Population Ecology

I. Population Demography
   A. Inputs and Outflows
   B. Describing a population
   C. Summary
II. Population Growth and Regulation
   A. Exponential Growth
   B. Logistic Growth
   C. What limits growth
   D. Population Cycles
   E. Intraspecific Competition
   F. Source and Sink populations

I. Population Demography

Population - a set of organisms belonging to the same species and occupying a particular place at the same time (capable of interbreeding).

Populations have traits that are unique

- birth rates
- death rates
- sex ratios
- age structure

All characteristics have important consequences for populations to grow

STATE FARM
Auto
Life
Fire
INSURANCE ®

Allstate ®/MD

A. Inputs and Outputs

basic processes that affect population size

- immigration
- births

basic processes that affect population size

- immigration
- births
- death
- emigration

Demography - statistical study of the size and structure of populations and changes within them

$$N_{t+1} = N_t + B - D + I - E$$

Task of demographer to account and estimate these values

B. Describing a population

Biological phenomena vary with age

- Reproduction begins at puberty
- Probability of survival dependent on age

Characteristics not fixed but subject to Natural selection

Must take age specific approach

How can we summarize mortality rates within population?

1. Life Tables

Allow for characterization of populations in terms of age-specific mortality or fecundity

Fecundity - potential ability of organism to produce eggs or young; rate of production

Life Table Columns

x = age

nx = # alive at age x

lx = proportion of organisms surviving from the start of the life table to age x

dx = number dying during the age interval x to x + 1

qx = per capita rate of mortality during the age interval x to x + 1

a. Two types of Life Tables

i. Cohort approach

consists of all individuals born during some particular time interval until no survivors remain most reliable method for determining age specific mortality

trace history of entire cohort

Could tabulate # surviving each age interval

This would give you survivorship directly!!

Very few data are available for human populations

Why???

Plants ideal for this type

sessile, can be tagged or mapped

Life table of the grass *Poa annua* (direct observations).

Age (x)*	Number Alive	Survivorship (l_x)	Mortality Rate (q_x)	Survival Rate (s_x)	Expectation of life (e_x)	
0	843	1.000	0.143	0.857	2.114	
1	722	0.857	0.271	0.729	1.467	
2	527	0.625	0.400	0.600	1.011	
3	316	0.375	0.544	0.456	0.685	
4	144	0.171	0.626	0.374	0.503	
5	54	0.064	0.722	0.278	0.344	
6	15	0.018	0.800	0.200	0.222	
7	3	0.004	1.000	0.000	0.000	
8	0	0.000				
*Number of 3-month periods: in other words, 3 = 9 months						

ii. Segment (static) approach

snap-shot of organisms alive during a certain segment of time

Not possible to monitor dynamics of populations by constructing a cohort table – rarely possible for animals

Examine whole population at a particular point in time

Get distribution of age classes during a single time period (cross section of the population)

Hunter harvest data

TABLE 10.3 Time-Specific Life Table for Red Deer on Isle of Rhum, 1957

x	N_x	l_x	d_x	q_x	e_x
		STAGS ♂			
1	1000	1.000	282	0.2820	5.81
2	718	0.718	7	0.0098	6.89
3	711	0.711	7	0.0098	5.95
4	704	0.704	7	0.0099	5.01
5	697	0.697	7	0.010	4.05
6	690	0.690	7	0.010	3.09
7	684	0.684	182	0.2660	2.11
8	502	0.502	253	0.5040	1.70
9	249	0.249	157	0.6306	1.91
10	92	0.092	14	0.1521	3.31
11	78	0.078	14	0.1794	2.81
12	64	0.064	14	0.2187	2.31
13	50	0.050	14	0.2799	1.82
14	36	0.036	14	0.3889	1.33
15	22	0.022	14	0.6363	0.86
16	8	0.008	8	1.0	0.50
		HINDS ♀			
1	1000	1.000	137	0.370	5.19
2	863	0.863	85	0.973	4.94
3	778	0.778	84	0.107	4.42
4	694	0.694	84	0.120	3.89
5	610	0.610	84	0.137	3.36
6	526	0.526	84	0.159	2.82
7	442	0.442	85	0.189	2.26
8	357	0.357	176	0.501	1.67
9	181	0.181	122	0.672	1.82
10	59	0.059	8	0.141	3.54
11	51	0.051	9	0.164	3.00
12	42	0.042	8	0.197	2.55
13	34	0.034	9	0.246	2.03
14	25	0.025	8	0.328	1.56
15	17	0.017	8	0.492	1.06
16	9	0.009	9	1.000	0.50

Source: V. P. W. Lowe 1969.

Assumptions

- individuals must be random sample of population you are studying
- population must be stable
- age-specific mortality and fecundity must be constant

Life Tables

1. allow to discover patterns of birth and mortality
2. uncover common properties shared by populations → understanding of population dynamics

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b. Calculations

Given any one column you can calculate the rest

Relationship

$$n_{x+1} = nx - dx$$

$$qx = dx/nx$$

$$lx = nx/no$$

c. Data used for ecological life tables

1. Survivorship directly observed (lx)

generates cohort life table directly and does not involve assumption that population is stable

2. Age at death observed – data may be used to estimate static life table

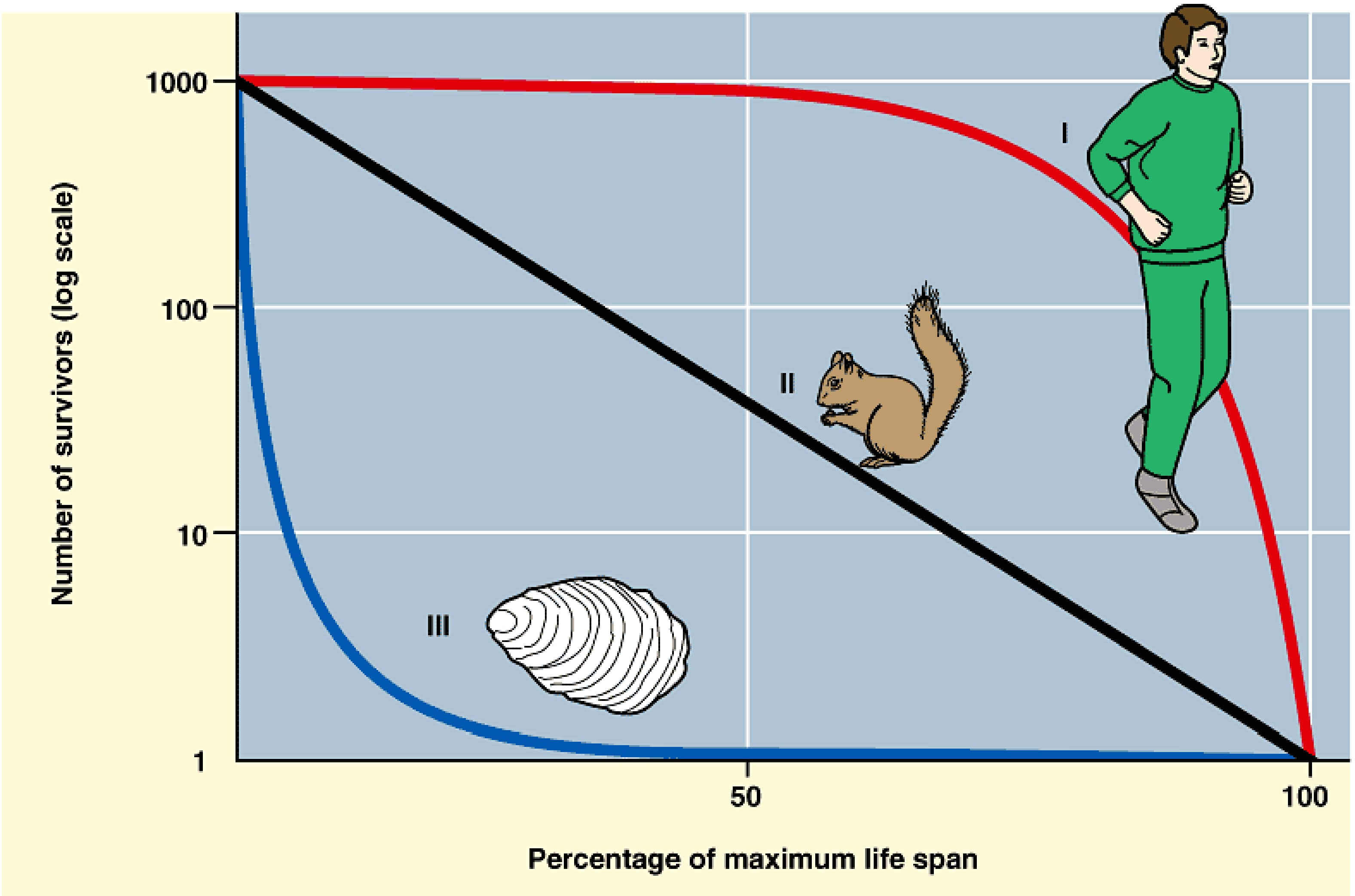
3. Age structure observed – can be used to estimate static life table, must assume constant age distribution

