

# BIOL 410 Population and Community Ecology

Age structured populations

# Variation in Carrying Capacity

- **Environmental Variation may cause carrying capacity to change over time**
- **Variation could be:**
  - 1. Random**
  - 2. Cyclic**

# Variation in Carrying Capacity

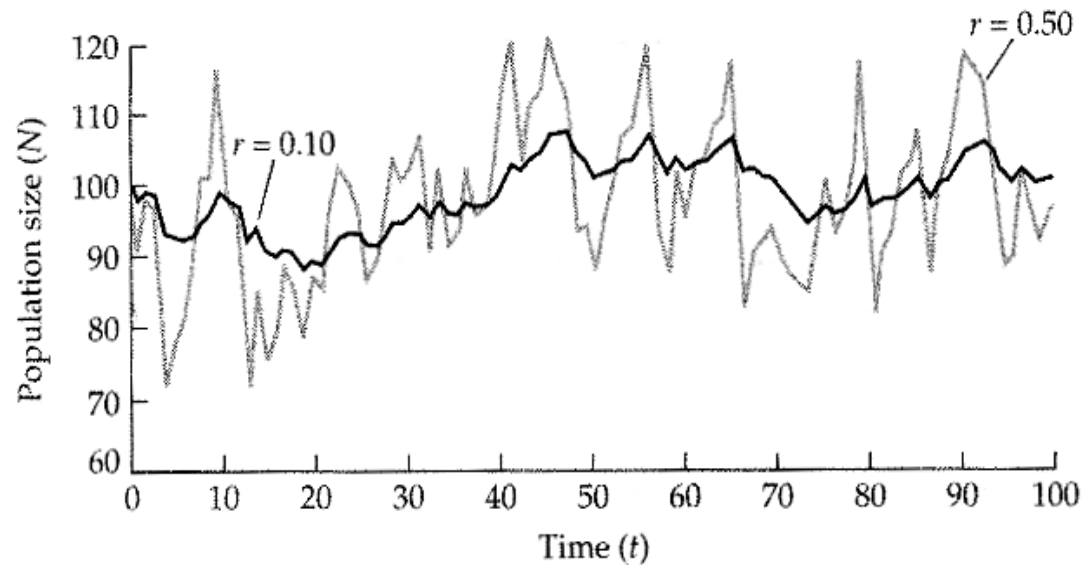
- **Random Variation in Carrying Capacity (K)**
- If  $r$  is not variable, but carrying capacity changes over time, result is complex growth patterns
- When a population is above the carrying capacity, it declines at a faster rate than it will increase if it is at a corresponding similar point *below* the carrying capacity.
- If the carrying capacity is described by a mean ( $\bar{K}$ ) with an associated variance ( $\sigma_K^2$ ), a rough approximation of the mean population size will be:

$$\bullet \quad \bar{N} = \bar{K} - \frac{\sigma_K^2}{2}$$

# Variation in Carrying Capacity

- **Random Variation in Carrying Capacity (K)**

- The more variable the environment, the smaller the average population size.
- If the intrinsic rate of increase ( $r$ ) is large, the population closely tracks changes in carrying capacity.
- if the small intrinsic rate of increase ( $r$ ) is small, the population do not fluctuate much in size as carrying capacity varies, but the population size ( $N$ ) will tend to be overall somewhat smaller than a population that has a rapid intrinsic growth rate.



# Variation in Carrying Capacity

- **Periodic (cyclic) variation in Carrying Capacity**
- **e.g. seasonal variation in resources**
- $K_t = k_0 + k_1 \cos\left(\frac{2\pi t}{c}\right)$
- $K_t$  = carrying capacity at time  $t$
- $k_0$  = is mean carrying capacity
- $k_1$  = the amplitude of the cycle
- $c$  = the length of the cycle

