Today:

- Lecture (Finish Population 1 & 2)
- Overview of Exam 1
- In-class assignment today (last ~25min)
  - Hand in beginning of lecture Tuesday

Populations in space & time

- Distribution: spatial extent of a species
  - What shapes species/population boundaries?
    - LOTS of things. History, Physical/Environmental limitations, Biological interactions
  - Within a distribution, how do we classify the spatial arrangement—**Dispersion** of organisms?
    - CLUMPED→RANDOM→UNIFORM
- Abundance: number of individuals in a population
  - **DENSITY** = # per unit Area
  - Already discussed estimating this (mark-recapture)
  - What about following it through time?
  - **Population dynamics**

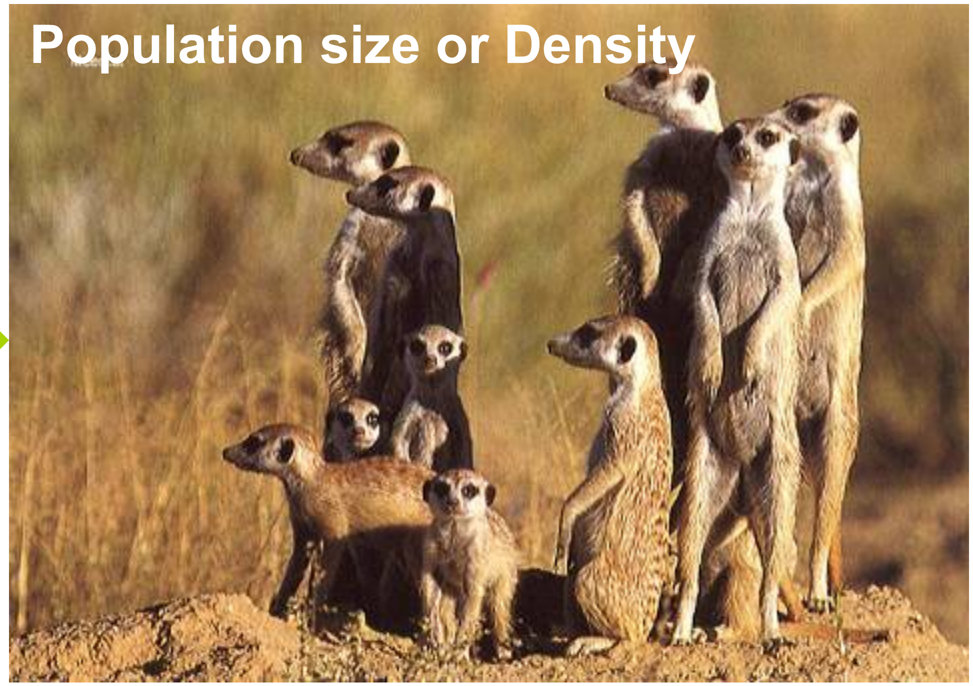
Population dynamics

- Abundance fluctuating through time
  - From last lecture: On average, one successful offspring per parent = Replacement rate = relatively stable population
    - Births (natality) = Deaths (mortality)
    - Emigration (out) = Immigration (in)

Demography: the study of these processes

Births

Immigration



Emigration

Deaths

General model of population growth:

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

Population dynamics

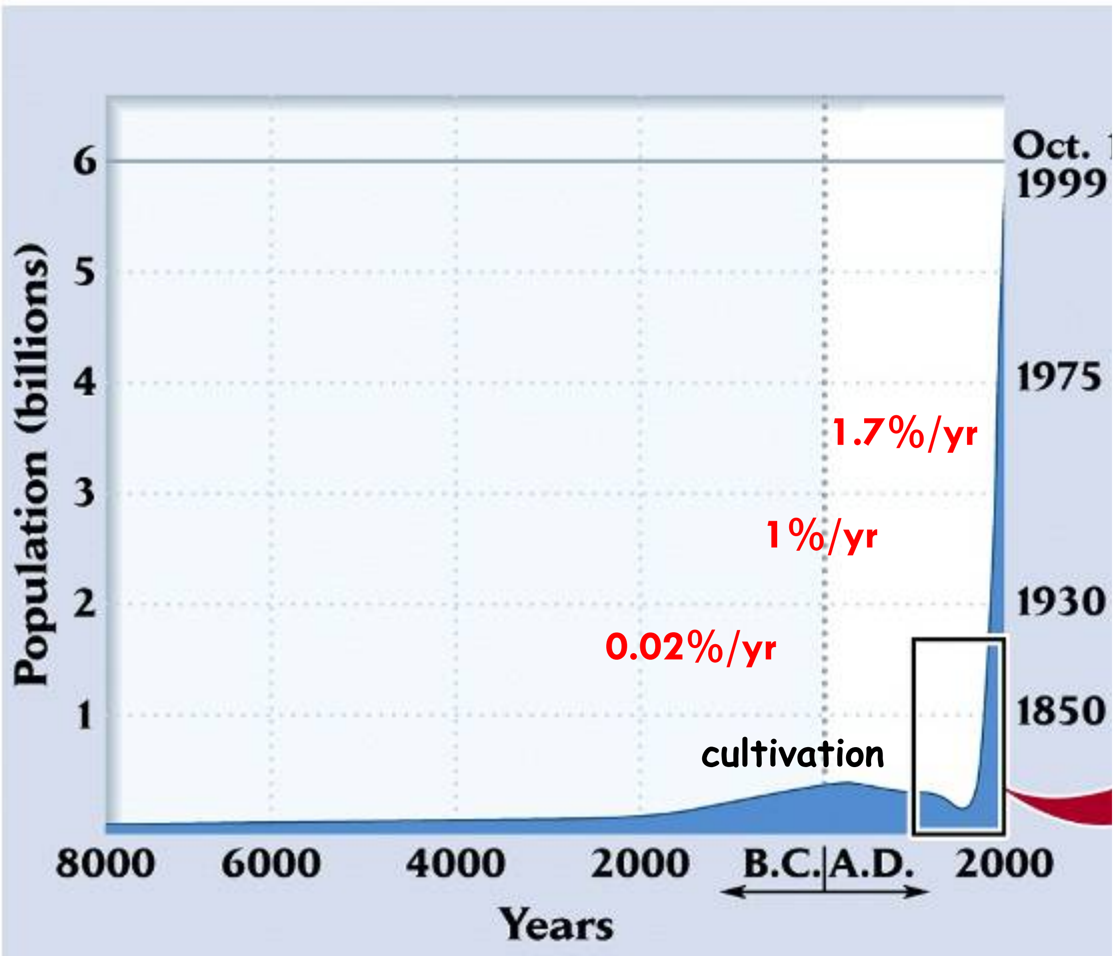
- Abundance fluctuating through time
  - From last lecture: On average, one successful offspring per parent = Replacement rate = relatively stable population
    - Births = Deaths
    - Emigration (out) = Immigration (in)
- Examples of
  - Rapid population growth?
    - Humans (special case)

How would you describe human population growth?

-what do we mean by exponential growth?

grows by a proportion of current population

(bigger pop contributes many more offspring)



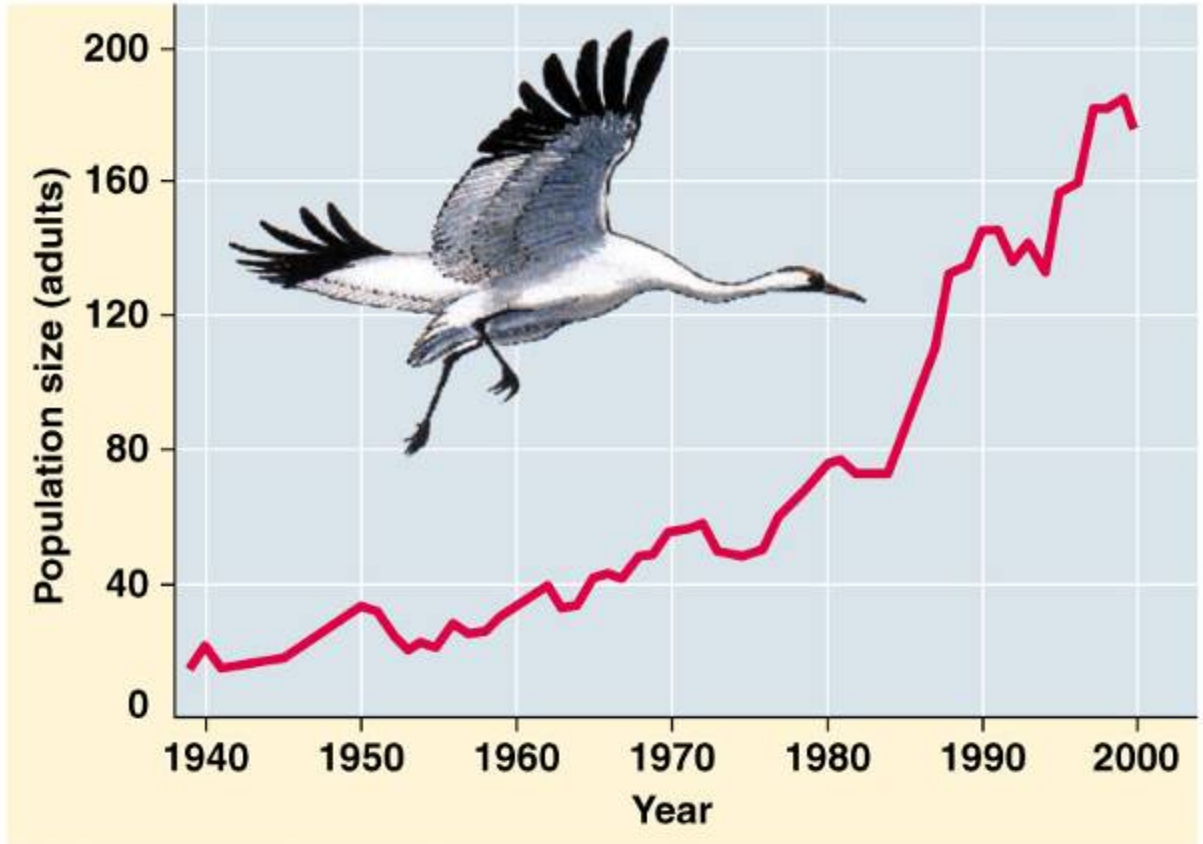
- **North Am. citizen uses six times more energy than the average person in the rest of the world**
- **4.7% of world population but 22% of carbon dioxide and CFC emissions**

Population dynamics

- Abundance fluctuating through time
  - From last lecture: On average, one successful offspring per parent = Replacement rate = relatively stable population
    - Births = Deaths
    - Emigration (out) = Immigration (in)
- Examples of
  - Rapid population growth?
    - Humans (special case)
    - Previously exploited species-now protected
      - But many never recover

Whooping Crane, *Grus americana*

Endangered Species



Why so low?

Sport hunting

Draining of wetlands

Collision with powerlines

Why recovering?

No more hunting

Captive breeding program

Migration corridor/wetlands still a problem

Population dynamics

- Abundance fluctuating through time
    - From last lecture: On average, one successful offspring per parent = Replacement rate = relatively stable population
        - Births = Deaths
        - Emigration (out) = Immigration (in)
- Examples of
    - Rapid population growth?
        - Humans (special case)
        - Previously exploited species-now protected
        - Newly introduced species

Scot's broom

Zebra mussel

Nutria

European starling

Population dynamics

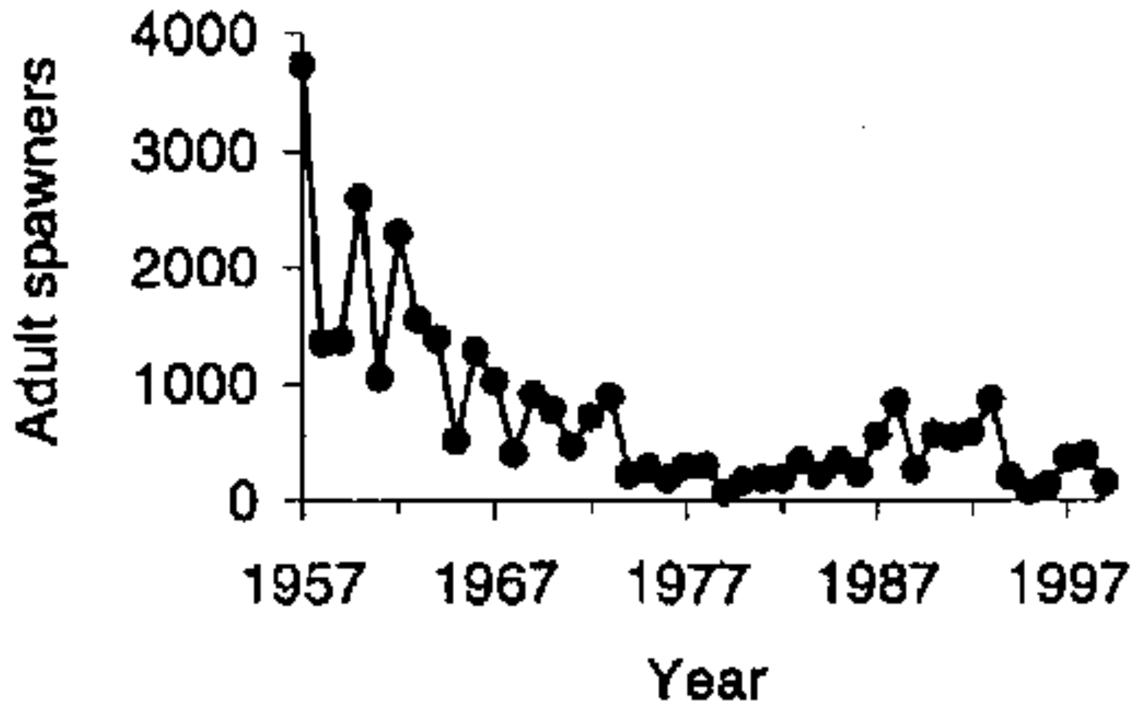
- Abundance fluctuating through time
  - From last lecture: On average, one successful offspring per parent = Replacement rate = relatively stable population
    - Births = Deaths
    - Emigration (out) = Immigration (in)
- Examples of
  - Rapid population growth?
  - Rapid population decline?
    - Currently exploited species
    - Endangered species
    - Songbirds, large mammals, amphibians…

Columbia River Chinook salmon

US listing as ‘endangered’