2. Survivorship curves

plot nx (lx) against x get survivorship curve

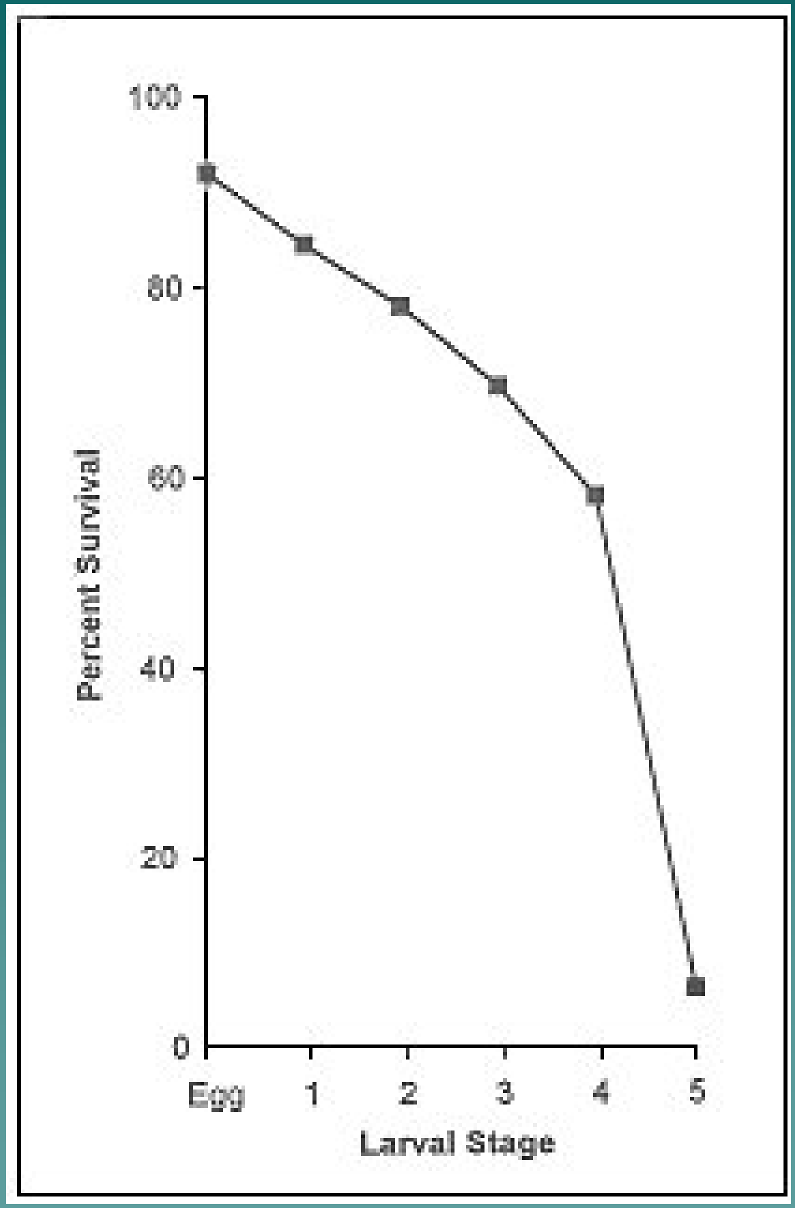
can detect changes in survivorship by period of life

a. 3 generalized types


1000
100
10
1
50
100
I
II
III
Number of survivors (log scale)
Percentage of maximum life span

Type I – characterized by low mortality up to physiological life span

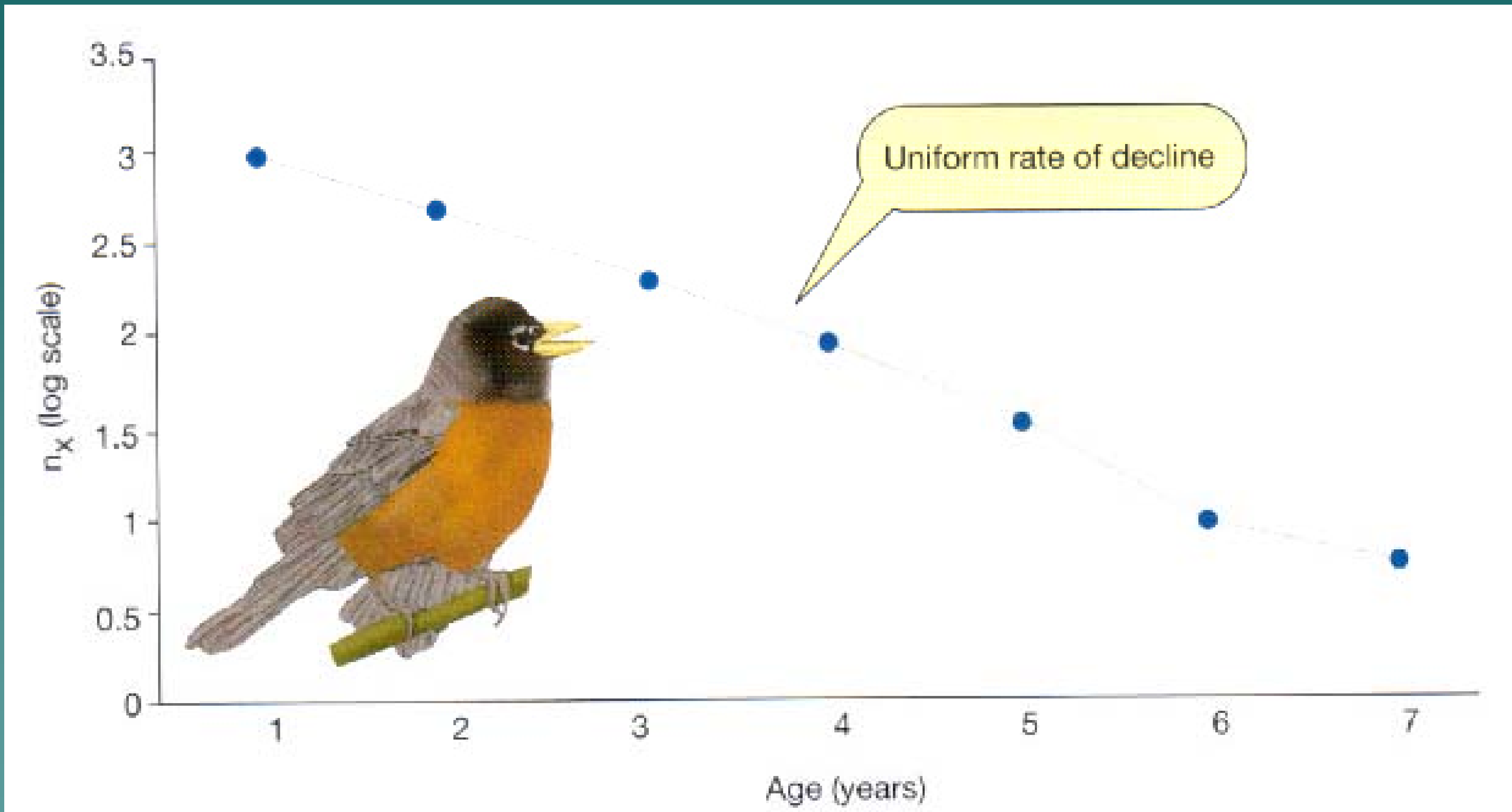
- humans
- animals in captivity
- some invertebrates