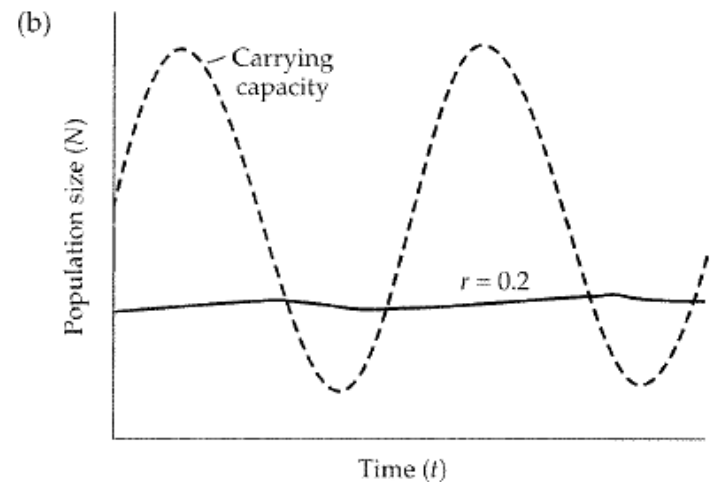
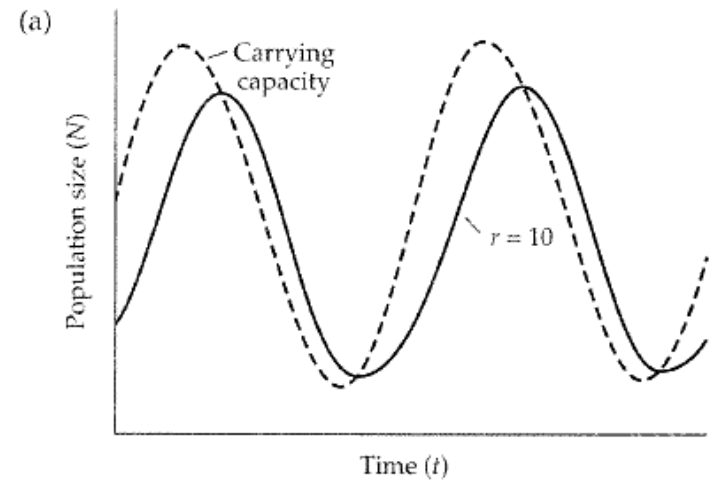
# Variation in Carrying Capacity

- **Periodic (cyclic) variation in Carrying Capacity**
- length of the cycle acts as a time lag, so the behavior of the model depends on the factor  $rc$  (as it did previously with  $r\tau$ )

# Variation in Carrying Capacity

- if  $rc$  is large ( $\gg 1.0$ ), then the population tends to track the fluctuations in the environment:
- $$N_t \approx k_0 + k_1 \cos\left(\frac{2\pi t}{c}\right)$$
- If  $rc$  is very small ( $\ll 1.0$ ), then the population tends to average out the fluctuations and persist at a level slightly below carrying capacity

- $$\bar{N} \approx \sqrt{k_0^2 - k_t^2}$$



# Age/stage structure populations





# Objectives

- Representing age structured populations
  - Cohort life tables
  - Static life tables
    - $R_0$ ,  $r$ ,  $G$
  - Matrix population models
    - Leslie Matrix
    - Lefkovich Matrix
  - Individual-based population models