A quagmire of likely contributors:

harvest, hatcheries, habitat, hydropower, and politics



Kareiva et al. 2000 Science

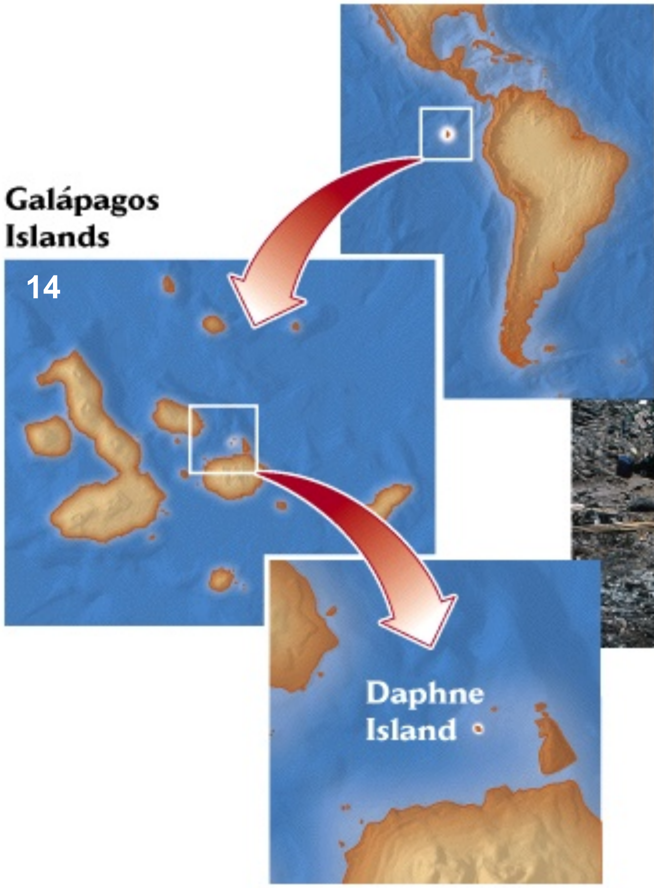
Characterizing population dynamics

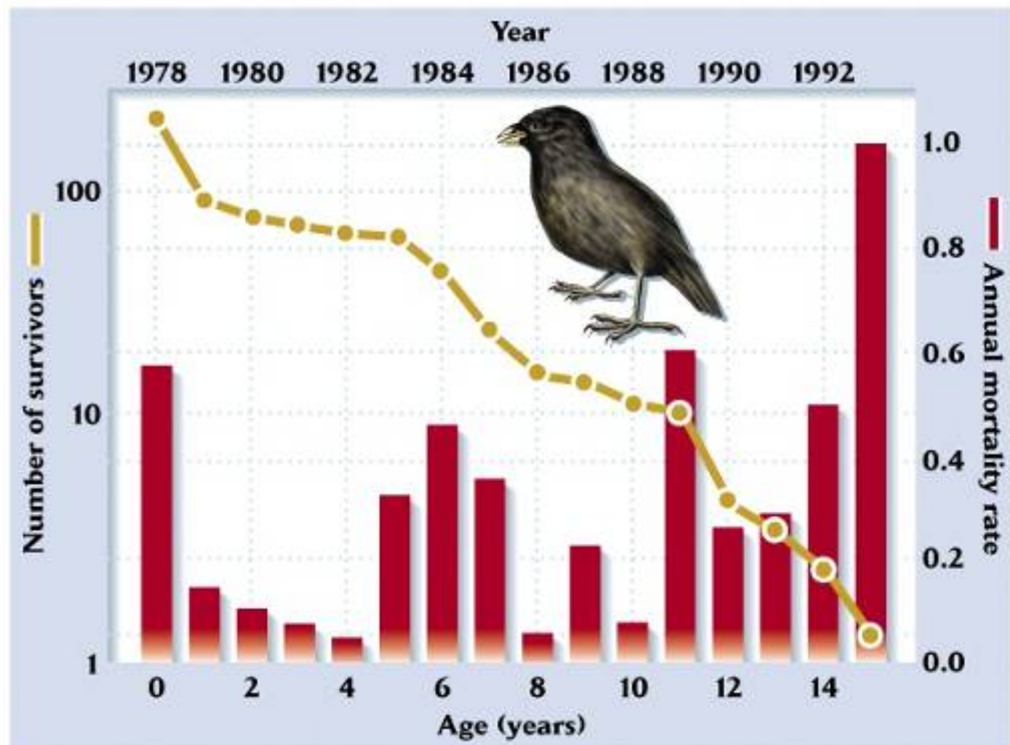
How fast does a population increase/decrease? (rate of change, population growth rate)

What will the population size be next year? (management)

- **Need to summarize Births & Deaths (age structure) of a population**
- **Cohort Life Table-follow one group from birth until the last one dies**
  - What kind of information might this give us?
    - How cohort numbers decline over time
    - Age specific survival
    - Age specific fecundity

Cohort Life Table Example





Followed entire cohort of Cactus finches born in 1978

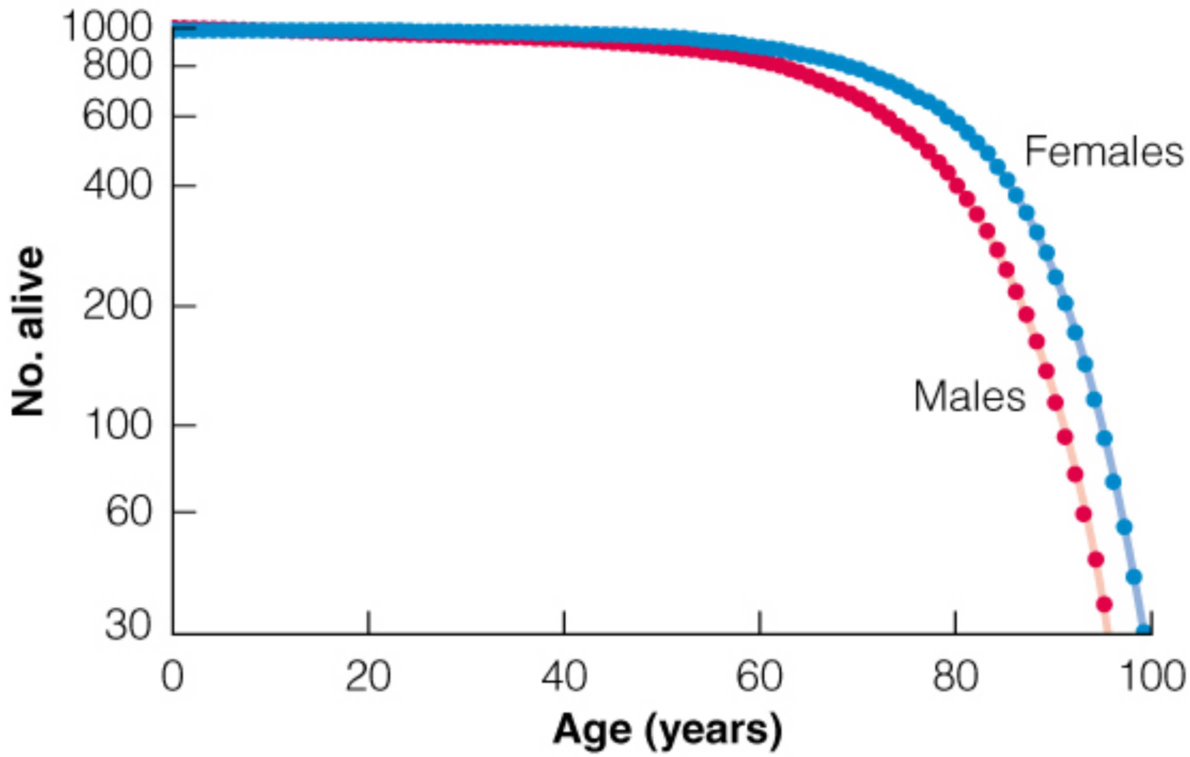
Last one died in 1993

…this method is SLOW for long-lived organisms!

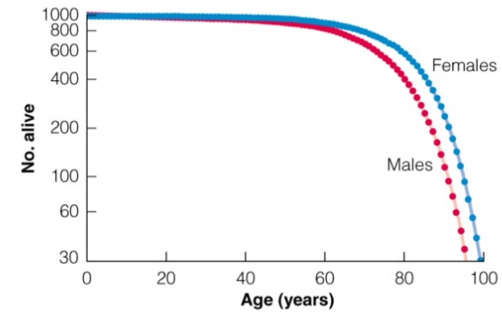
…also difficult to follow highly mobile organisms

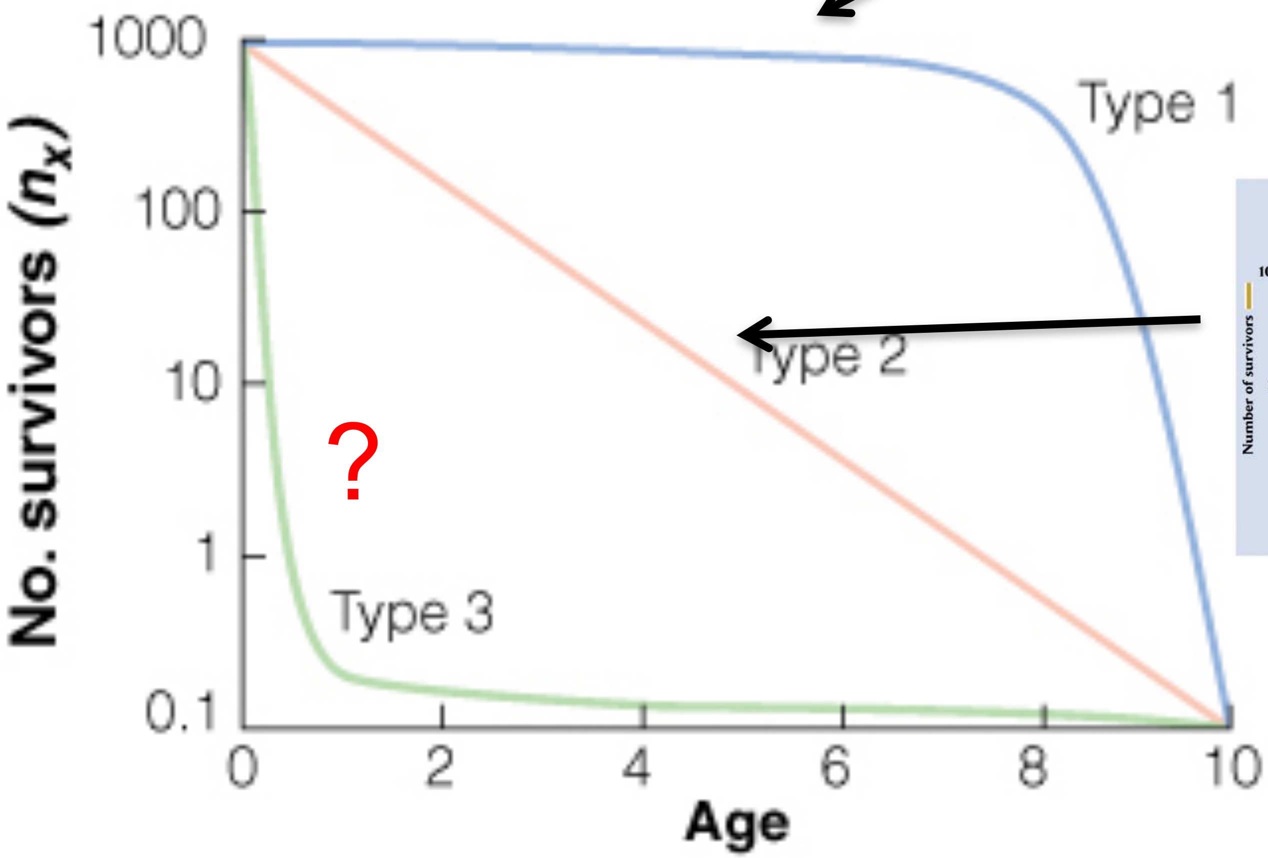
Cohort 'schedule' for humans

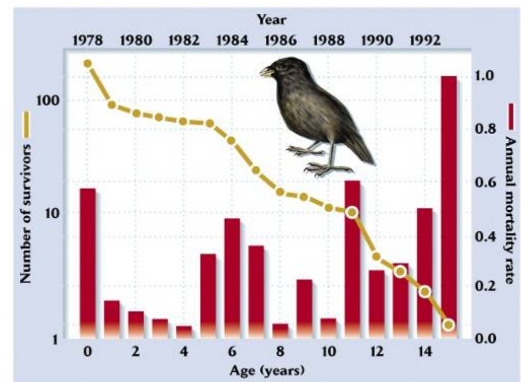
followed 1000 individuals from birth to death



Survivorship curves







(a)

Characterizing population dynamics

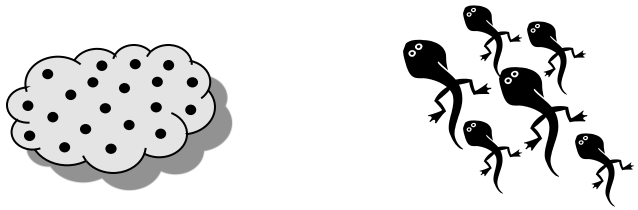
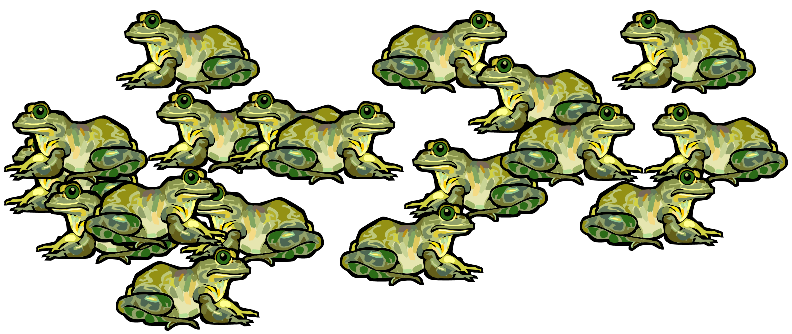
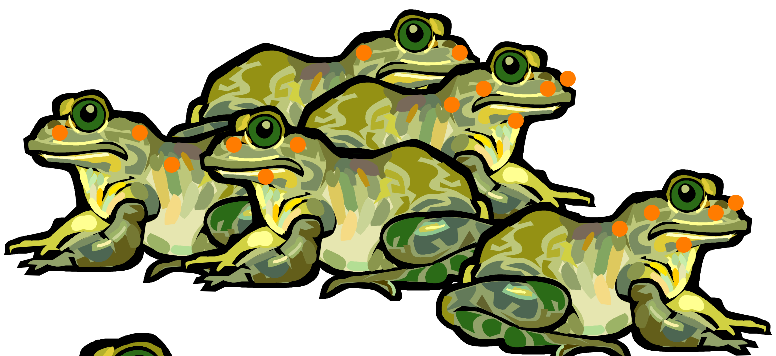
- Need to summarize Births & Deaths (age structure) of a population

- Cohort Life Table-follow one group from birth until the last one dies

- Static Life Table-census population for abundance in each age/stage multiple times – to estimate survival and reproductive output by age/stage

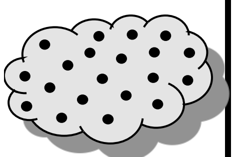
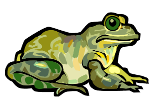
  - Limitations?
    - Must be able to age/stage each organism (not so easy)

Cohort life table for Cascades frog

	Survival schedule	Fecundity
	100 eggs (some live to be tadpoles)	0
	25 grow and survive to become metamorphs	0
	5 grow and survive to become young frogs, try to reproduce	20 eggs
	3 grow and survive to become older frogs, reproduce then die	50 eggs