Spruce Sawfly

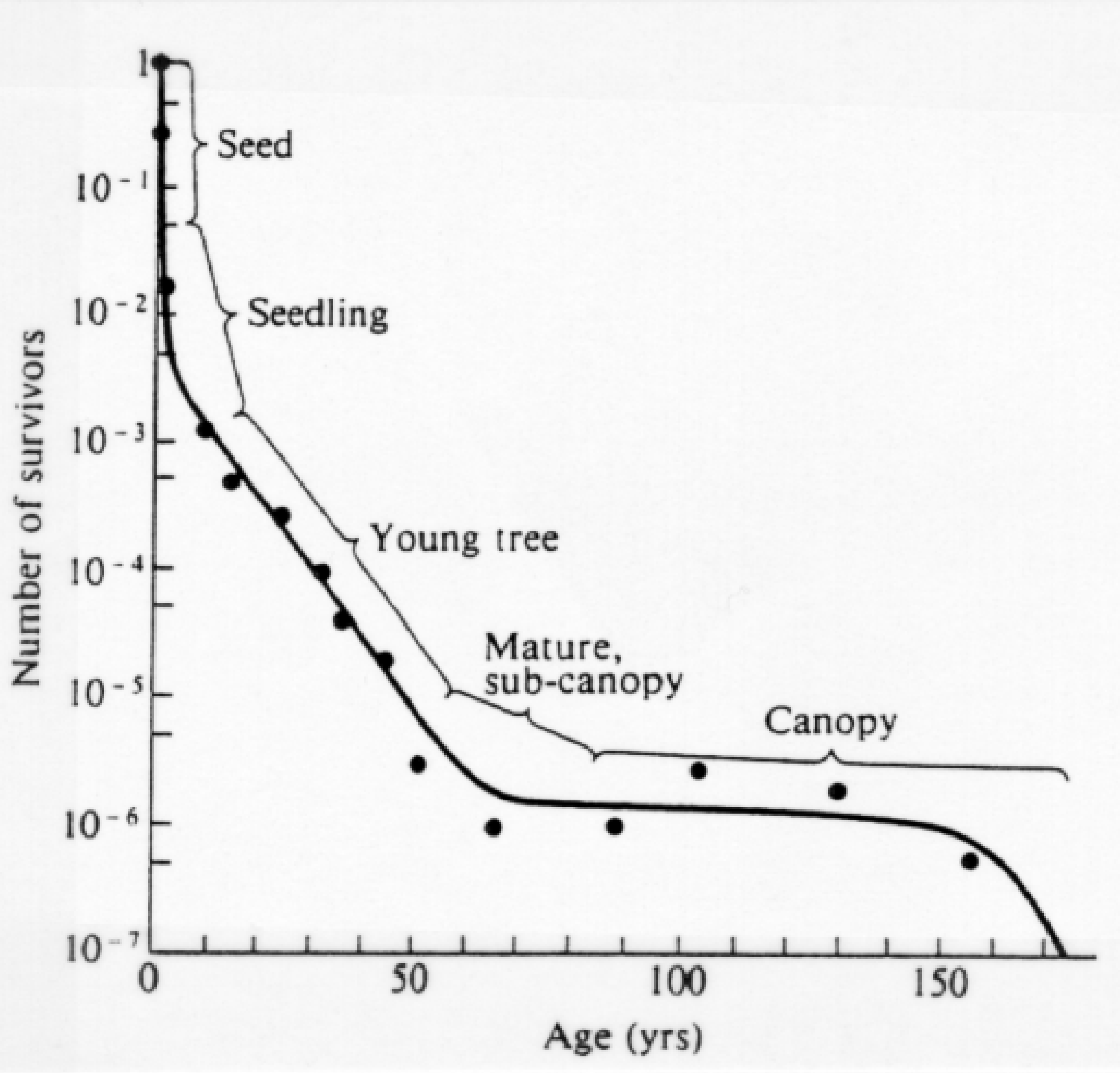
Type II – Constant mortality, environment important here