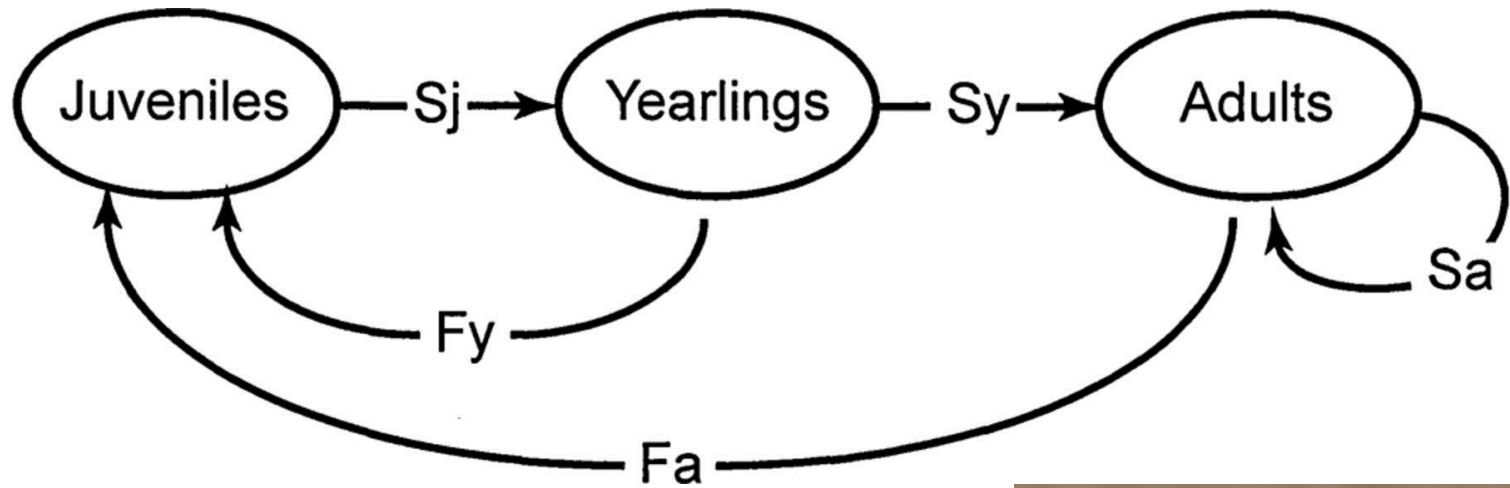
# Age-structured Populations

$$N_{t+1} = N_t + b \cdot N_t - m \cdot N_t$$

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

- Exponential models assume no age-structure in populations
- For many organisms, this may be an unrealistic assumption
  - Delays in contribution to population birth rates
  - Differences in death rates during different phases of an organism's life history

# Age/stage life history diagram



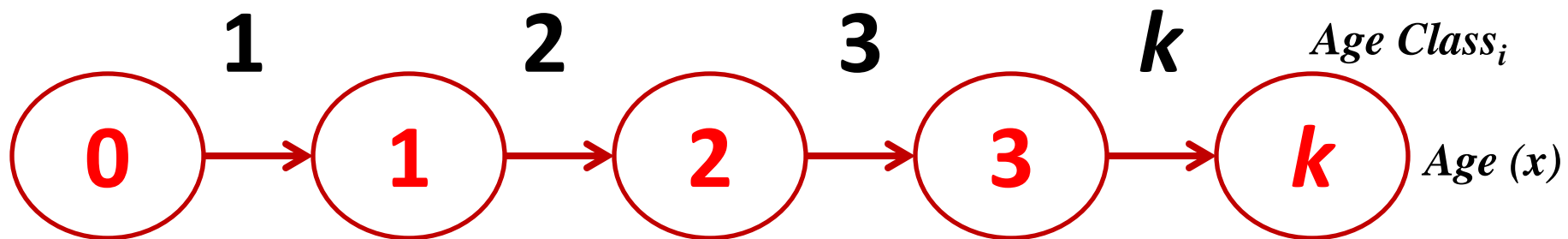
*Journal of Mammalogy*, 92(2):433–443, 2011