Cohort life table for Cascades frog

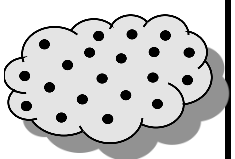
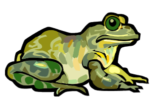
In this case the time step between ages is 1 year

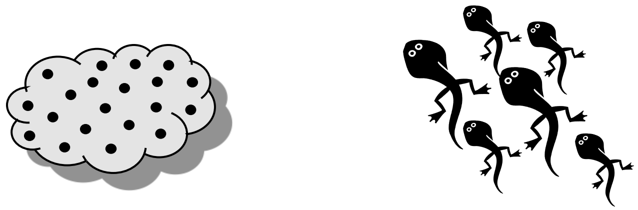
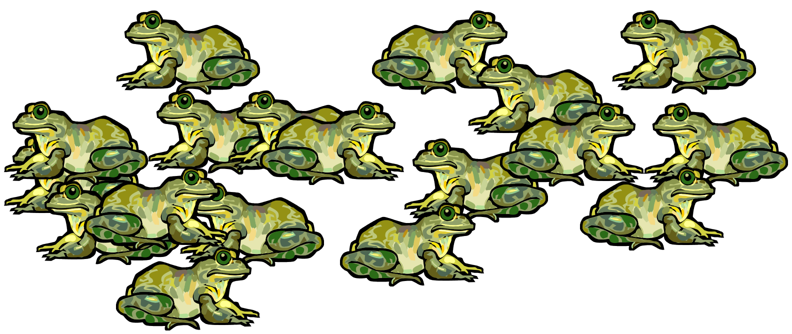
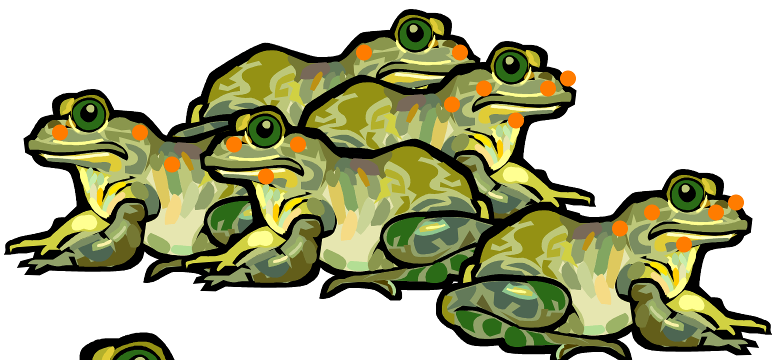
Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100			
1	25			
2	5			
3	3			

Cohort life table for Cascades frog

In this case the time step between ages is 1 year

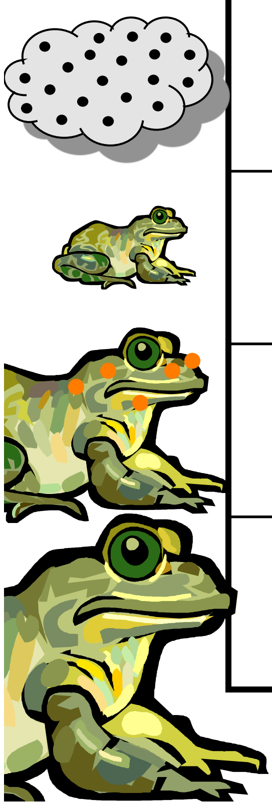



Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100			0
1	25			0
2	5			20
3	3			50

	Survival schedule	Survival (s_x)
	100 eggs (some live to be tadpoles)	=25/100
	25 grow and survive to become metamorphs	=5/25
	5 grow and survive to become young frogs, try to reproduce	=3/5
	3 grow and survive to become older frogs, reproduce then die	What goes here?

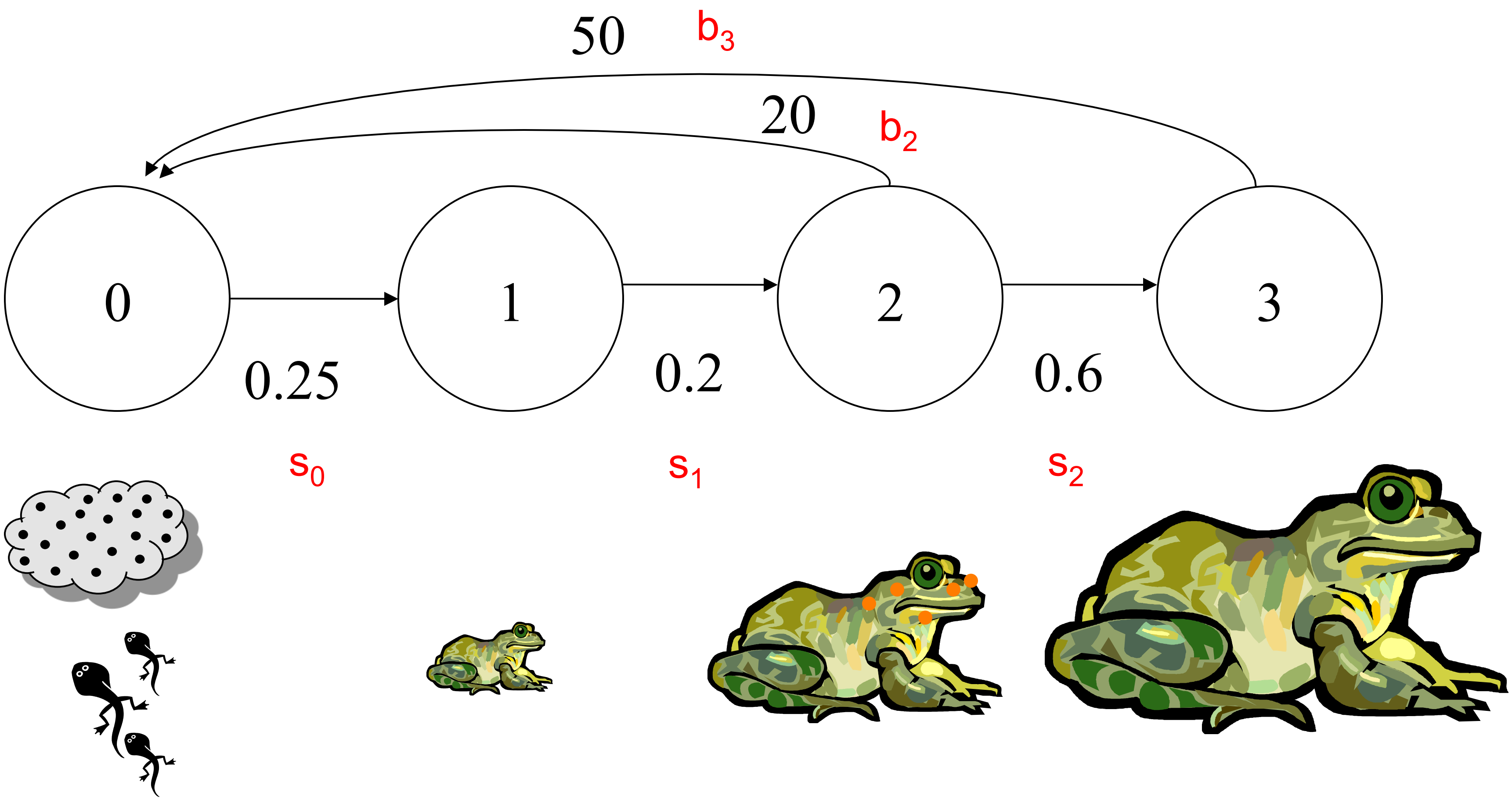
Cohort life table for Cascade frog

Survival from x to x+1



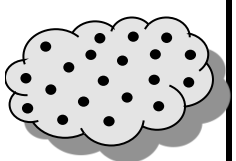
Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100		0.25	0
1	25		0.2	0
2	5		0.6	20
3	3		n/a	50

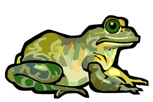
Compare to life history diagram

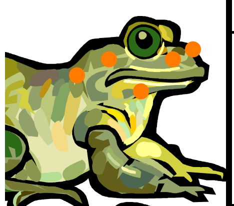


Cohort life table for Cascades frog

Survival from birth up to x



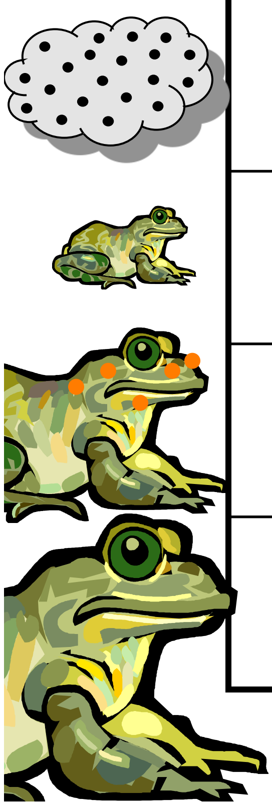




Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100	1	0.25	0
1	25		0.2	0
2	5		0.6	20
3	3		n/a	50

Cohort life table for frog example

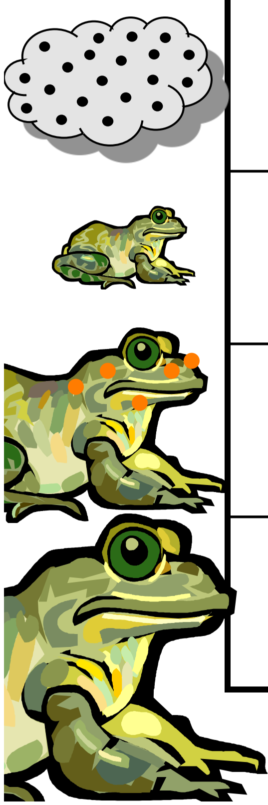
Survival from birth up to x



Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100	1	0.25	0
1	25	0.25	0.2	0
2	5		0.6	20
3	3		n/a	50

Cohort life table for frog example

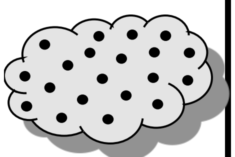
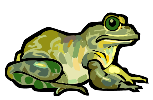
Survival from birth up to x



Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100	1	0.25	0
1	25	0.25	0.2	0
2	5	0.05	0.6	20
3	3		n/a	50

Cohort life table for frog example

Ok. Now what do we do with this??

Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)
0	100	1	0.25	0
1	25	0.25	0.2	0
2	5	0.05	0.6	20
3	3	0.03	n/a	50

Life table terms

- x = age
- n_x = number alive at age x
- l_x = survivorship up to age x (proportion living)
- s_x = survival rate from age x to age x+1
- b_x = fecundity (births) at age x

- Want to know if on average each individual replaces itself…

Called the net reproductive rate

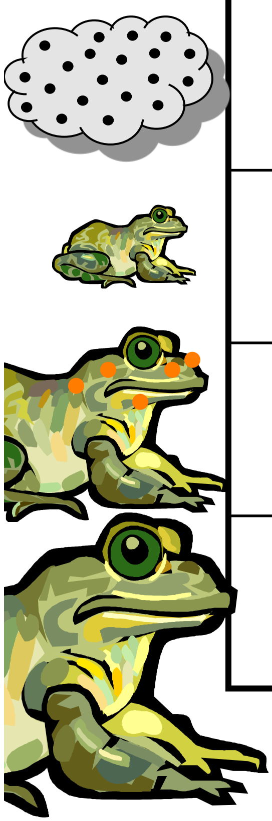
Net reproductive rate

- R_0
  - "R nought"
  - net reproductive rate, that is, number of offspring produced by average individual over her entire lifetime (or generation)

- $R_0 = \Sigma\, l_x\, b_x$

- In words: *The probability of making it to each age, times the fecundity at that age, summed across all ages (lifetime)*

Cohort life table for frog example



Age (x)	Number alive (n_x)	Survivorship (l_x)	Survival rate (s_x)	Fecundity (b_x)	$l_x b_x$
0	100	1	0.25	0	0
1	25	0.25	0.2	0	0
2	5	0.05	0.6	20	0.05 x 20 = 1
3	3	0.03	n/a	50	0.03 x 50 = 1.5

$R_0 = \Sigma\, l_x\, b_x$ =2.5

Net reproductive rate

- R_0 does not determine population growth rate, which depends on both how many and when offspring are produced
  - Offspring produced earlier lead to higher population growth
  - Why?
  - So, changes in age structure lead to changes in population growth rate
- Need to include average age at which an individual gives birth (generation time)

  G = generation time = $\Sigma\, x\, l_x b_x / \Sigma\, l_x b_x$

  For frog example, G =(6.5)/(2.5) = 2.6

  - These time steps need not be "years" but in this case they are

Estimate intrinsic rate of population growth

- $r_a = \ln(R_0) / G$

- For frog example:

$\ln(2.5)/2.6 =$

$(0.92)/2.6 =$

0.35

$r > 0$ population growing
$r = 0$ population stable
$r < 0$ population declining

What does this say about the population of Cascades frogs??


naturalvisions.co.uk

Population dynamics

- How to quantitatively describe population change?
  - Estimate R_0, r_a from life-table
  - Simple population growth (decline) models
    - Estimate the rate of change with time
  - 1. Geometric
  - 2. Exponential
  - 3. Logistic
    - Remember that these are all *models*
- We'll work through some examples
- IN-CLASS Exercise (~25 min)

From last lecture:

Births

Immigration

Emigration

Deaths

General model of population growth:

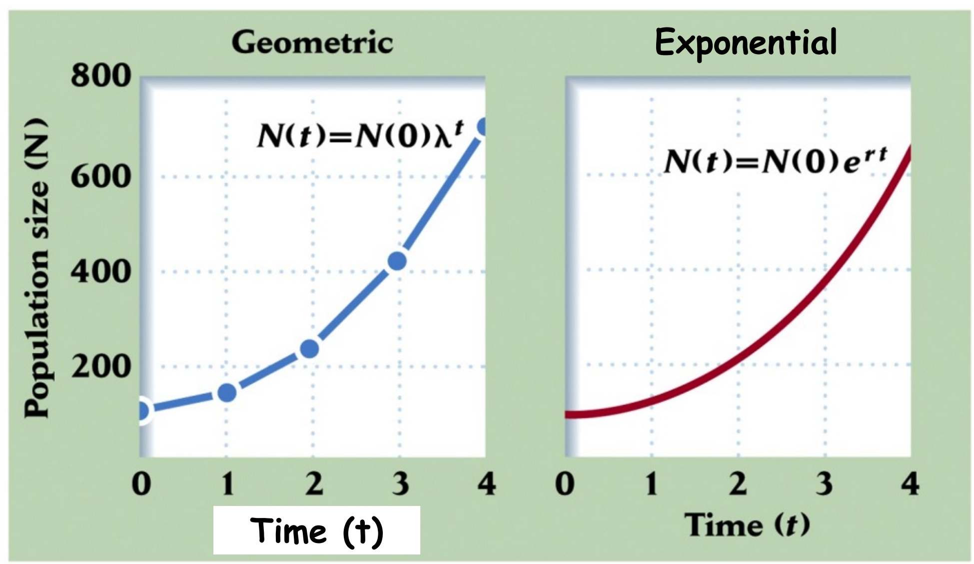
$$N_{t+1} = N_t + B_t - D_t + \cancel{I_t} - \cancel{E_t}$$

Population dynamics

- Simple models describe how idealized populations would grow in an infinite environment…
- Is the population growing "un-checked" over the short term?
  - If yes, then density-independent model may be reasonable approx.