• birds after nest-leaving

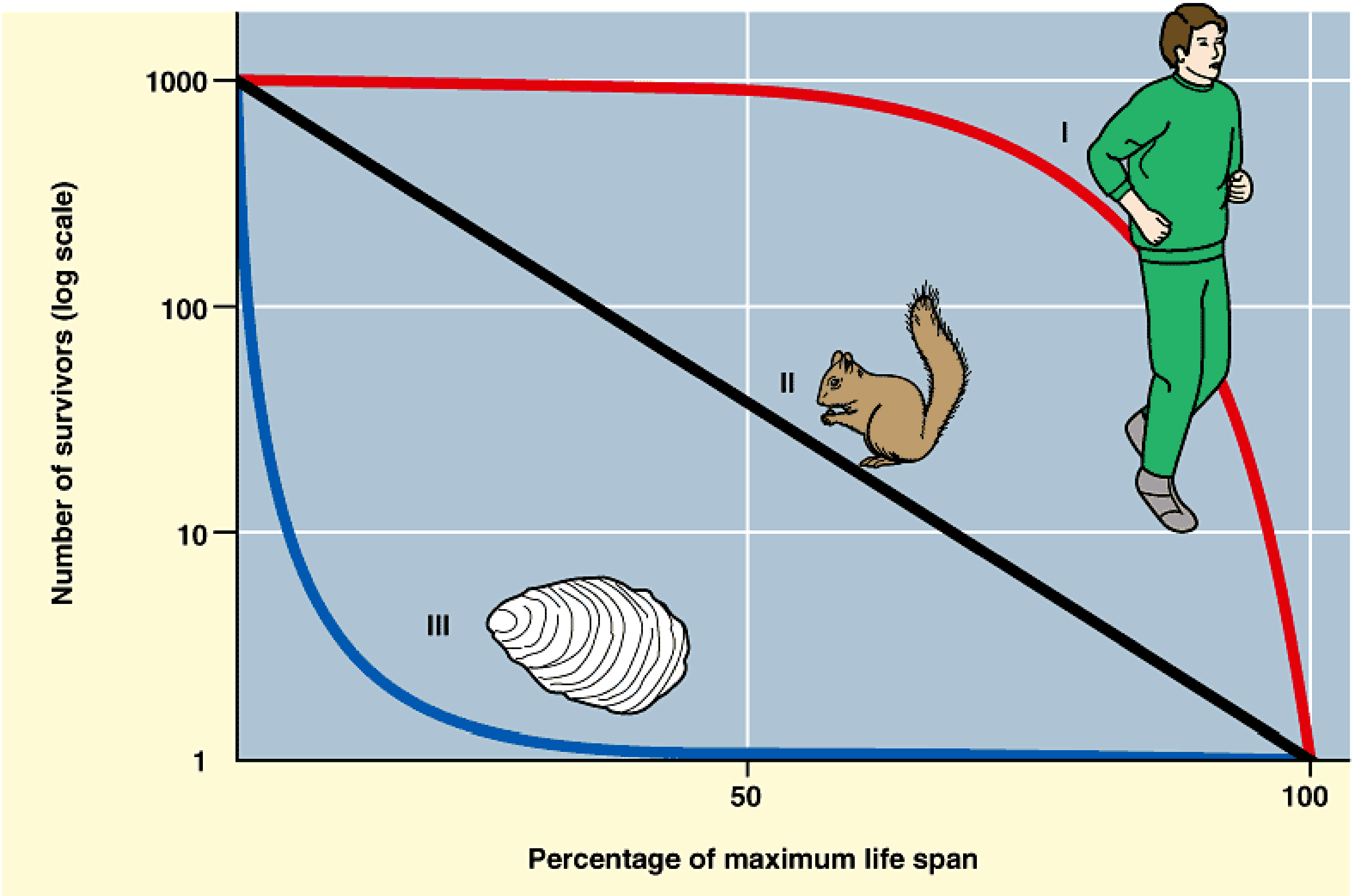

Uniform rate of decline
3.5
3
2.5
2
1.5
1
0.5
0
n_x (log scale)
1
2
3
4
5
6
7
Age (years)

Type III – high juvenile mortality then low mortality to physiological life span

- insects
- plants
- fish



Seed
Seedling
Young tree
Mature,
sub-canopy
Canopy
Number of survivors
1
10 - 1
10 - 2
10 - 3
10 - 4
10 - 5
10 - 6
10 - 7
0
50
100
150
Age (yrs)



1000
100
10
1
50
100
Number of survivors (log scale)
Percentage of maximum life span
I
II
III

b. Plotting data

Most survivorship curves are plotted on a logarithmic scale

Consider 2 populations both reduced by ½ over 1 unit of time

100 → 50

10 → 5

100 → 50 ---- slope = -50

10 → 5 ---- slope = -5

Both cases population reduced by ½ but when plotted slopes will be much different

If you use the log scale slope will be identical in each case.

c. Difficulty with generalizations

As a cohort ages it may follow more than one survivorship curve.

Generalizations regarding age-specific birth rates more straightforward

Basic distinction between species

semelparous – reproduction 1 in life

Iteroparous – reproduction many times during life

Typically

Pre-reproductive period

Reproductive period

Post-reproductive period

3. Net Reproductive Value & Intrinsic Capacity for Increase

How can we determine net population change?

Alfred Lotka – method to combine reproduction and mortality for population

intrinsic capacity for increase

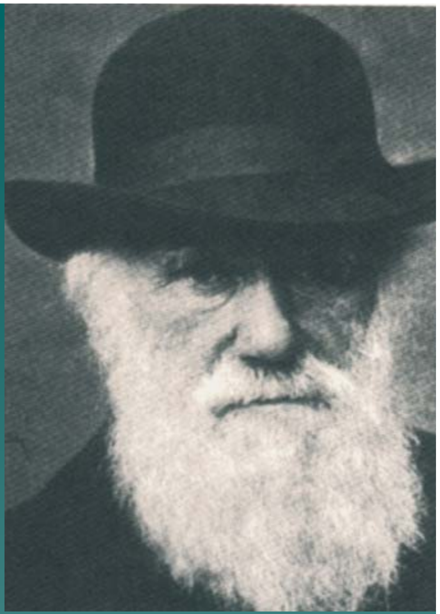
aka – biotic potential (slope of population growth curve) = = r_{max}

r = per capita rate of increase per unit time

Darwin calculated

2 elephants →

19 mil in just 150 years



r_{max} – depends on

- fertility of species
- longevity
- speed of development

To determine rate of growth (or decline)

need to know how birth and death rates vary with age

- Natality or Fertility Life Table

bx - # female offspring produced per unit time, per female age x

x	lx	bx
9	0.989	0
14	0.988	0.002
19	0.986	0.123
24	0.983	0.264
29	0.980	0.277
34	0.977	0.181
39	0.971	0.065
44	0.964	0.013
49	0.953	0.0005

US Women 1989

Not many live to realize full potential for reproduction …

Need to estimate # offspring produced that suffers average mortality –

Net Reproductive Rate

$R_0 = \sum lx*bx$

Net reproductive rate (R_0) – avg # age class 0 female offspring produced by an average female during lifetime

R_0 multiplication rate per generation, temper birth rate by fraction of expected survivors

$R_0 =$

0.907

x	lx	bx
9	0.989	0
14	0.988	0.002
19	0.986	0.123
24	0.983	0.264
29	0.980	0.277
34	0.977	0.181
39	0.971	0.065
44	0.964	0.013
49	0.953	0.0005

Sagebrush Lizards – Tinkle 1973. Copeia 1973:284

What kind of survivorship curve would you expect?

x	lx	bx	lx* bx
0	1.0	0	0
1	0.230	0	0
2	0.143	2.9	0.415
3	0.076	3.9	0.296
4	0.034	4.4	0.150
5	0.013	4.4	0.057
6	0.007	4.4	0.031
7	0.003	4.4	0.013
8	0.002	4.4	0.009
9	0.001	4.4	0.004
		GRR = 33.2	Ro = 0.975

If survival were 100%, $R_0 = \sum bx$ (Gross reproductive rate)

$R_0 = 0.975$

for every female in population there are 0.975 female offspring

If $R_0 = 1.0$ population stays the same and is replacing itself

If $R_0 < 1.0$ population declining

If $R_0 > 1.0$ population increasing

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Model Organism

- Parthenogenic
- Lives 3 yrs. then dies
- 2 young at 1 yr.
- 1 young at 2 yr.
- 0 young at 3 yr.

$R_0 = ?$

x	lx	bx	lxbx	
0	1	0	0	
1	1	2	2	
2	1	1	1	
3	1	0	0	
4	0		R_0 = 3	

Generation Time

Timing of reproduction varies -

- begin immediately after birth
- delayed until late in life

Time of first reproduction = A

Time of last reproduction = Ω

Generation time – mean period elapsing between birth of parents and birth of offspring.