**Adult survival and population growth rate in Colorado big brown bats  
(*Eptesicus fuscus*)**

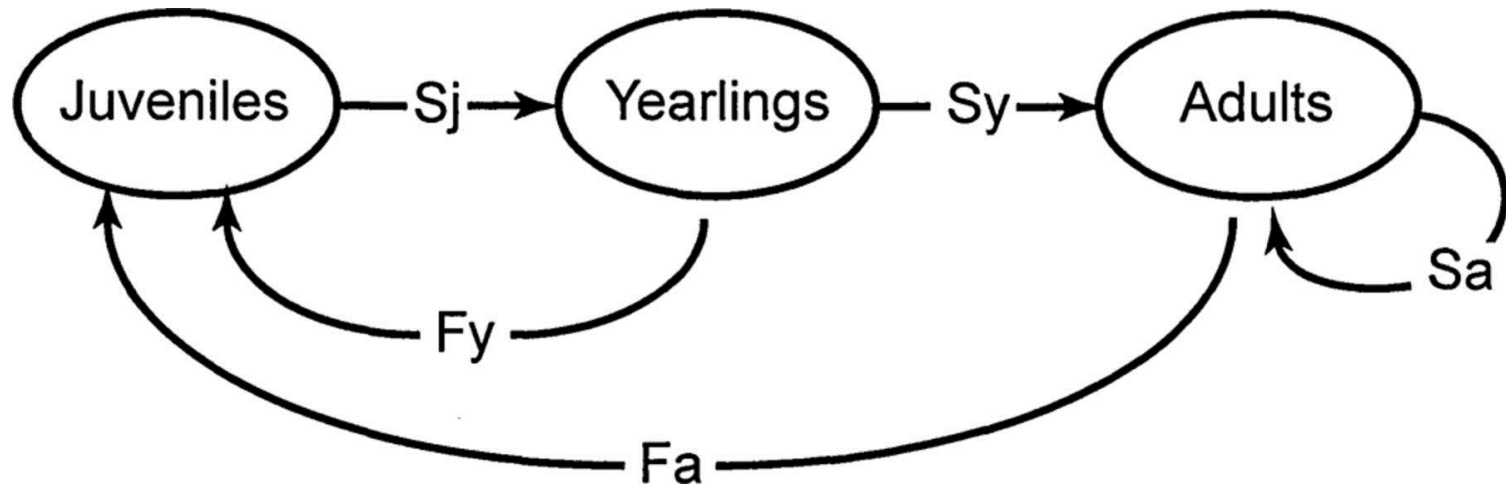
THOMAS J. O'SHEA,\* LAURA E. ELLISON, AND THOMAS R. STANLEY

# Age-structured populations

- Define by Age Class ( $i$ )
- Individuals within age class ( $i$ ) are between the age of  $i-1$  and  $i$ .
- Age classes run from 1- $k$ .
- Age structure: define fecundity and mortality rates for age classes based on time spans of significance to the life history of the species
- Simplification of continuous processes (death)