- Two forms:
  - Geometric
  - Exponential

•Two options: 1) increase to infinity or 2) decrease to zero….just a matter of time (rate)



Geometric growth

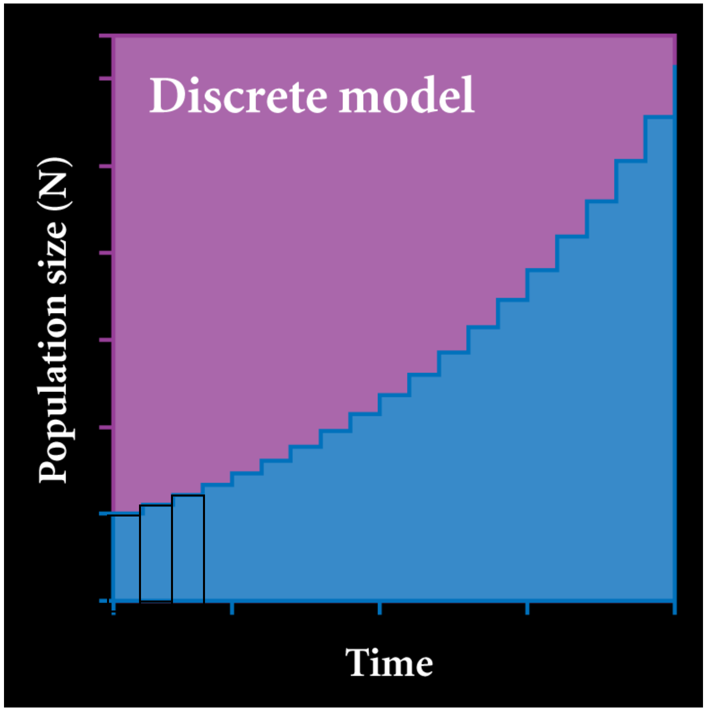
•Populations reproduce only at limited times—say once a year (results in stair step changes).

•How do we describe the RATE of change with time?

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

λ is the rate of geometric pop'n growth (proportional increase)

$$\lambda = N_{t+1} / N_t$$



•Density-independent
(λ does not change with pop size)
•Resources not limiting

Exponential growth

•Populations reproduce continuously—results in smooth changes in population size with time.

•How do we describe the RATE of change with time?

$$dN/dt = rN$$

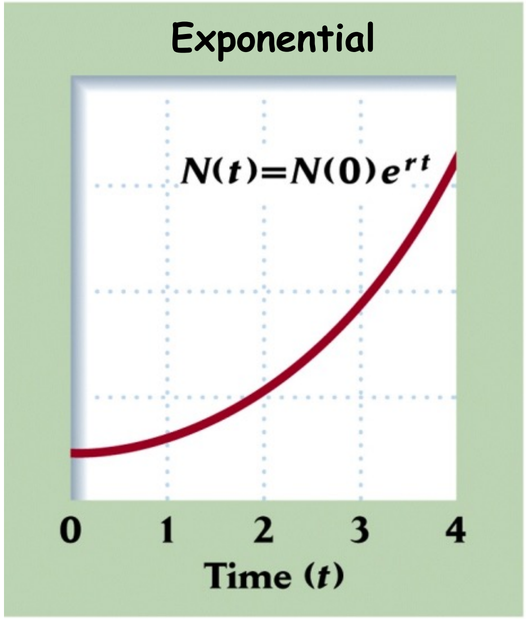
r is the per capita growth rate (per individual increase)

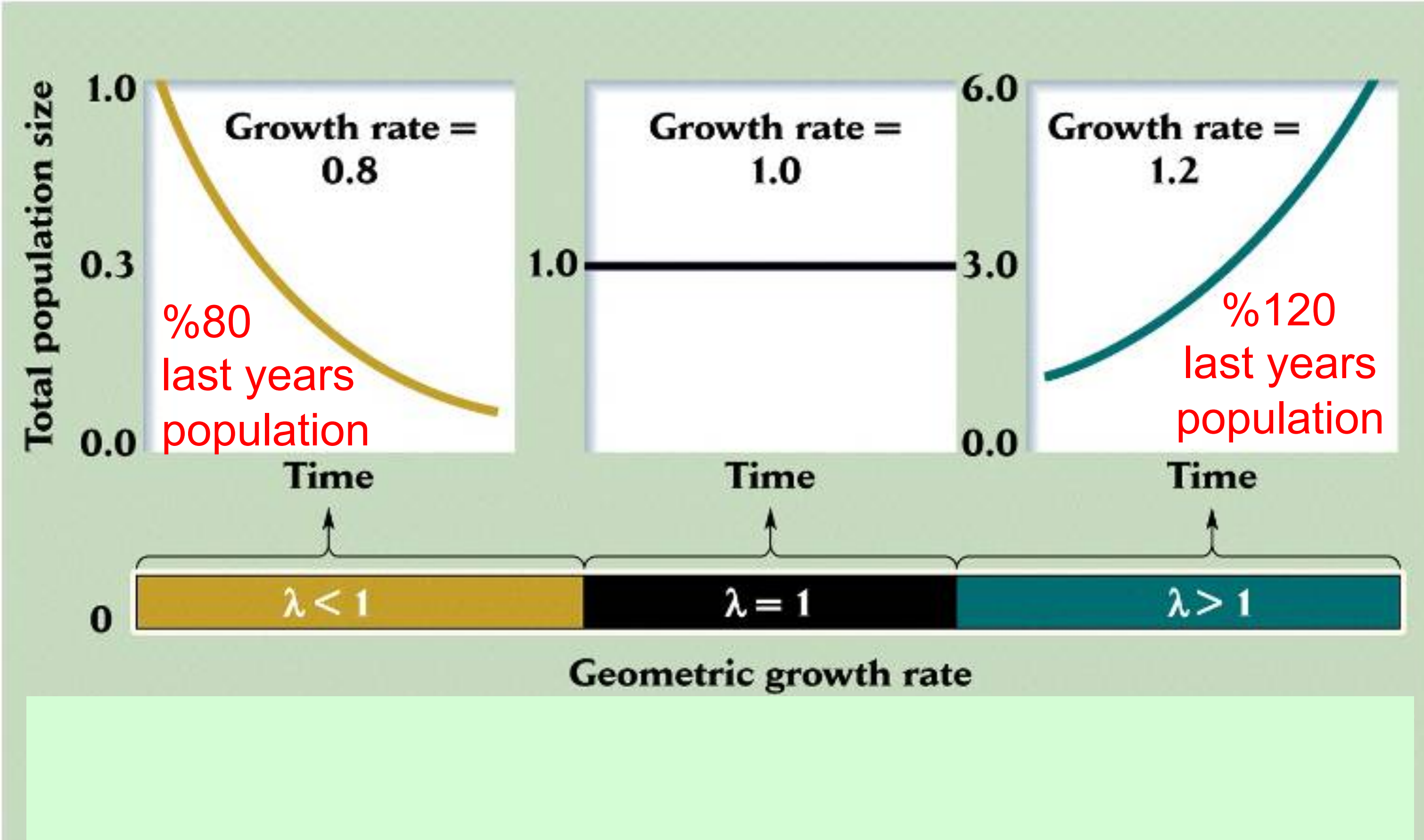
Can be re-written in discrete time (integrated)

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

•Density-independent (r does not change with pop size)

•Resources not limiting

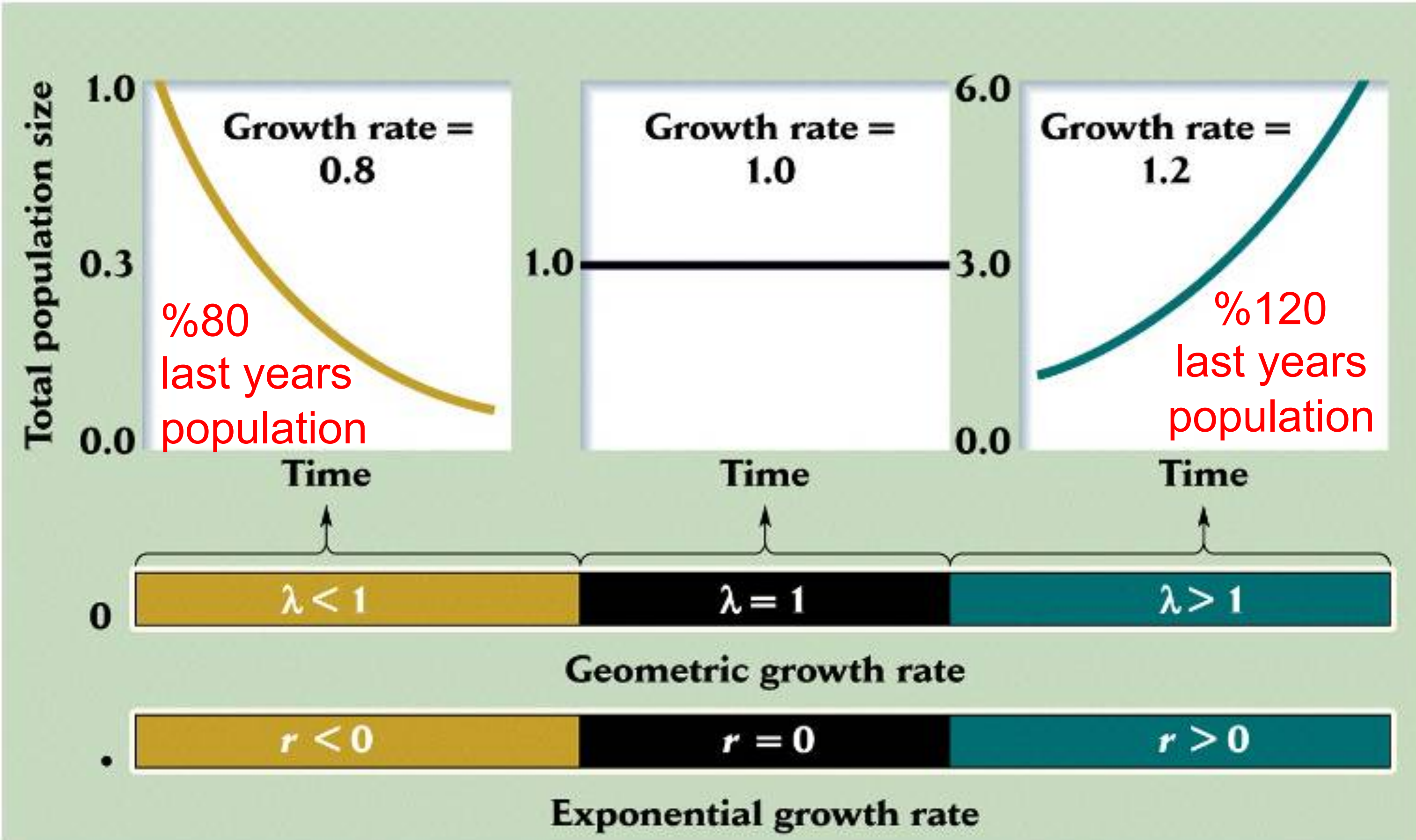




$N_{t+1} = N_t\lambda$

where λ measures the proportional change in the population (varies between 0-infinity)

Figure 14.6



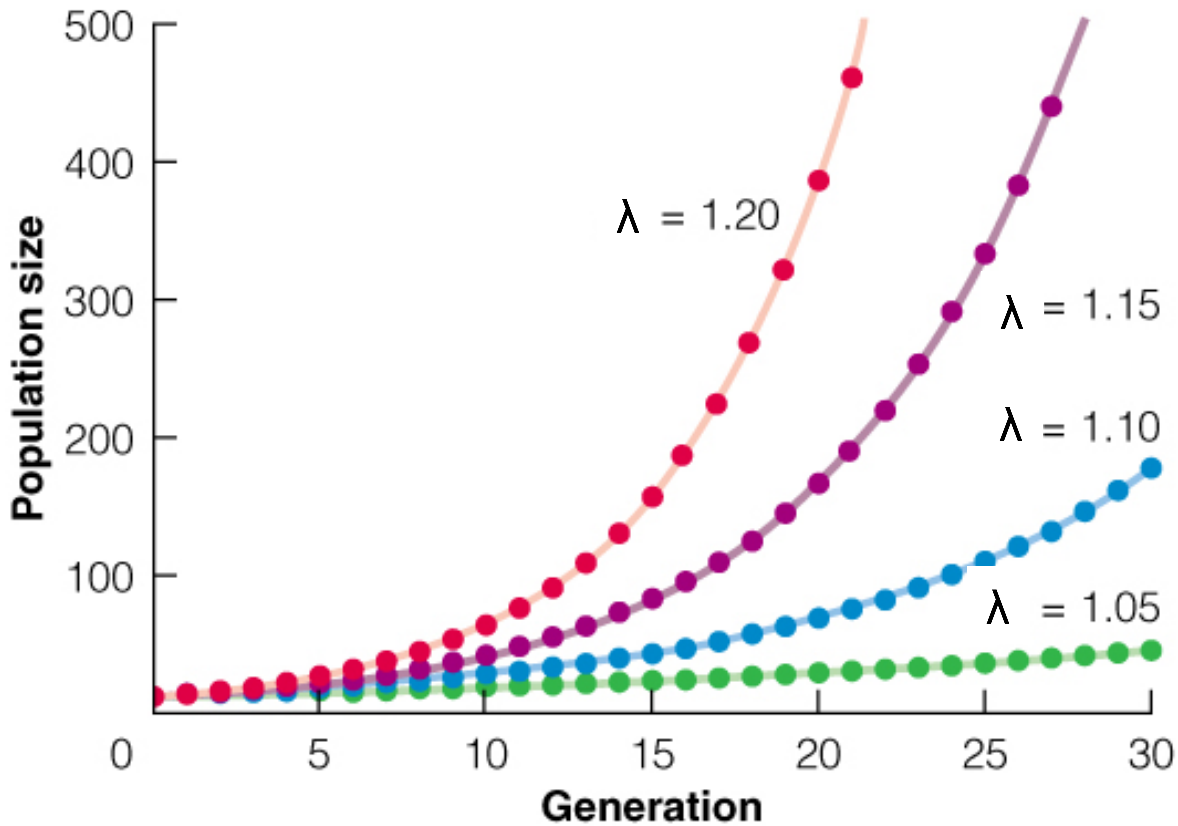
$N_t = N_0 e^{rt}$

where r measures the rate of population change (varies between ±infinity)

Geometric and exponential equations are roughly interchangeable because $r = \ln(\lambda)$

Figure 14.6

Increasing the rate of geometric population growth (λ)



Okay, but we know most populations don't grow unchecked!

Limits on Population Growth

- Density Dependent Limits?
  - Food/prey
  - Water
  - Shelter, nest sites, territories
  - Disease
  - Mates
- Density Independent Limits?
  - Weather
    - Includes stochastic events: hurricanes, fires
  - Climate
    - But sometimes climate effects become density dependent….example: El nino in the Galapagos Is.