Semelparous organisms –

generation time = A

Species with overlapping generations – more difficult to define.

parental population continues to contribute individuals while older offspring do as well

Aphid – 4.7 days

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Mathematically we can define generation time for a population with overlapping generations as -

$$G = \frac{\underline{E}\ lx*bx*x}{R_0}$$

Calculate generation time for this organism

x	lx	bx	lxbx	lxbxx
0	1	0	0	0
1	1	2	2	2
2	1	1	1	2
3	1	0	0	0
4	0		$R_0 = 3$	

G = 4/3 = 1.33

Average time between birth of parents and birth of offspring = 1.33 age categories

Intrinsic Rate of Natural Increase

If $R_0 > 1$ we know??

The population is growing but at what rate??

Intrinsic rate of natural increase – measure of instantaneous rate of change of a population

per unit time per individual

r difficult to calculate

only determined through iteration using

Euler's Implicit Equation

$$Ee^{-rx}\,lx*bx = 1$$

e = 2.718

r = intrinsic rate of natural increase

lx, bx

r can be estimated

$r = \log e\,(R_0) / G$

G = generation time

loge = log base e, natural log

for model organism

$R_0 = 3.0$

$G = 1.33$

$r = \text{loge } (3.0) / 1.33$

r = 0.826 individuals added per individual per unit time

For overlapping generations

G is approximation & r is approximation

r > 0 growing population

r < 0 declining population

r = 0 stable population

$$r = \text{loge}\,(R_0) / G$$

r inversely proportional to G

What does this mean???

higher the G ---- lower r

$r = \text{loge}\ (R_0) / G$

r is positive when R_0 is greater than 1

$(\ln 1 = 0)$

$$r = \log e\,(R_0) / G$$

When R_0 is as high as possible the maximal rate of r is realized (r_{max})

Calculate *r* for this squirrel population.

x	lx	bx		
0	1.0	0		
1	0.3	2		
2	0.15	3		
3	0.09	3		
4	0.04	2		
5	0.01	0		

$R_0 = \underline{E}\ lx*bx$

$r = \log e\ (R_0)\ /\ G$

$$G = \frac{\underline{E}\ lx*bx*x}{R_0}$$

x	lx	bx	lxbx	
0	1.0	0	0	
1	0.3	2	0.6	
2	0.15	3	0.45	
3	0.09	3	0.27	
4	0.04	2	0.08	
5	0.01	0	0	
$\underline{E}$			1.4	

$R_0 = 1.4$

$R_0 = \underline{E}\ lx*bx$

x	lx	bx	lxbx	xlxbx
0	1.0	0	0	0
1	0.3	2	0.6	0.6
2	0.15	3	0.45	0.9
3	0.09	3	0.27	0.81
4	0.04	2	0.08	0.32
5	0.01	0	0	0
E			1.4	2.63

$R_0 = 1.4$

$G = 2.63/1.40 = 1.88$

$$G = \frac{E\ lx*bx*x}{R_0}$$

x	lx	bx	lxbx	xlxbx
0	1.0	0	0	0
1	0.3	2	0.6	0.6
2	0.15	3	0.45	0.9
3	0.09	3	0.27	0.81
4	0.04	2	0.08	0.32
5	0.01	0	0	0
E			1.4	2.63

$R_0 = 1.4$

$r = \text{loge}\ (R_0)\ /\ G$

$G = 1.88$

$r = 0.336\ /\ 1.88 = 0.179$

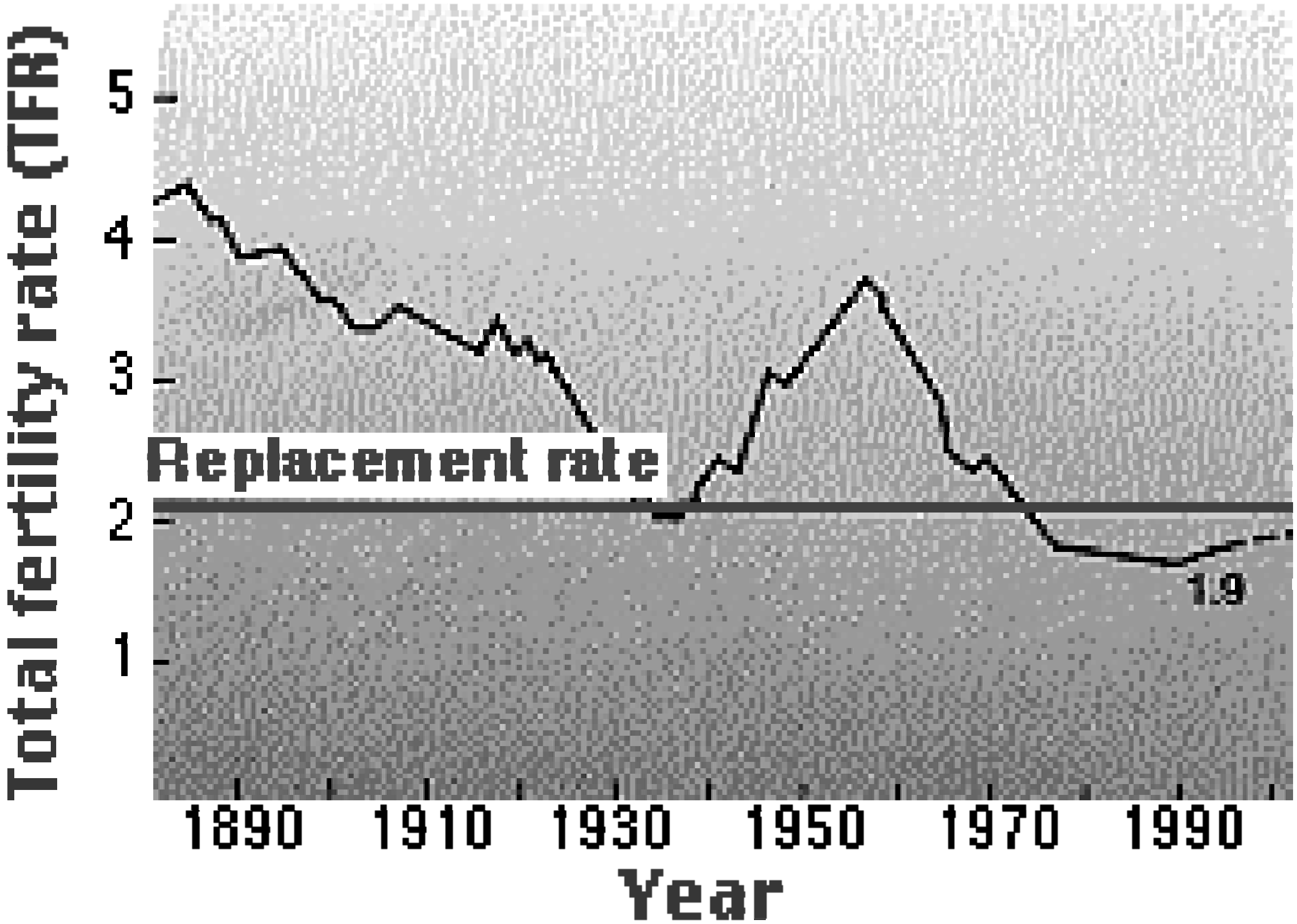
What can we conclude about this population?