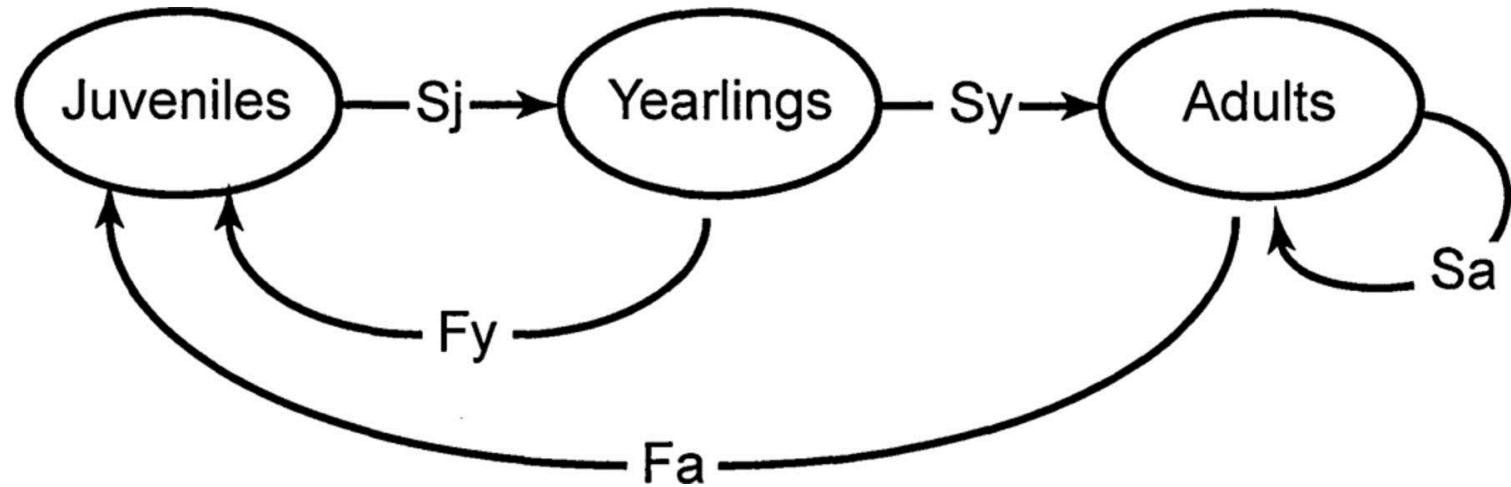


# Stage structured populations



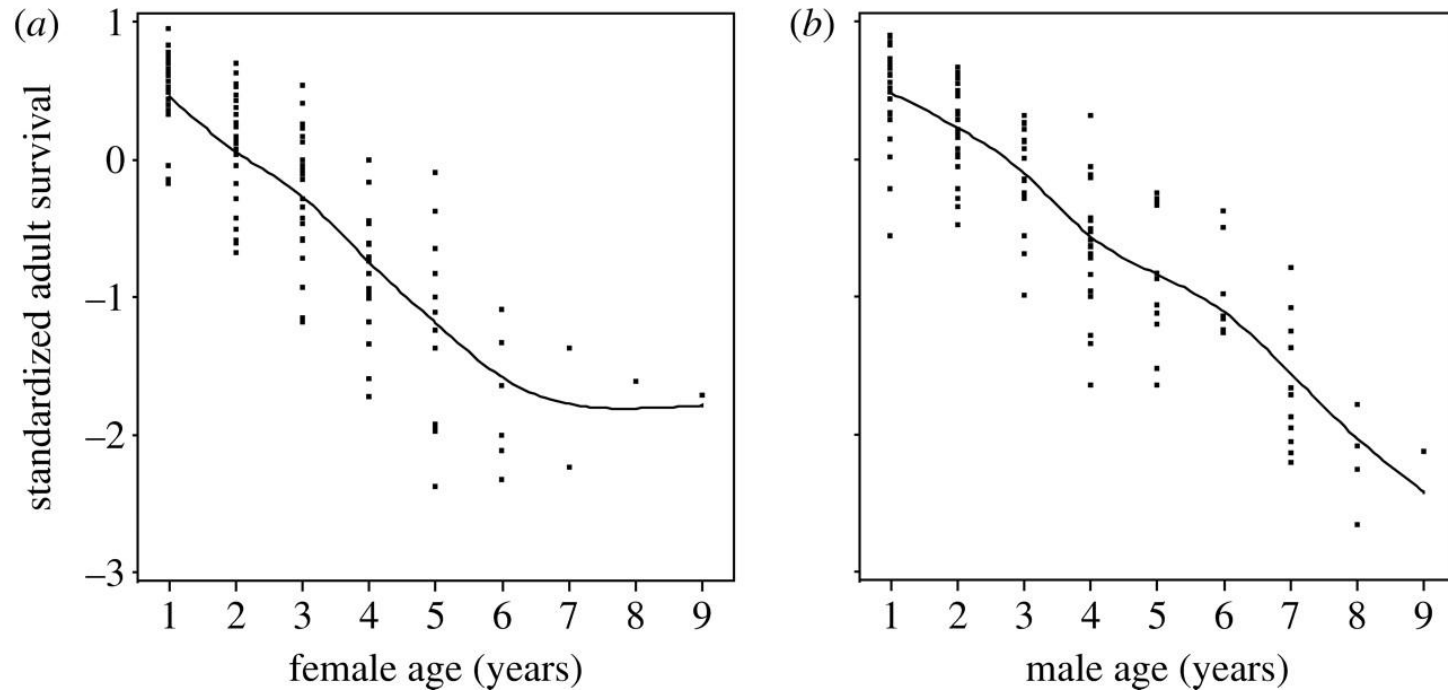
- Stage Structure: define fecundity and survivorship rates for age groups based on time spans of significance to the life history of the species
- Further simplification of continuous demographic changes and age structure