Logistic Population Growth

•Exponential population growth with a limit

growth rate diminishes as limit is approached

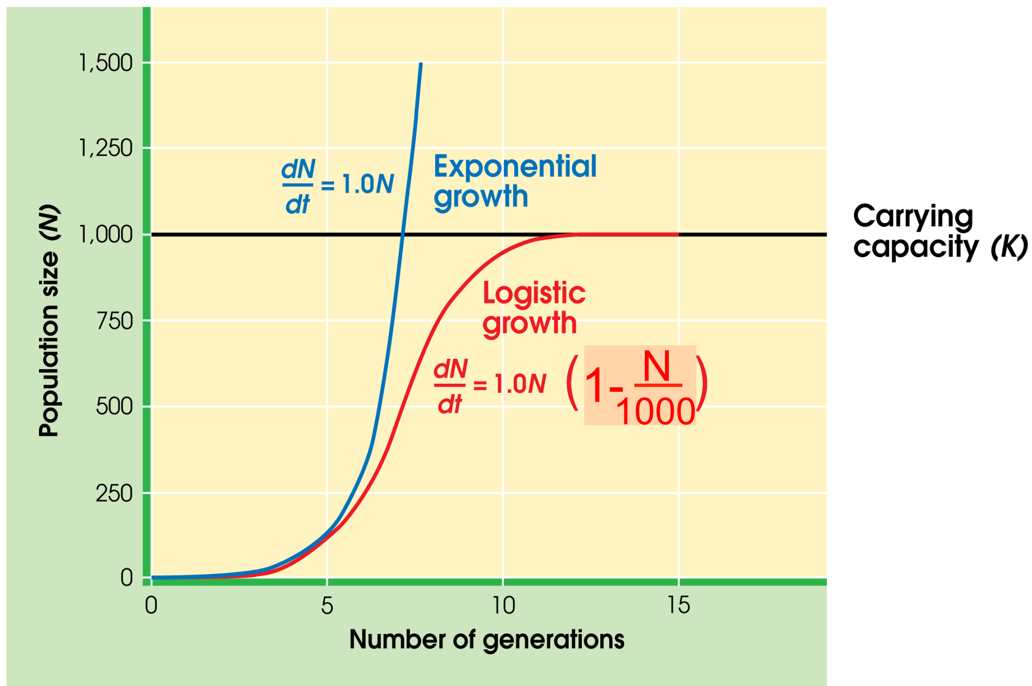
Carrying capacity (K) = max # individuals that can be supported in the environment

$$dN/dt = r_0 N(1 - N/K)$$

r_0 is the equivalent of the exponential growth rate

$$r_{realized} = r_0 (1 - N/K)$$

rate of growth slows to zero as K is reached



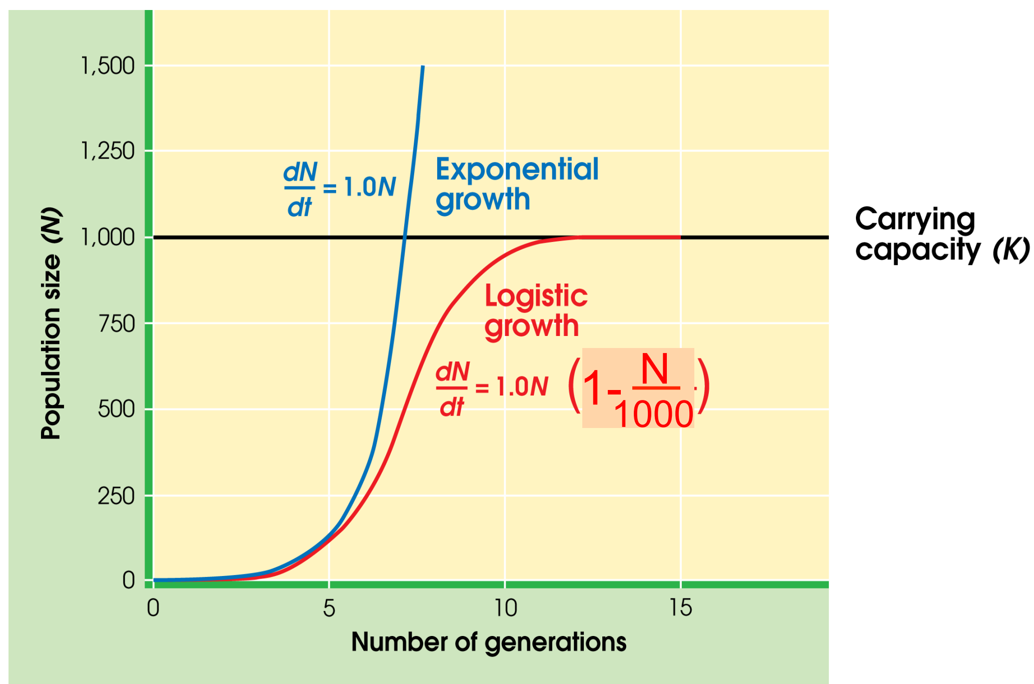
Logistic Population Growth

$$dN/dt = r_0 N\,(1 - N/K)$$

Can be written in discrete form:

$$N_t = \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right) e^{-rt}}$$

This is burdensome….but appreciate that we could project a population next year if we knew N this year, r, and K.



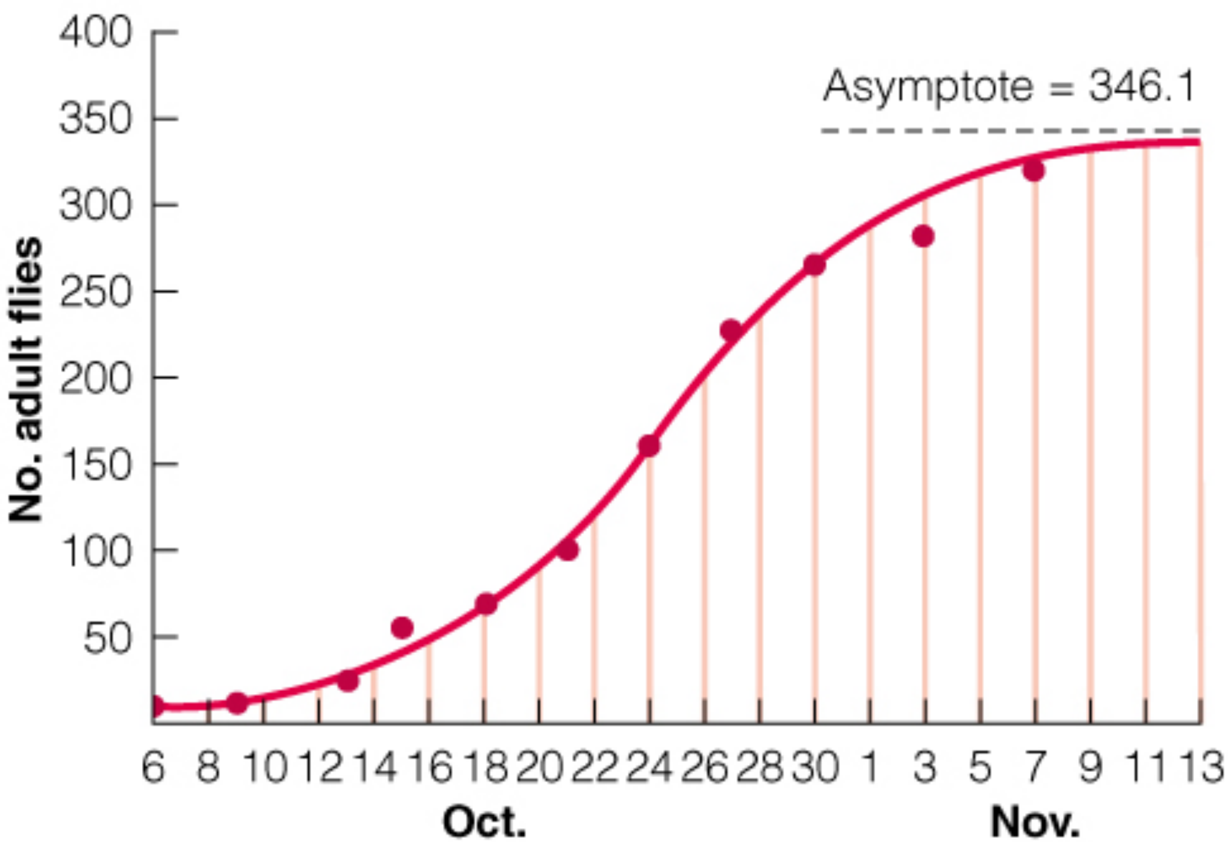
How to recognize density dependence

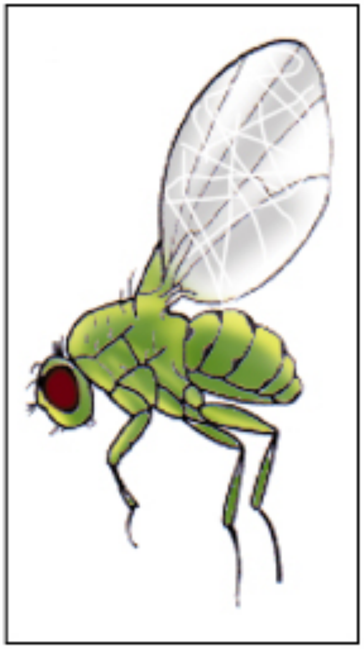
- Manipulate density of an organism
  - Record individual performance across a range of densities (growth, survival, reproduction)
    - Pearl (1927) as a classic example

- Or, observe the success of individuals as a function of the number of adults.
  - Examples-reproduction:
    - Fisheries stock-recruit relationships
    - Song sparrows

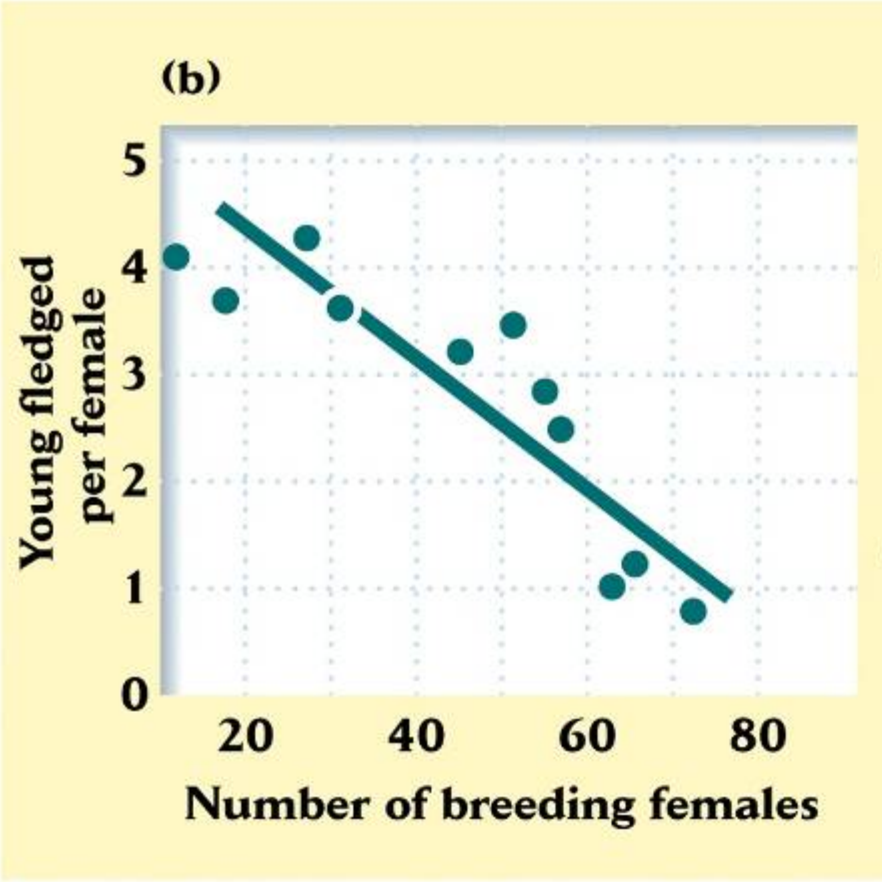
One of the first laboratory 'tests' Pearl (1927)

Maintained *Drosophila* colonies in bottles with fixed amount of yeast



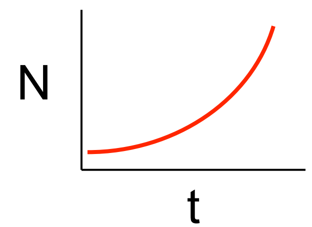


Density dependence in Song sparrows



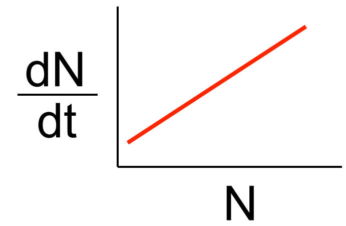
Ways to look at simple dynamics of populations
(density dep. & density indep.)

1. Time series
   - Number of individuals (N) at each time t



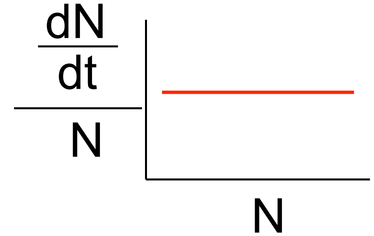
2. Population rate of change
   - $dN/dt = N_{t+1} - N_t$

   # New added versus pop' n size (N)



3. Per capita rate of change
   - $dN/dt/N = (N_{t+1} - N_t)/N_t$

   Does pop' n growth rate change with N?

