$)	$l_x m_x e^{-rx}$
2	0	1000	1.000	0	0.000	0.000
3	1	253	0.253	1.28	0.324	0.311
4	2	116	0.116	2.28	0.264	0.244
5	3	89	0.089	2.28	0.203	0.179
6	4	58	0.058	2.28	0.132	0.112
7	5	39	0.039	2.28	0.089	0.072
8	6	25	0.025	2.28	0.057	0.044
9	7	22	0.022	2.28	0.050	0.038
10	8	0	0.000	0	0.000	0.000
11						
12					Euler	1
13						
14				R_0	1.120	
15				r	0.0413	

$r = 0.0413$

Finite rate of increase, λ

- Finite rate of increase, λ, is N_{t+1}/N_t
- This can be estimated as e^r
- For the squirrels this is $e^{0.041} = 1.04$
- This population is increasing 4% per year

Generation time (G)

- Average difference in age between parent and offspring
- $G = \Sigma l_x m_x x / R_0$

	A	B	C	D	E	F	G
1	Age	Number alive (n_x)	Survivorship (l_x)	Fertility (m_x)	Offspring per ind. ($l_x m_x$)	$l_x m_x e^{-rx}$	$l_x m_x x$
2	0	1000	1.000	0	0.000	0.000	0.000
3	1	253	0.253	1.28	0.324	0.311	0.324
4	2	116	0.116	2.28	0.264	0.244	0.529
5	3	89	0.089	2.28	0.203	0.179	0.609
6	4	58	0.058	2.28	0.132	0.112	0.529
7	5	39	0.039	2.28	0.089	0.072	0.445
8	6	25	0.025	2.28	0.057	0.044	0.342
9	7	22	0.022	2.28	0.050	0.038	0.351
10	8	0	0.000	0	0.000	0.000	0.000
11							
12						Sum:	3.13
13						G	2.79
14				R_0	1.120		
15				r	0.0413		
16				λ	1.042		

On average, squirrel parents are 2.79 years older than offspring

r can also be approximated with $\ln(R_0)/G = 0.040$

Calculating stable age distribution

- The distribution of ages that results in smooth change in population size is called the **stable age distribution**
- For the population to be increasing or decreasing smoothly, the proportion of individuals in each age class needs to be:

$$c_x = \frac{l_x e^{-rx}}{\sum l_x e^{-rx}}$$

	A	B	C	D
1	Age (x)	Survivorship (l_x)	$l_x e^{-rx}$	c_x
2	0	1.000	1.000	0.647
3	1	0.253	0.243	0.157
4	2	0.116	0.107	0.069
5	3	0.089	0.079	0.051
6	4	0.058	0.049	0.032
7	5	0.039	0.032	0.021
8	6	0.025	0.020	0.013
9	7	0.022	0.016	0.011
10	8	0.000	0.000	0.000
11				
12		Sum:	1.5451	
13		r	0.0413	

Assumptions

- Growth rate is based just on the cohort
  - Immigration isn't included
  - Permanent emigration is indistinguishable from mortality – growth rate will be accurate, but cause will be mis-attributed
- Constant environment
  - The growth rate is estimated from a single cohort, but the population is made up of multiple, overlapping cohorts
  - Growth rate will only be accurate if the cohort used for the life table has the same properties as all the cohorts in the population
  - This will only be true if the environment is stable, relatively unchanging

Period life tables

- Instead of using a cohort followed throughout its lifetime, can use a sample of individuals of each age
  - Age is used in place of time
  - Age-specific reproduction is estimated for m_x
  - Reduction in numbers of individuals of each age are assumed to reflect mortality
- Period table will be the same as a cohort table if:
  - Population is stationary = not changing in size, at stable age distribution
  - No change in the environment
  - Geographically closed (no immigration/emigration)

Example – mosquitofish sample

- Sample a population of mosquitofish in a pond
- Count how many are in each age class (based on size)

	A	B
1	Age class (days)	Num. In class
	0	130
2	30	190
3	60	240
4	90	120
5	120	60
6	150	15
7	180	3
8	210	1
10	240	0
10		
12	Sum	759

Building n_x from a sample

- Recognize that all of the fish in the sample were at one time in age class 0 – sum the age classes, assign to 0
- Recognize that all the individuals at 30 d or older lived to 30 d – sum from 30 d or more, assign to 30 d
- Continue through rest of ages

	A	B	C
1	Age class (days)	Num. In class	n_x
	0	130	759
2	30	190	629
3	60	240	439
4	90	120	199
5	120	60	79
6	150	15	19
7	180	3	4
8	210	1	1
10	240	0	0
10			
12	Sum	759	

Rest of the calculations are the same

	A	B	C	D	E	F	G
1	Age class (days)	Num. In class	n_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
2	0	130	759	1.000	0	0.000	0.000
3	30	190	629	0.829	0	0.000	0.000
4	60	240	439	0.578	0	0.000	0.000
5	90	120	199	0.262	24	6.292	566.324
6	120	60	79	0.104	0	0.000	0.000
7	150	15	19	0.025	29	0.726	108.893
8	180	3	4	0.005	32	0.169	30.356
9	210	1	1	0.001	0	0.000	0.000
10	240	0	0	0.000	0	0.000	0.000
11							
12	Sum	759			R0	7.187	
13					G	98.172	
14					r	0.020	
15					lambda	1.020	
16							

Estimate m_x separately

Advantages and disadvantages of period life tables

- Advantages
  - Can estimate growth rate from age distribution of a single sample, at a point in time + reproductive estimates for each age
  - Don’t need to follow a cohort through its entire life
- Disadvantages
  - Assumptions are hard to meet, and the method is unreliable if they are violated
  - Better ways of estimating growth rate from demographic data are available, which we will learn next time