# Age/stage dependent processes



- Survivorship
- Fecundity

# Age and survival



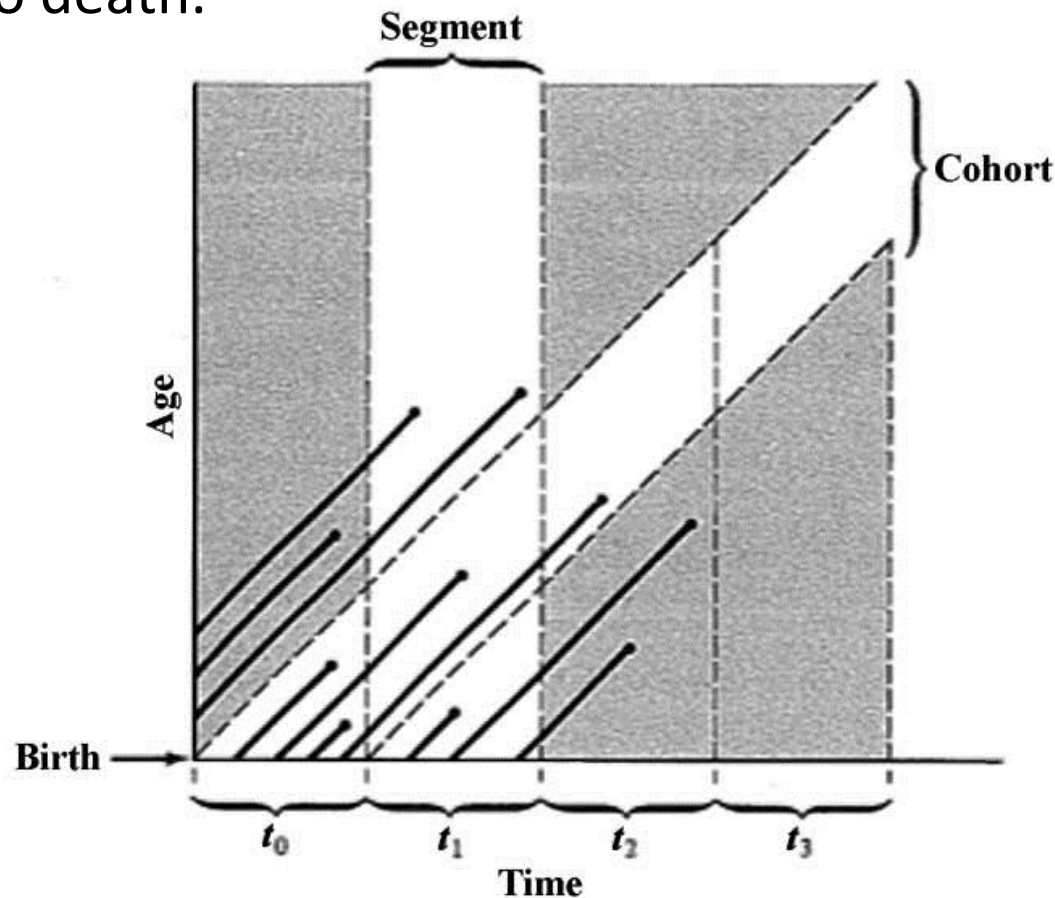
L.F Keller et al. Proc. R. Soc. B 2008;275:597-604

**Age-specific variation in (year-standardized) annual adult survival in (a) female and (b) male song sparrows on Mandarte Island**



# Survivorship $l(x)$

- Survivorship Schedule  $l(x)$
- Cohort – group of individuals born at the same time and followed to death.





# Survivorship $l(x)$

- Survivorship Schedule  $l(x)$
- Cohort – group of individuals born at the same time and followed to death.
- Cohort Survival -  $S(x)$  – *number of the original cohort still alive at start of age  $(x)$*
- Survivorship Schedule –  $l(x)$  – *proportion of the original cohort that survives to age  $(x)$*
- $l(x) = \frac{S(x)}{S(0)}$