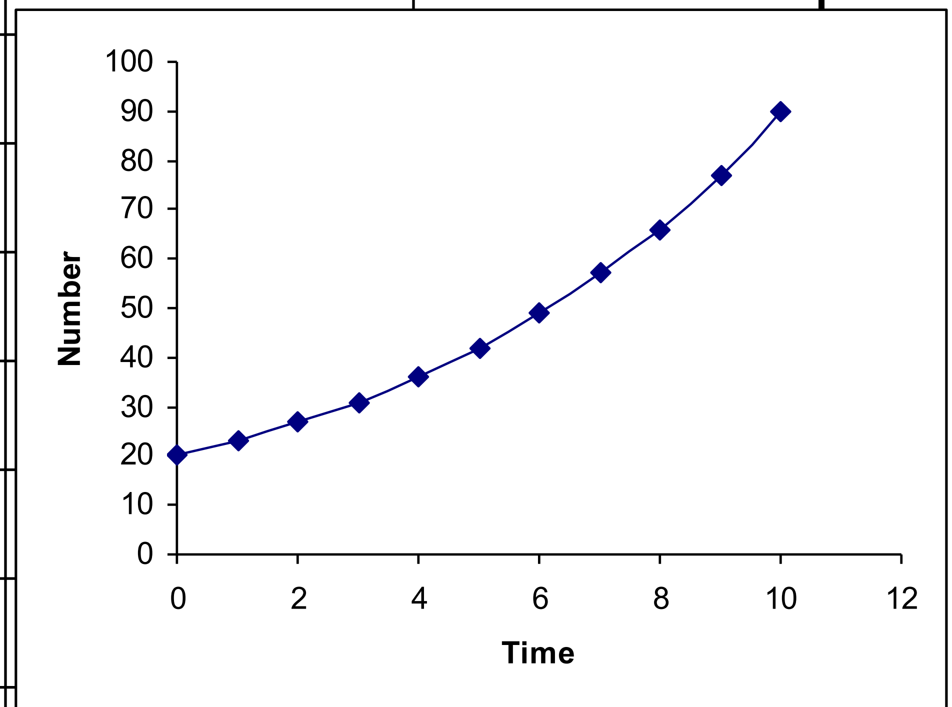


Geometric increase

Time	N	dN/dt	dN/dt/N
0	20		
1	23		
2	27		
3	31		
4	36		
5	42		
6	49		
7	57		
8	66		
9	77		

Geometric increase

Time	N	dN/dt	dN/dt/N
0	20		
1	23		
2	27		
3	31		
4	36		
5	42		
6	49		
7	57		
8	66		
9	77		

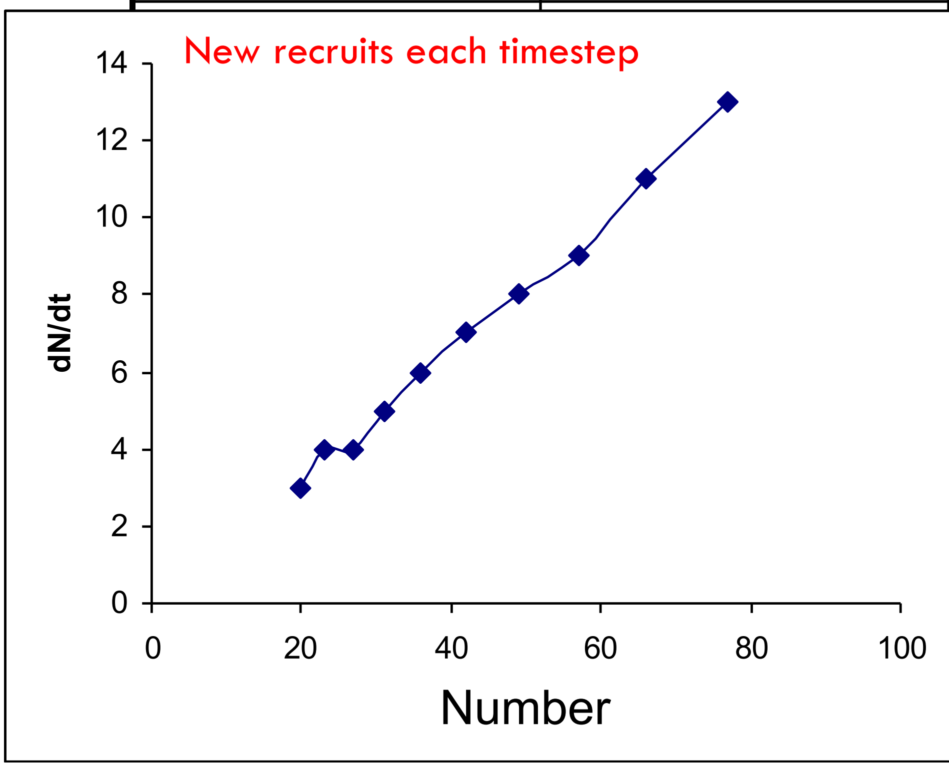


Geometric increase

Time	N	dN/dt	dN/dt/N
0	20	23-20 = 3	
1	23	27-23 = 4	
2	27		
3	31		
4	36		
5	42		
6	49		
7	57		
8	66		
9	77		

Geometric increase

Time	N	dN/dt	dN/dt/N
0	20	23-20 = 3	
1	23	27-23 = 4	
2	27	4	
		5	
		6	
		7	
		8	
		9	
		11	



Geometric increase

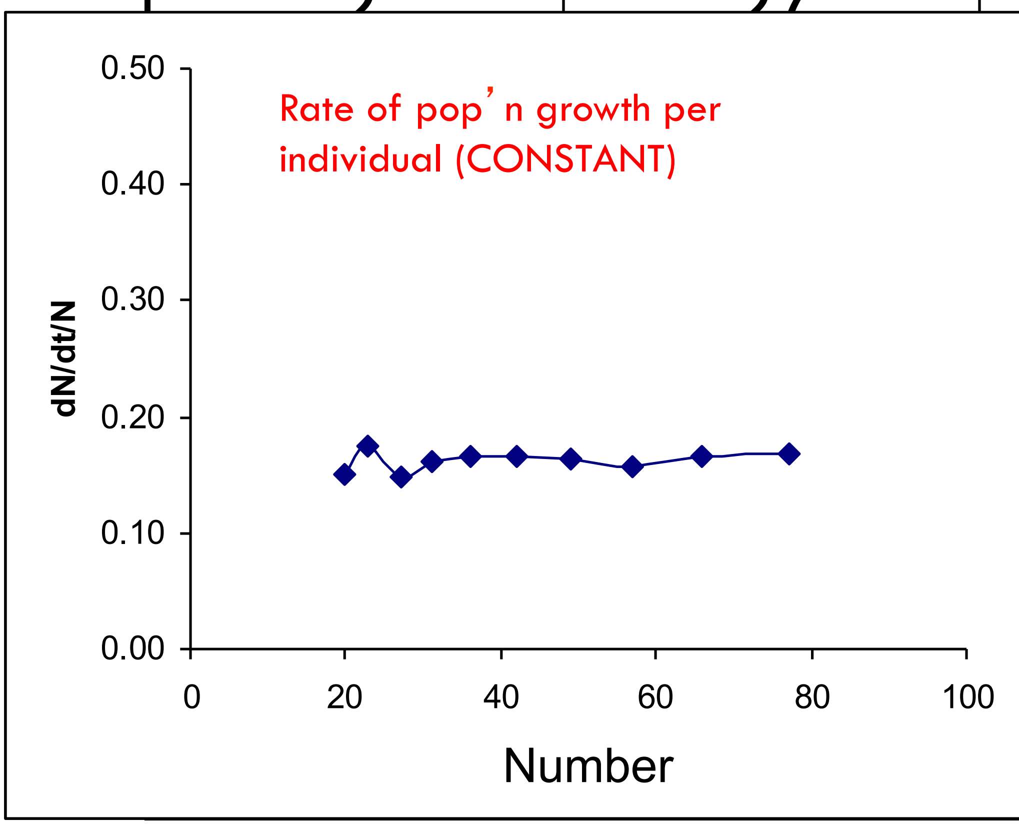
Time	N	dN/dt	dN/dt/N
0	20	3	3/20 =0.15
1	23	4	4/23=0.17
2	27	4	4/27=0.15
3	31	5	
4	36	6	
5	42	7	
6	49	8	
7	57	9	
8	66	11	
9	77		

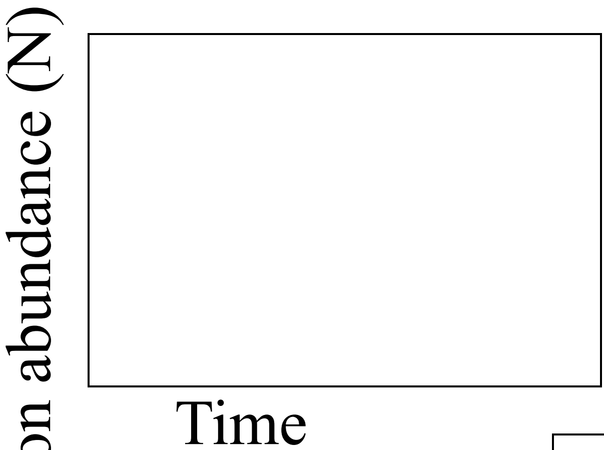
Geometric increase

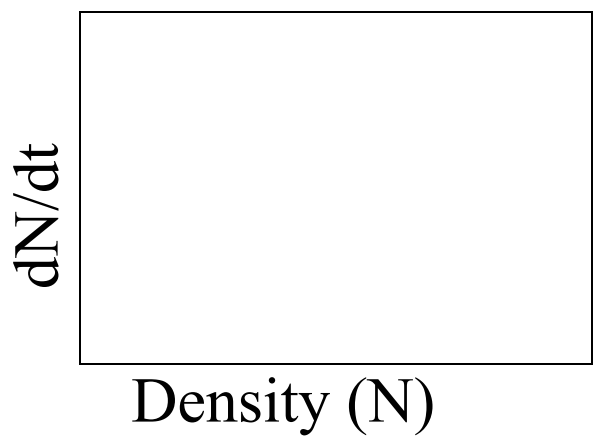
Time	N	dN/dt	dN/dt/N
0	20	3	3/20 =0.15
1	23	4	4/23=0.17
2	27	4	4/27=0.15
3	31	5	0.16
4	36	6	0.17
5	42	7	0.17
6	49	8	0.16
7	57	9	0.16
8	66	11	0.17
9	77		

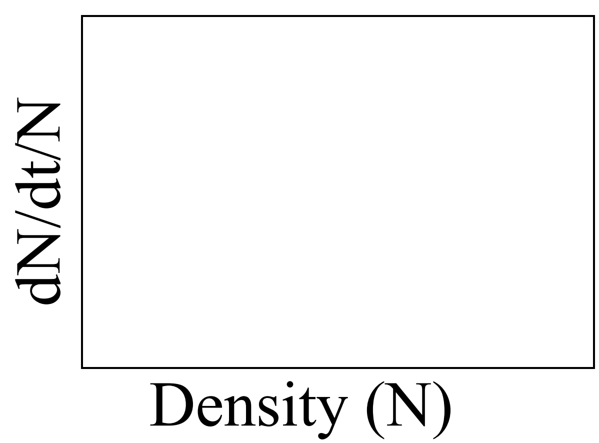
Geometric increase

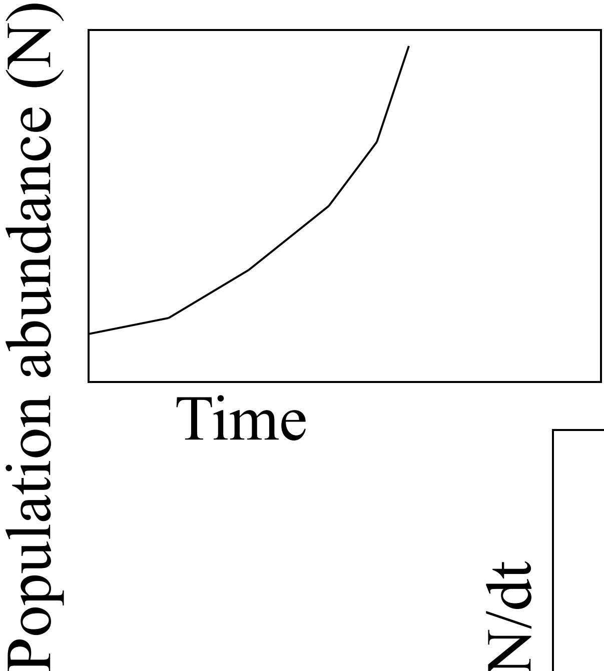
Time	N	dN/dt	dN/dt/N
0	20	3	3/20 =0.15
1	23	4	4/23=0.17
2	27	4	4/27=0.15
[illegible]	[illegible]	5	0.16
[illegible]	[illegible]	6	0.17
[illegible]	[illegible]	7	0.17
[illegible]	[illegible]	8	0.16
[illegible]	[illegible]	9	0.16
[illegible]	[illegible]	11	0.17




Population abundance (N)
Time

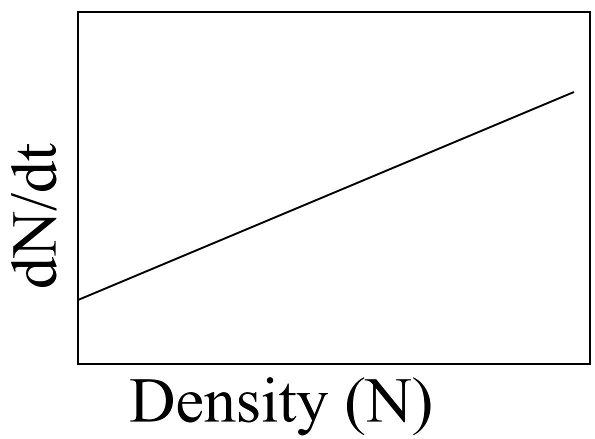

dN/dt
Density (N)


dN/dt/N
Density (N)

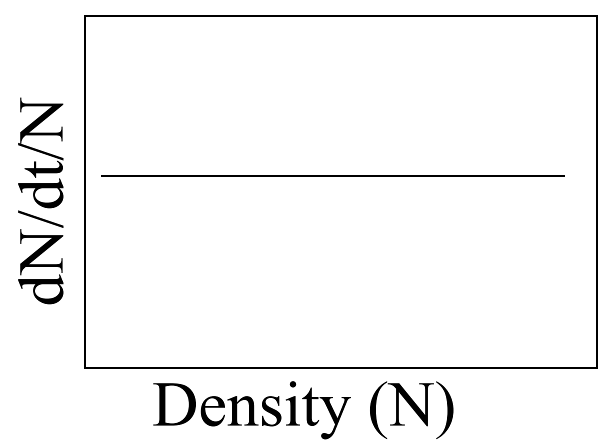


Geometric Population Growth

(same pattern for exponential)



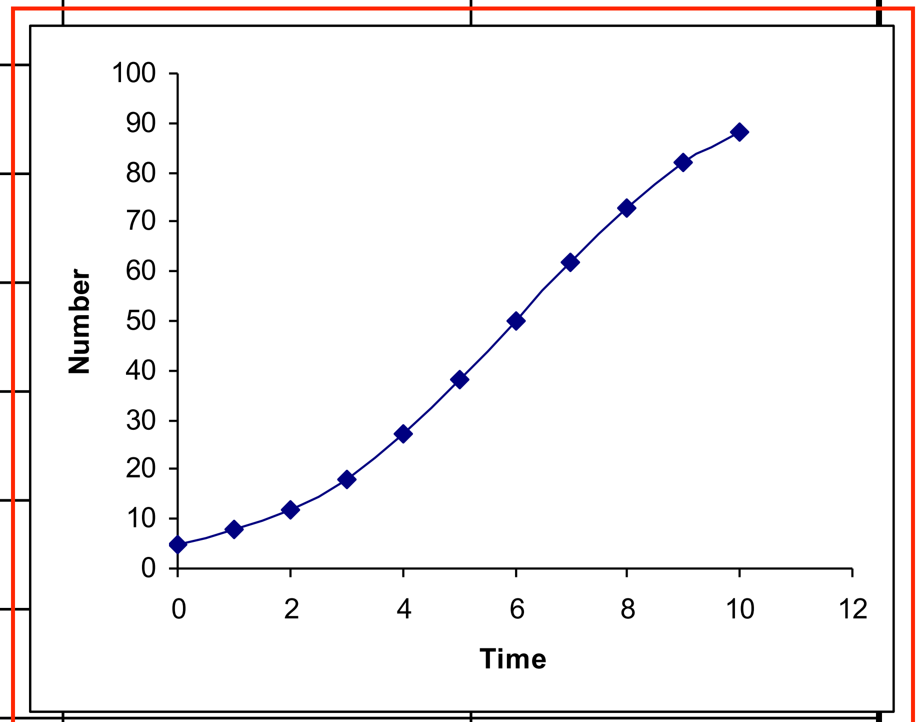
Accelerating population increase



Constant per capita increase

Logistic

Time	N	dN/dt	dN/dt/N
0	5		
1	8		
2	12		
3	18		
4	27		
5	38		
6	50		
7	62		
8	73		
9	82		