$r = 0.179$

thus the population is increasing by 0.179 individuals added/individual/unit time

Demographers can also calculate the replacement rate for a population –

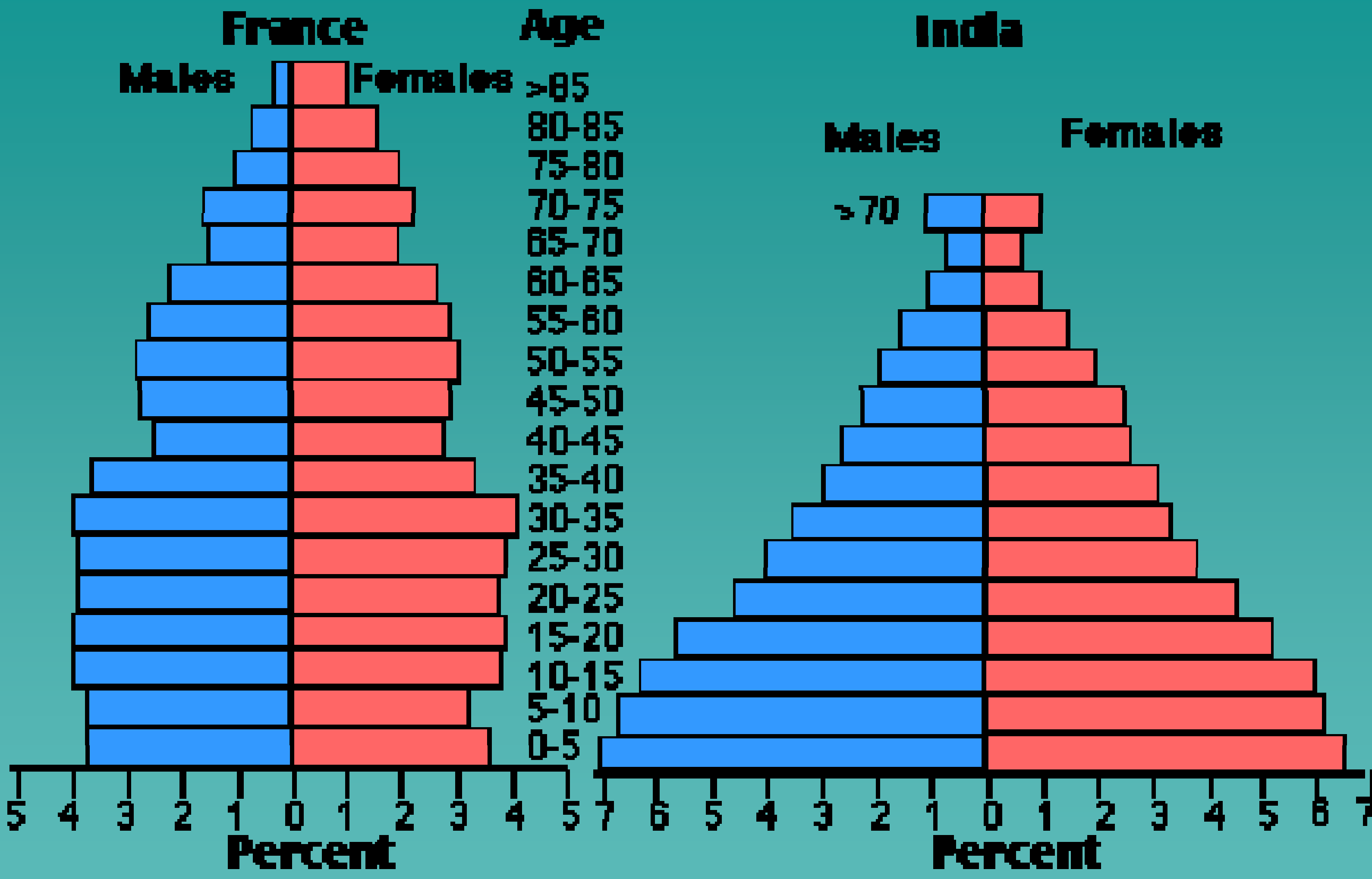
the rate of reproduction that will result in 0 population growth.



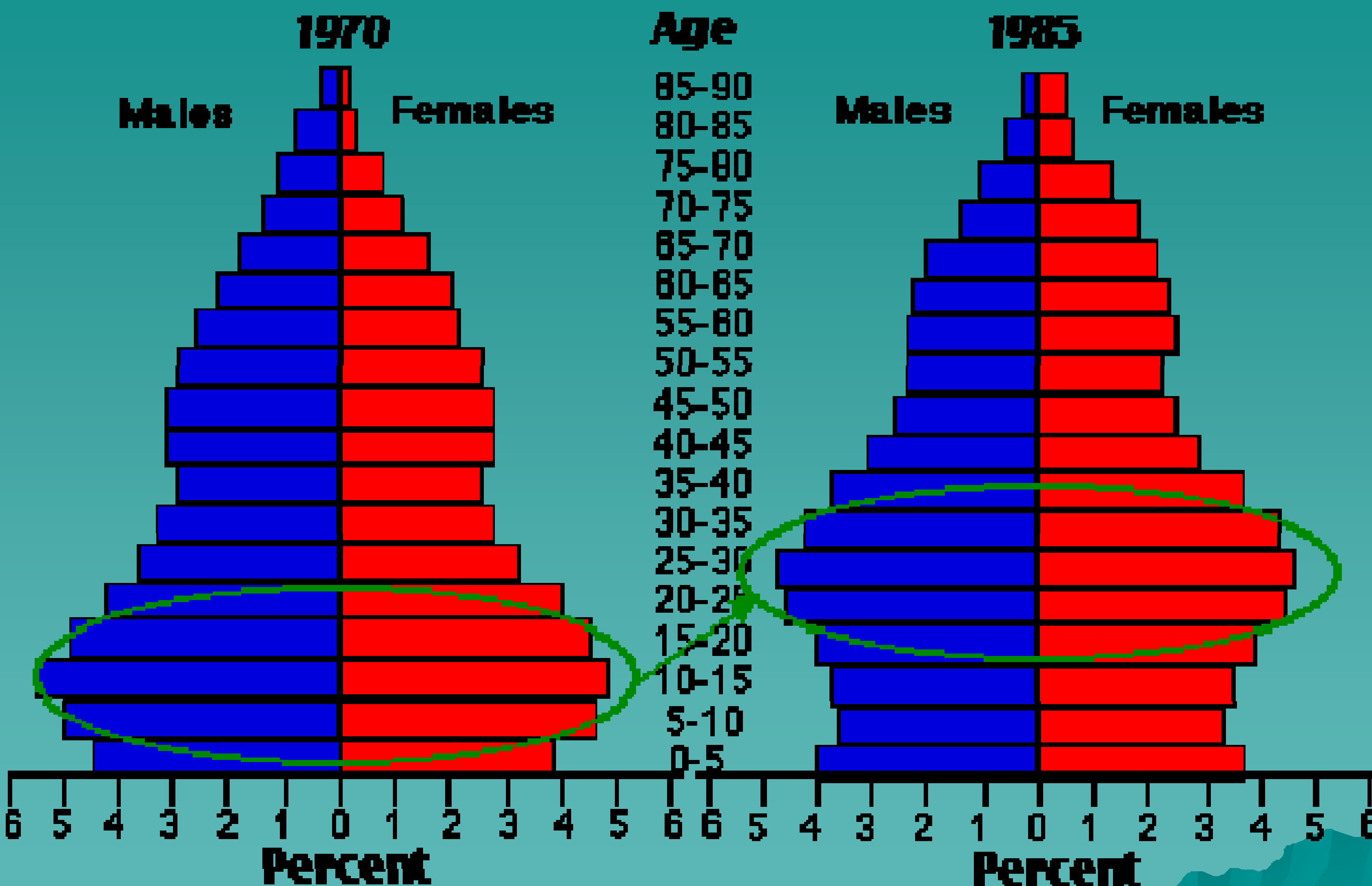
Total fertility rate (TFR)
5
4
3
2
1
Replacement rate
1.9
1890
1910
1930
1950
1970
1990
Year

4. Stable Age Distribution

Age distribution (age structure) determines (in part) population reproductive rates, death rates, and survival.