$x$	$S(x)$	$l(x)$
0	500	1.0
1	400	0.8
2	200	0.4
3	50	0.1
4	0	0

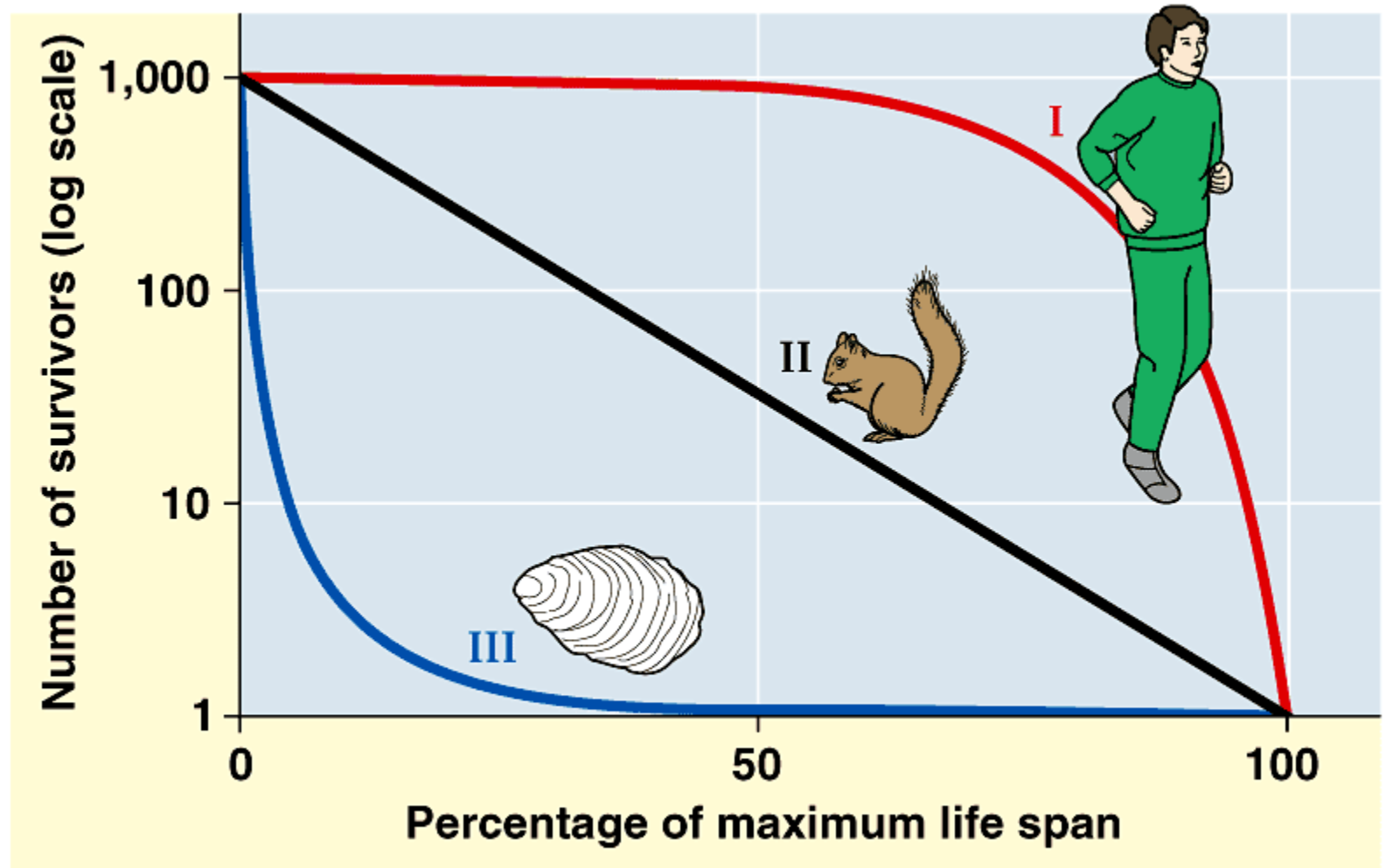
# Survival Probability $g(x)$

- To compare the survival of different ages directly, we must determine the probability of survival [ $g(x)$ ] from age ( $x$ ) to age ( $x+1$ ), given that an individual has already survived to age  $x$ .

- $$g(x) = \frac{l(x+1)}{l(x)}$$

$x$	$S(x)$	$l(x)$	$g(x)$
0	500	1.0	0.8
1	400	0.8	0.5
2	200	0.4	0.25
3	50	0.1	0
4	0	0	