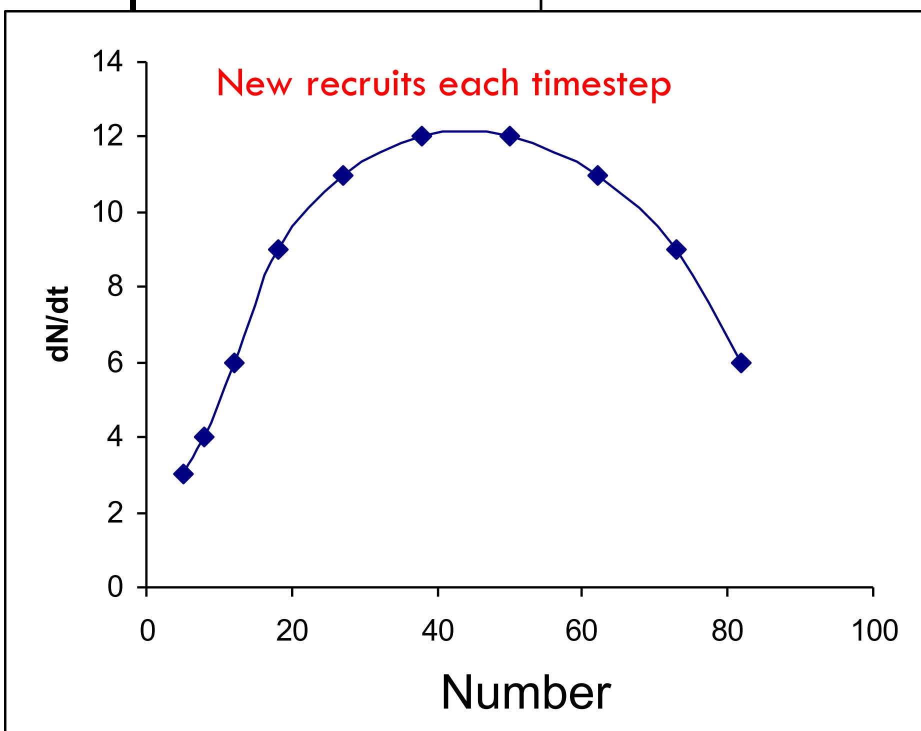


Logistic

Time	N	dN/dt	dN/dt/N
0	5	8-5=3	
1	8	12-8=4	
2	12		
3	18		
4	27		
5	38		
6	50		
7	62		
8	73		
9	82		

Logistic

Time	N	dN/dt	dN/dt/N
0	5	8-5=3	
1	8	12-8=4	
2	12	6	
		9	
		11	
		12	
		12	
		11	
		9	
		6	

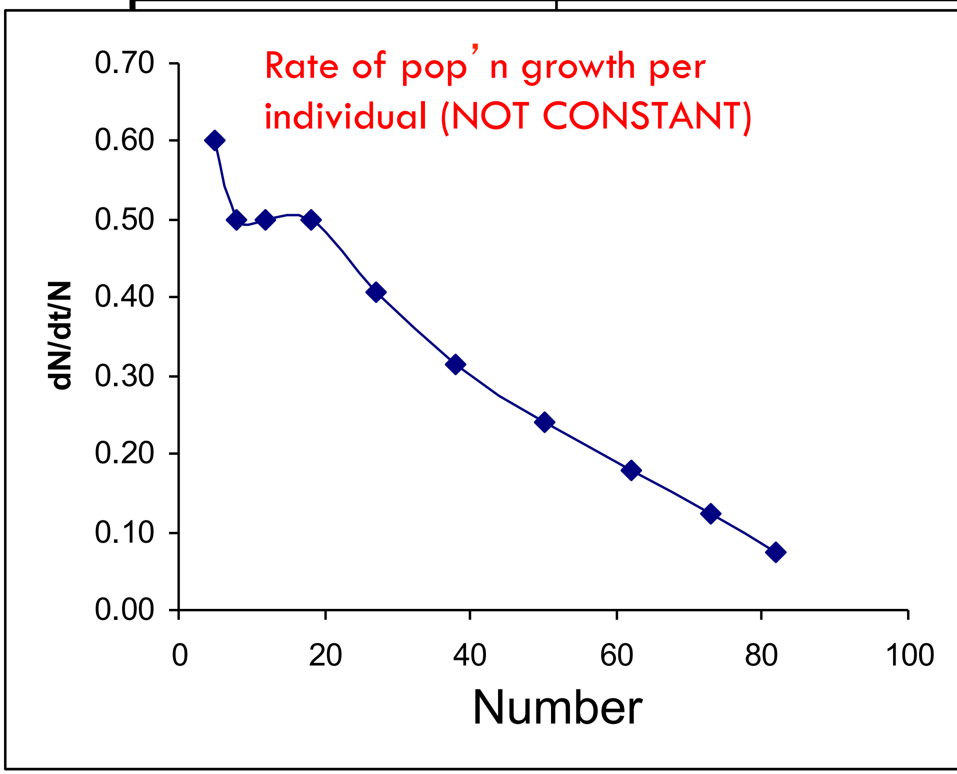


Logistic

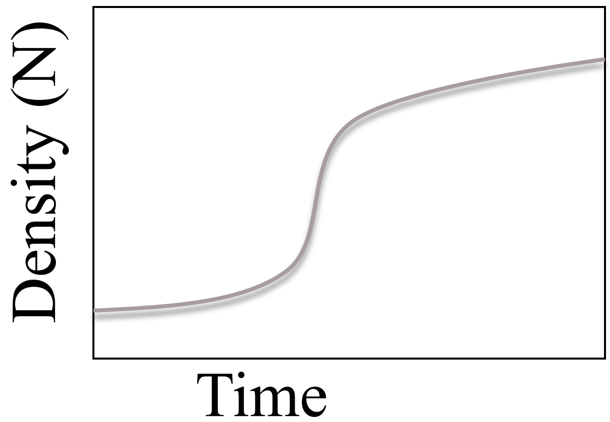
Time	N	dN/dt	dN/dt/N
0	5	3	3/5=0.6
1	8	4	4/8=0.5
2	12	6	6/12=0.5
3	18	9	
4	27	11	
5	38	12	
6	50	12	
7	62	11	
8	73	9	
9	82	6	

Logistic

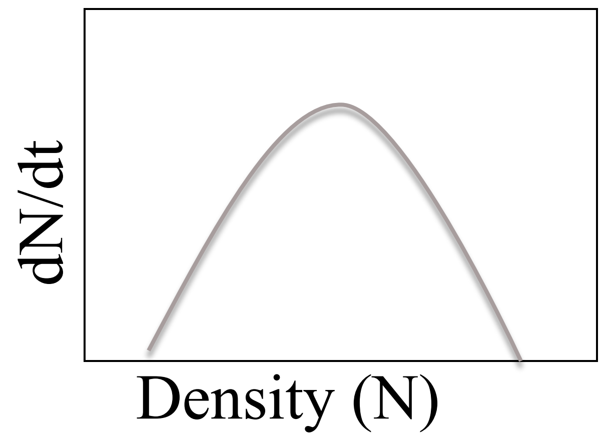
Time	N	dN/dt	dN/dt/N
0	5	3	3/5=0.6
1	8	4	4/8=0.5
2	12	6	6/12=0.5
		9	0.5
		11	0.4
		12	0.32
		12	0.24
		11	0.18
		9	0.12
		6	0.07



Logistic Population Growth



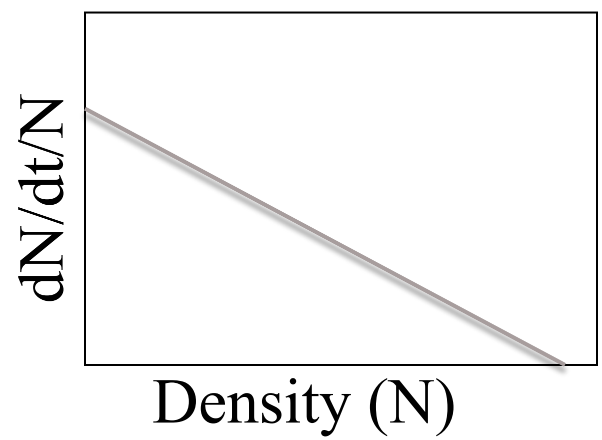
Population
Rate of
Change



Highest population increase at intermediate densities

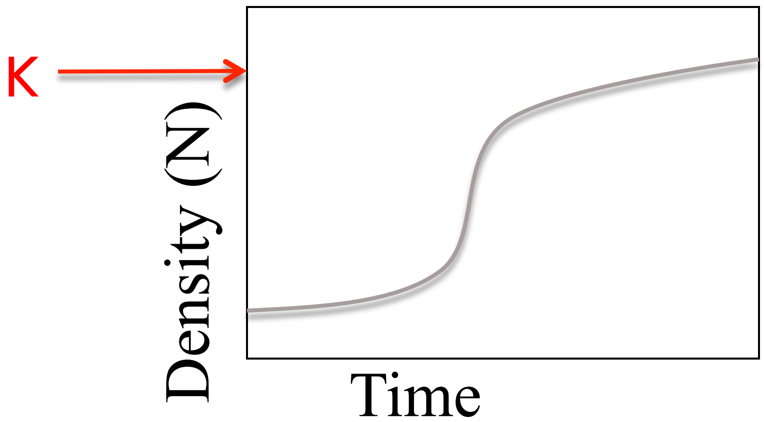
Declining per capita contribution

Per
Capita
Rate of
Change



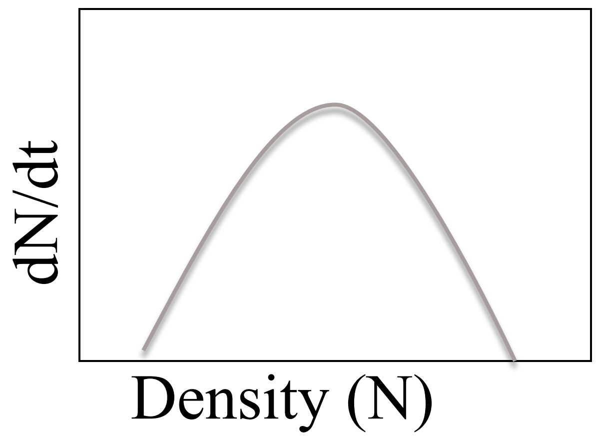
Logistic Population Growth

K = carrying capacity
(max # individuals that can be supported in the environment)

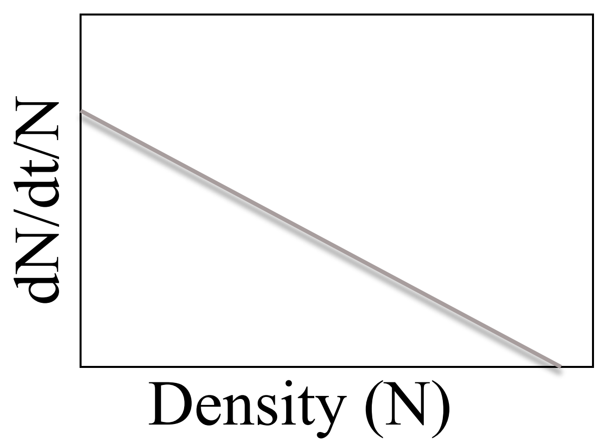


Where is K in each graph?

Population Rate of Change



Per Capita Rate of Change



1st Exam

- **Expectations:**
  - Non-programmable calculator permitted (**no cell phones**)
  - Closed book
  - Sign an 'honor pledge' on your exam
    - *"I did not give or receive aid on this exam"*
  - 1 hour 50 minutes time limit (designed to take ~1hr)
  - Mix of questions: short answer, fill in the blank, graphical interpretation, calculations, 1-2 longer or multi-part questions

1st Exam

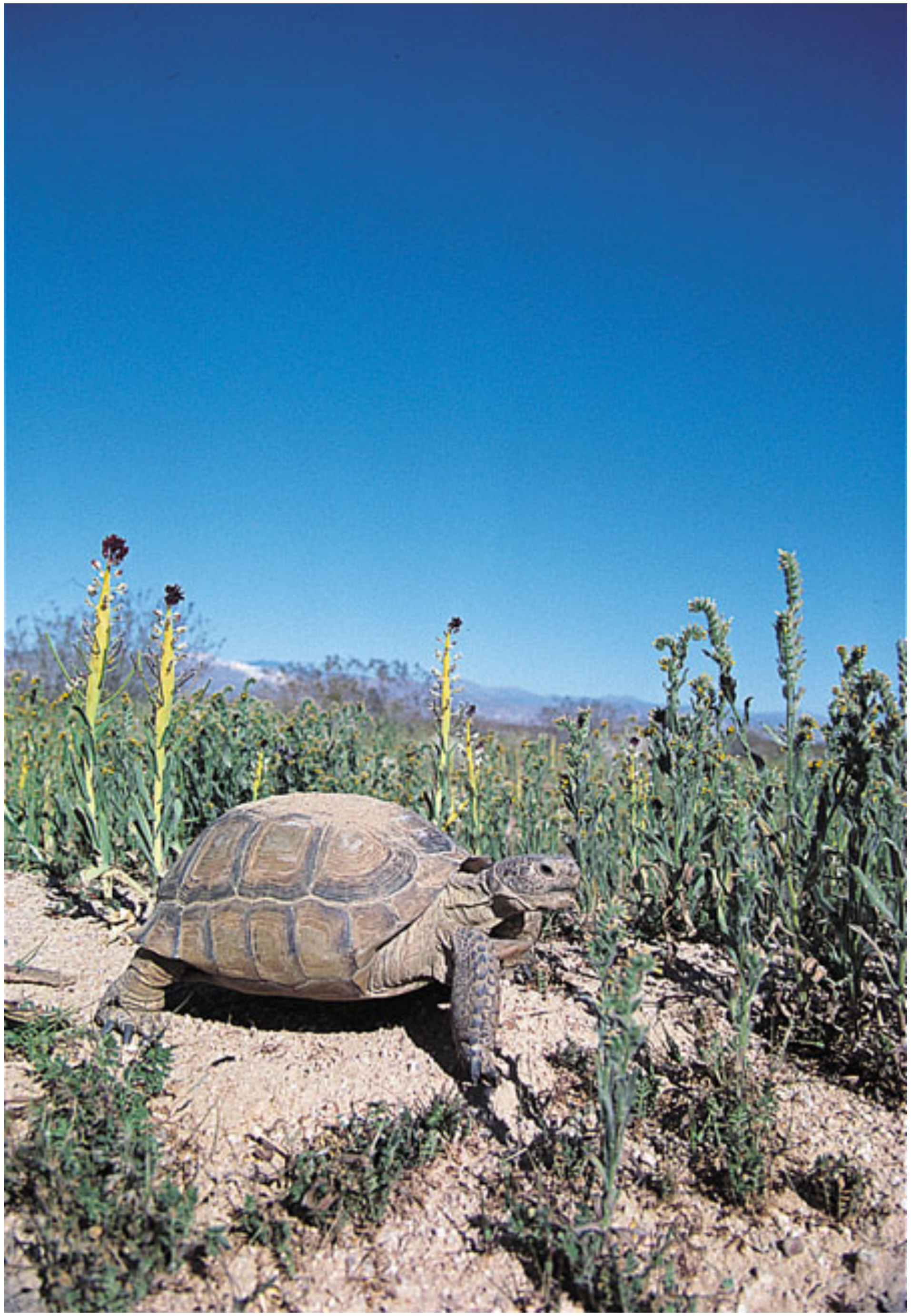
- **What to study?**
  - Lecture notes, in-class assignments
  - Book is for your reference only
  - Use posted slides to refresh your memory.