France
Age
India
Males
Females
>85
80-85
75-80
70-75
65-70
60-65
55-60
50-55
45-50
40-45
35-40
30-35
25-30
20-25
15-20
10-15
5-10
0-5
Males
Females
>70
5 4 3 2 1 0 1 2 3 4 5
7 6 5 4 3 2 1 0 1 2 3 4 5 6 7
Percent
Percent



1970
Age
1985
Males
Females
Males
Females
85-90
80-85
75-80
70-75
65-70
60-65
55-60
50-55
45-50
40-45
35-40
30-35
25-30
20-25
15-20
10-15
5-10
0-5
6 5 4 3 2 1 0 1 2 3 4 5 6
6 5 4 3 2 1 0 1 2 3 4 5 6
Percent
Percent

Theoretically… all continuously breeding populations tend toward a <u>stable</u> age distribution.

Stable age distribution – *ratio* of each group in a growing population remains the same.

IF – age-specific birth rate and age-specific death rate do not change.

Lotka proved that any pair of unchanging lx and bx schedules eventually give rise to a stable age distribution

Each age class grows at a constant rate - λ

the rate of population change – λ, the finite multiplication rate

$\lambda = e^r$

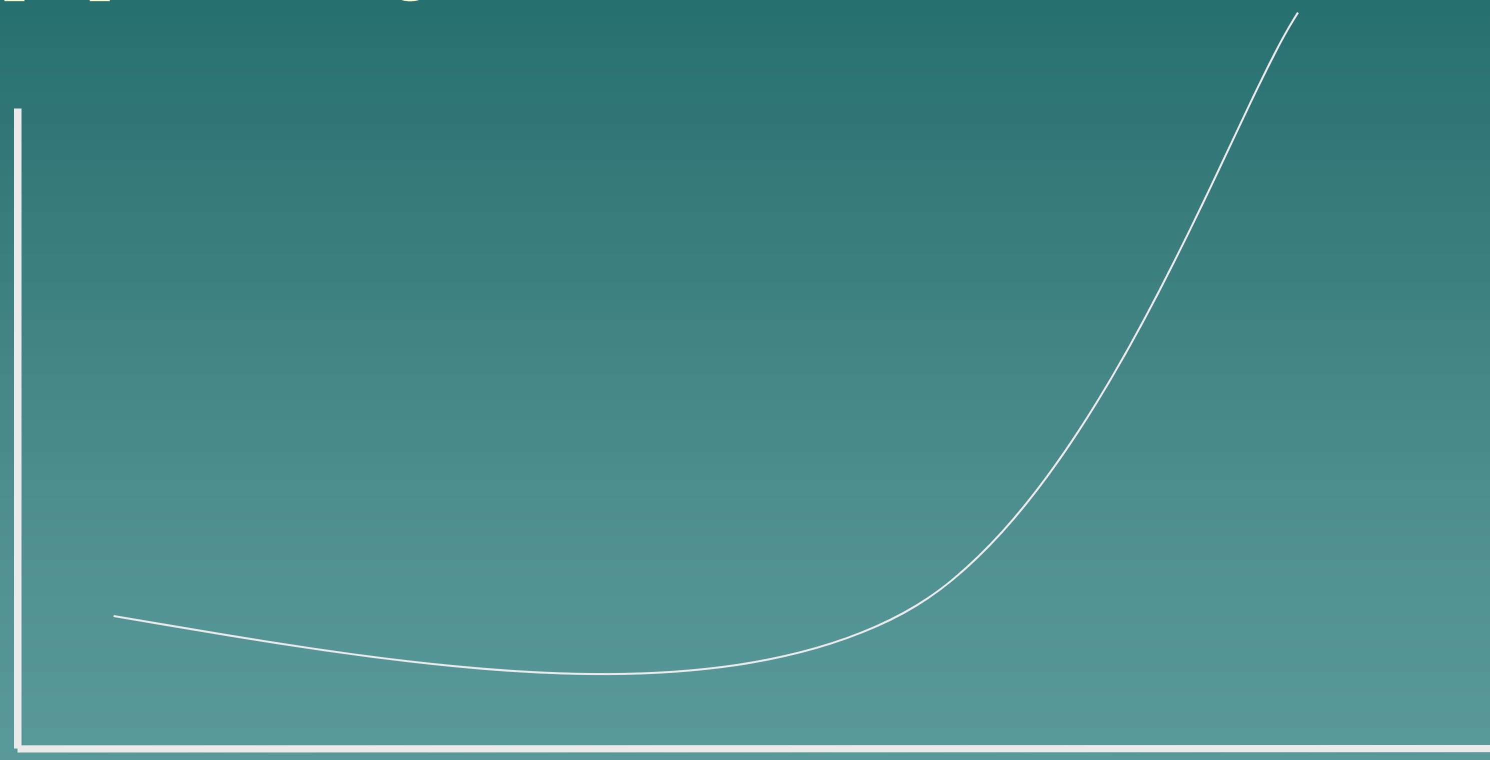
$e = 2.718$

$\lambda = 1.2$

$Nt = N_0\lambda^t$

used to project but not predict population size

If this occurs then we get exponential population growth



$Nt = N_0\lambda^t$

This equation can be rewritten as

$Nt = N_0\ e^{rt}$

or

$dN/dt = rN$

A population will grow and grow exponentially as long as r is positive and constant!

C. Summary

The rate of increase ($Nt = N_0\ e^{rt}$) is ultimately a function of age specific mortality and natality

What value is knowing *r* ?

• used to compare between different species

• used to compare actual against what species is capable of

How does modifying life history characteristics affect *r*?

1. change # of offspring produced

(change bx column – affects R_0)

2. change longevity

(change lx column – affects R_0)

3. change age at first reproduction

(change bx, and G)

GRR = 3 but difference in age at 1st reproduction

x	lx	bx	lx*bx		lx	bx	lx*bx	
0	1	0	0		1	1	1	
1	0.5	1	0.5		0.5	1	.5	
2	0.2	1	0.2		0.2	1	.2	
3	0.1	1	0.1		0.1	0	0	
			R_0 = 0.8				R_0 = 1.7	

Population 1, r = -0.149

Population 2, r = 1.001

so, age at first reproduction can have big affect on r

Characteristics of species with high and low *r* values

High values – occupy temporary harsh environments, unpredictable

selection has put premium on high *r* before environment turns bad

high r species good colonizers

Low values – live in stable predictable environments, little need for rapid population growth

environment is saturated

selection puts premium on competitive ability rather than reproduction.

II. Population Growth and Regulation

Central process of ecology – population growth

No population grows forever, so must be some regulation.

Demographic variables useful because permits prediction of future changes.