- **Have questions?**
  - Use tutorials, office hours
    - Please do not ask for a 1:1 meeting unless you have used all other avenues
  - Be as specific as possible
  - Don't wait until the last minute!
  - Do not expect urgent emails to be answered

***Please be respectful in your interactions with me and your TA's**

In class assignment

- Work in groups of ~4
- Fill out separate worksheets
- Use the definitions and equations on your handout
- Hand in Tuesday @ beginning of lecture



Desert tortoises, *Gopherus spp.*

- Federally listed in 1990
- Dramatic declines in population density (~90%) occurred between 1970-1990's (especially breeding females)
- Ecologically important "ecosystem engineer"--creates habitat for many other desert critters
- ~30% of carcasses recovered showed mortality due to gunshots
- Other factors (all human facilitated):
    - Collection as pets
    - Off-road vehicle crushing
    - Introduced respiratory disease
    - Increased predation by ravens
    - Habitat fragmentation

Desert tortoise range, *Gopherus agassizii*

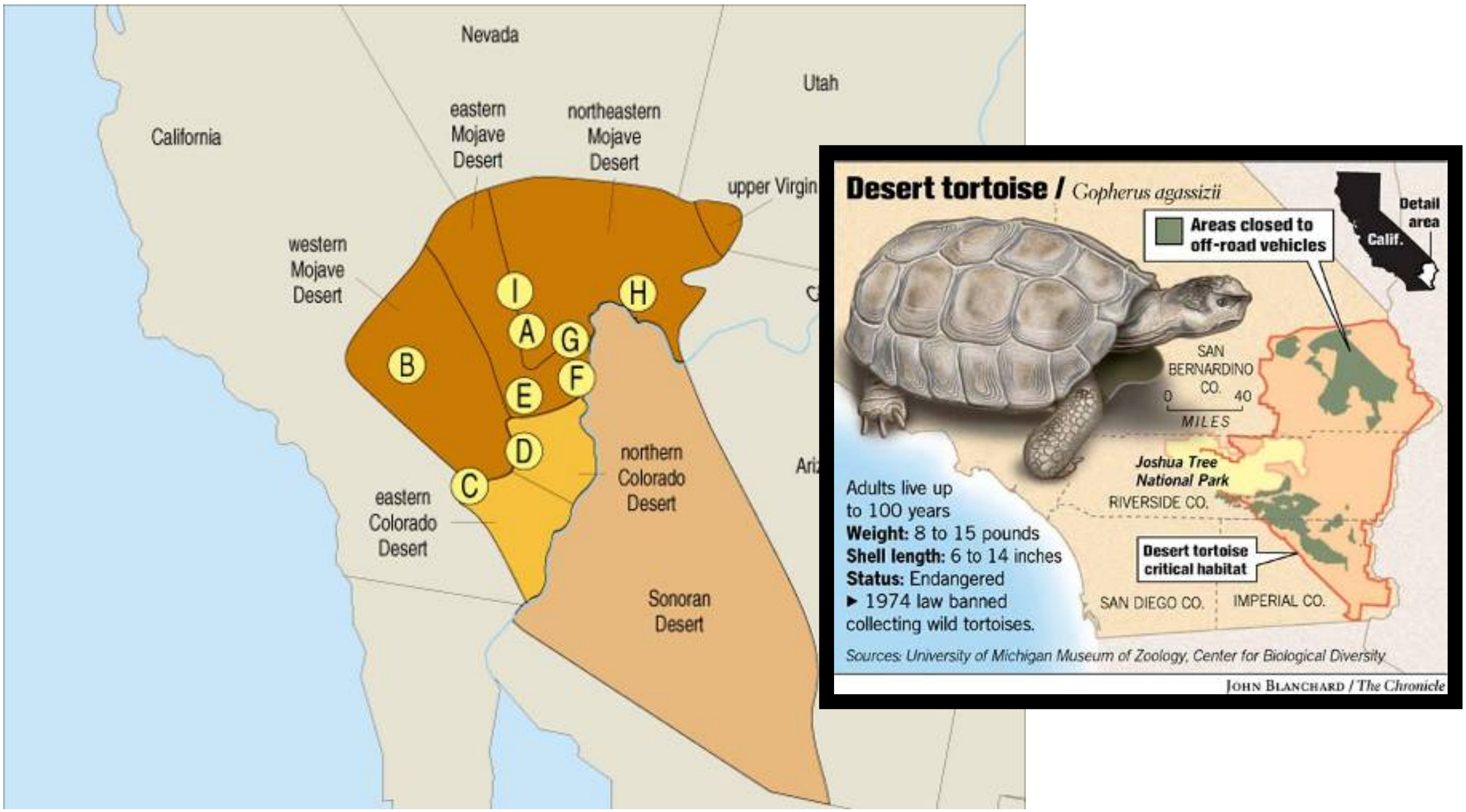
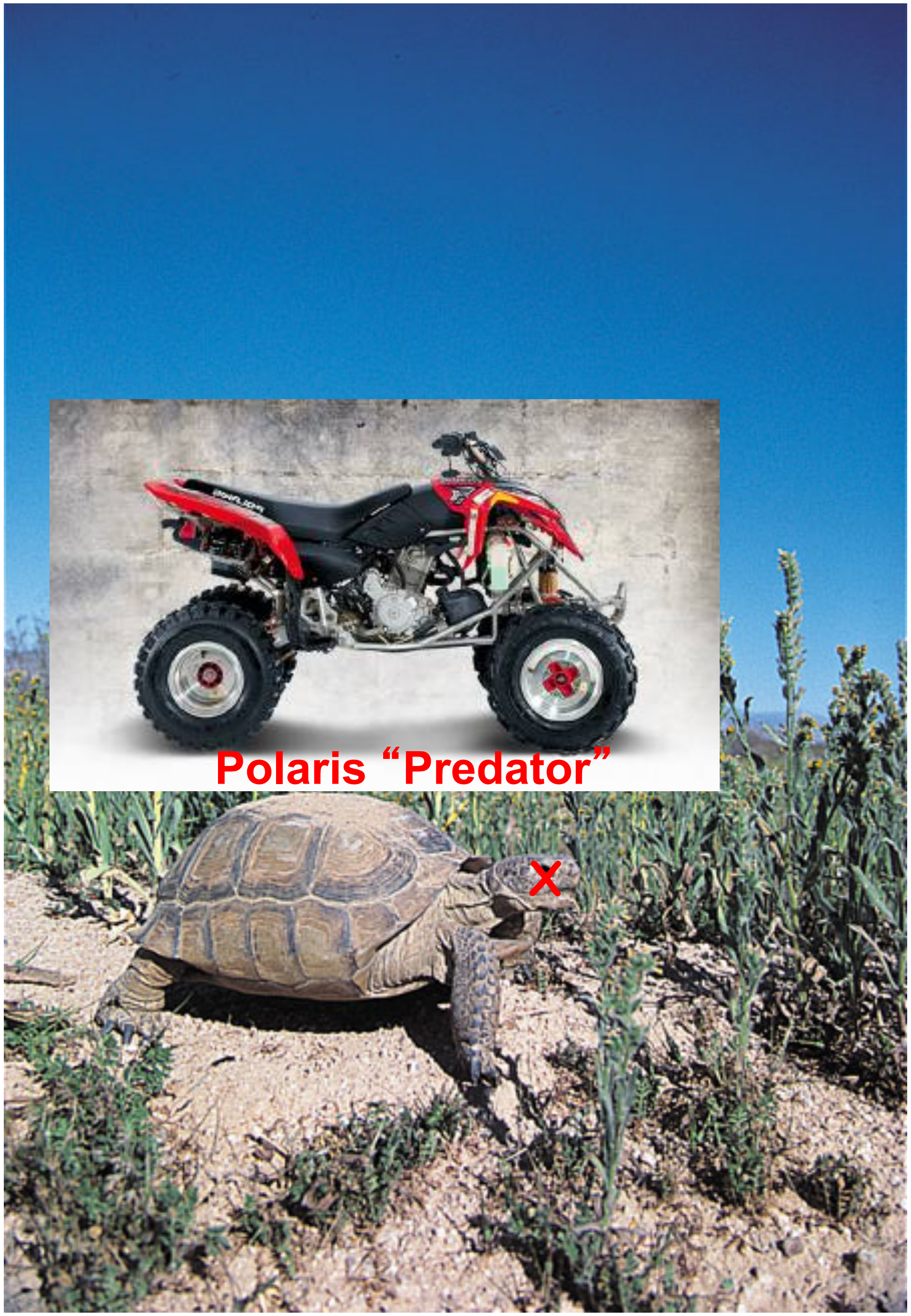


Fig. 1. U.S. range of the desert tortoise (*Gopherus agassizii*). The six population segments for desert tortoises federally listed as threatened occur in parts of the Mojave and Colorado deserts that lie north and west of the Colorado River.



Desert tortoises, *Gopherus spp.*

- Life History (life in the slow lane)
  - Highly vulnerable to predators in first 10 years of life
  - …then their shells get hard.
  - Mature at ~5-6 yrs
  - Don't lay that many eggs 1-4
  - Active from late Spring-October (when annual plants available)
  - Hibernate other times of the year

YOUR JOB TODAY
(to hand in Tuesday @ beginning of lecture):

- Based on real mark-recapture data--
  - Fill in the "holes" of a **static life table**
    (Good practice for calculating all the parts of the table)
  - Estimate exponential rate of increase (r_a) using this life table
  - Answer a few questions designed to make you work through all the calculations and THINK about what the numbers mean.
  - Use the collective intellect of your group to make sure you all understand these calculations.
- If you do all this and discuss it as a group—I guarantee you'll get a better grade on the 1st exam.

Life table terms

- x = age
- l_x = survivorship up to age x (proportion living)
- s_x = survival rate from age x to age $x+1$
- b_x = fecundity (births) at age x

- Want to know if on average each individual replaces itself…

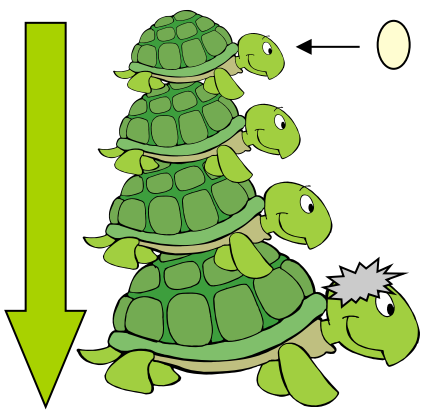
Called the net reproductive rate

Desert tortoises, *Gopherus spp.*

Mark-recapture data following individuals over 3 surveys (one survey every 5 years)

Survival from x to x+1

Survival from birth up to x

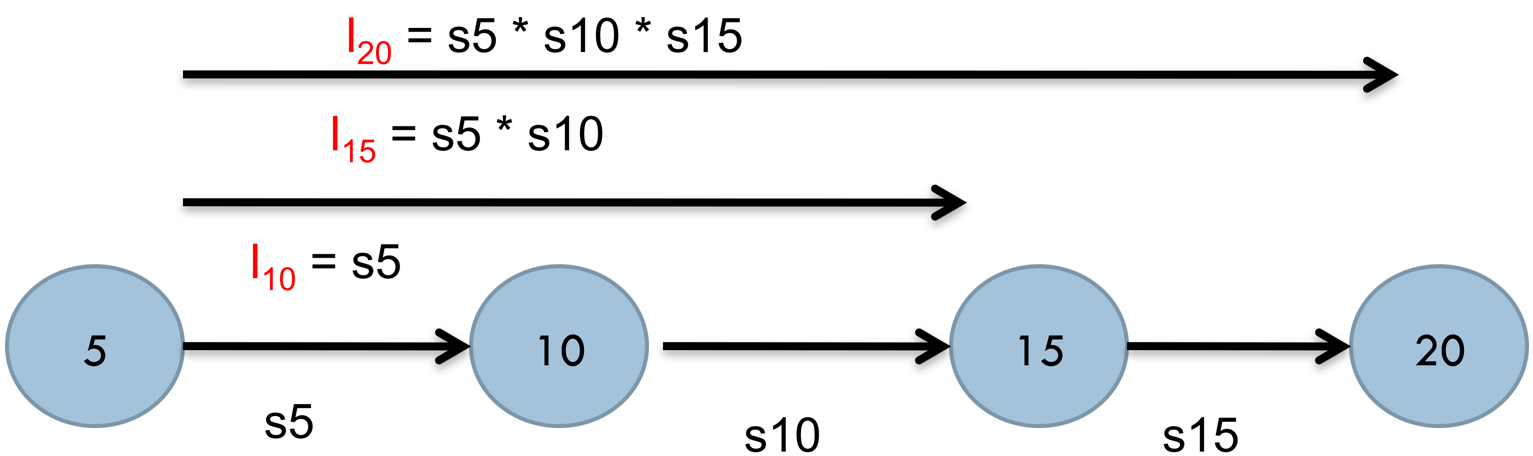


Stage	Surveys			Survey 1 compared to 2				Survey 2 compared to 3			
x	N_1	N_2	N_3	s_x	l_x	b_x	$l_x\ b_x$	s_x	l_x	b_x	$l_x\ b_x$
5	548	408	180	0.27	1.00	0.00		?	1.00	0.00	
10	180	147	97	0.24		3.22				2.27	
15	69	43	15	0.21		7.71				5.44	
20	21	14	5	n/a		9.84		n/a		6.94	
						R_0=				R_0=	

Net reproductive rate R_0

$R_0 = \Sigma\ l_x b_x$

Average number of offspring produced per individual taking into account survival and fecundity



I_{20} = s5 * s10 * s15
I_{15} = s5 * s10
I_{10} = s5
5
10
15
20
s5
s10
s15

- Generation time (G)
  - Average age at which reproduction occurs

$$G = \Sigma x l_x b_x \, / \, R_0$$

- Estimate intrinsic rate of population growth (r_a)

$$r_a = \ln (R_0) \, / \, G$$

$r_a > 0$ (growing), $r_a = 0$ (stable), $r_a < 0$ (declining)