1. apply demographic parameters to description of growth and regulation
2. examine difficulties in analyzing and predicting growth

A. Exponential Growth

Continuous growth in unlimited environment

modeled by

$$dN/dt = rN$$

Assumes *r* is constant

Does exponential ever really occur in nature?

YES!

Under certain circumstances

- short period of time
- unlimited resources

Case Studies

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1. Exponential growth in trees

Pleistocene – N. Hemisphere pines followed retreating glaciers northward

Examine sediments in lakes and ID pollen

Estimated population sizes by counting pollen

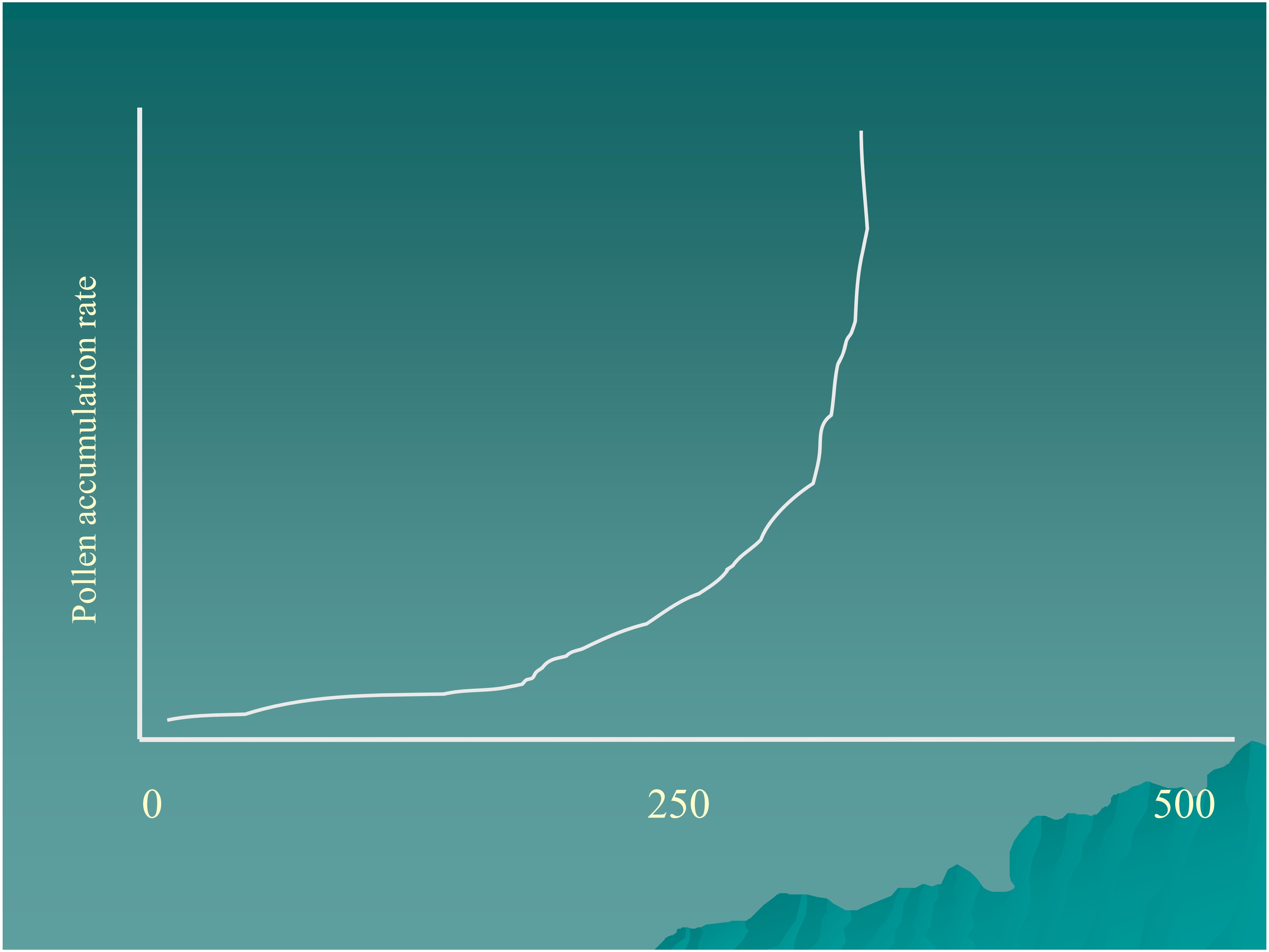
#/cm^2

What is assumption?

K. Bennett 1983. Nature 303:164

Rate of pollen deposition is proportional to # of trees

Trees found to grow at exponential rate.

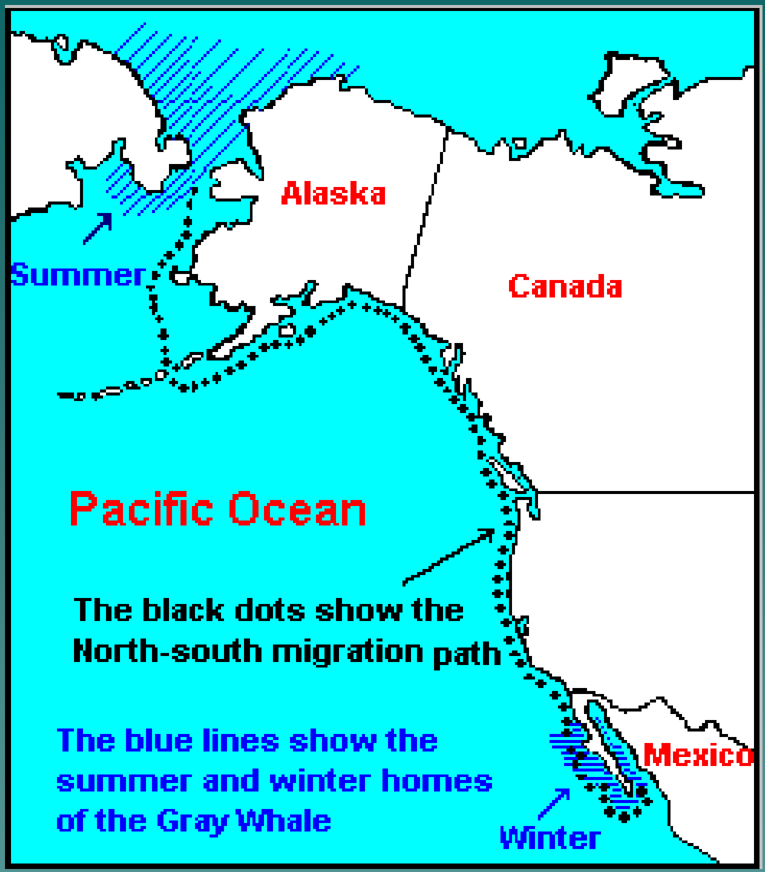


Pollen accumulation rate
0
250
500

Two subpopulations
Western – severly decimated (10-100s)
Eastern – recovered (22,000)

- Whaling along CA coast began 1845
- Average take – 370/yr
- By 1874 population so low not profitable to hunt
- 1946 International Agreement

Migration Route



- 1971 estimated pop trends by construction of Life Table
- r= 0.041
- rmax is low, gestation 13mo, lactation 7 mo, 3-4 mo no reprod, age at first reproduction = 8,

- 1983 annual counts estimated r= 0.037
- 1991 est 21,000

As different as these organisms are, circumstances for exponential growth share several things

What are they?