# Natural Survivorship



# Age and clutch size (Fecundity)

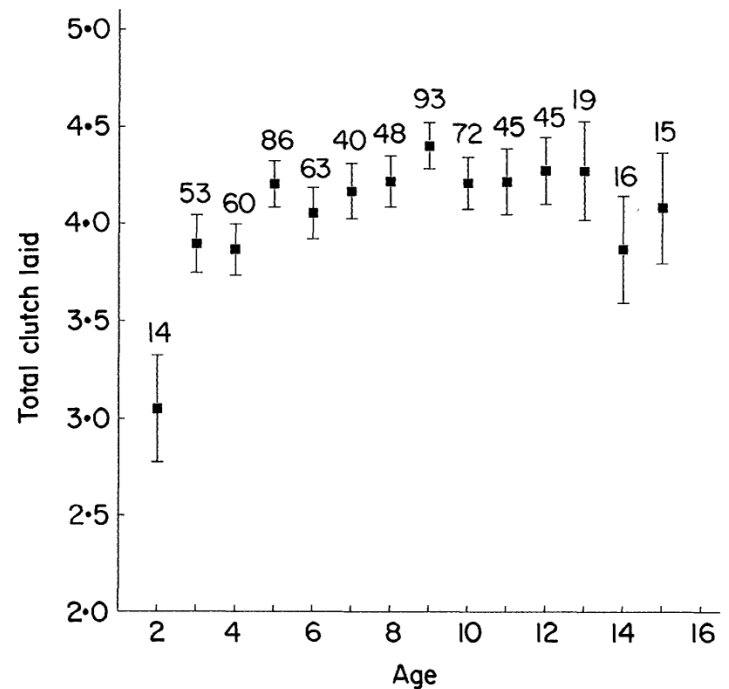
*Journal of Animal Ecology* 1993,  
**62**, 323–333

## Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry

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**Fig. 2.** The distribution of clutch size with respect to age for lesser snow geese at La Pérouse Bay. Least square means and associated standard errors were estimated from an ANOVA model including age and year. The values are those expected under a balanced design with covariate (year) effects removed (SAS Institute 1990). Age-classes 9 and above include both known and minimum age individuals. Age-class 15 is a composite of individuals 15 and older. Sample sizes are indicated.

# Fecundity $b(x)$

- Fecundity Schedules
- Average number of female offspring born per unit time to an individual female of a particular age.

- Represented by age as births,  $b(x)$ , or maternity,  $m(x)$
- If individuals do not reproduce within particular age categories, their fecundity schedule for that age is zero.

$x$	$S(x)$	$l(x)$	$b(x)$
0	500	1.0	0
1	400	0.8	2
2	200	0.4	3
3	50	0.1	1
4	0	0	0

Types of Fecundity Schedules:

Semelparous/monocarpic – reproduce only once in lifetime

Iteroparous/ polycarpic – reproduce multiple times through lifetime

# Life Tables

- What is a life table?
  - “a table of age-specific survival and fecundity rates for a population”
  - A “bookkeeping” device used by ecologists and actuaries to track population numbers and vital rates across age
  - Often focused on tracking survival, but is useful for understanding population change
  - Life table analysis
    - Allows us to calculate key rates and population properties
      - Net reproductive rate per individual  $R_0$
      - Generation Time ( $G$ )
      - Instantaneous growth rate ( $r$ )

# Net Reproductive Rate $R_0$

- Net Reproductive Rate ( $R_0$ ) – the mean number of female offspring produced per female over her lifetime.

$$R_0 = \sum_{x=0}^k l(x)b(x)$$

$x$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$l(x) b(x)$
0	500	1.0	0.8	0	0.0
1	400	0.8	0.5	2	1.6
2	200	0.4	0.25	3	1.2
3	50	0.1	0	1	0.1
4	0	0		0	0.0
					$\Sigma = 2.9$

# Generation Time ( $G$ )

- $R_0$  measures the increase in the population as a function of *generation time*.
- To derive the intrinsic rate of increase in the population ( $r$ ), we need to scale  $R_0$  to Generation Time ( $G$ )



# Generation Time (G)

- Generation Time (G) - the average age of the parents of all offspring produced by a single cohort

$$G = \frac{\sum_{x=0}^k l(x) b(x) x}{\sum_{x=0}^k l(x) b(x)}$$

**G is typically greater than 1.0 for most populations.**

# Generation Time (G)

$x$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$l(x) b(x)$	$l(x) b(x) x$
0	500	1.0	0.8	0	0.0	0.0
1	400	0.8	0.5	2	1.6	1.6
2	200	0.4	0.25	3	1.2	2.4
3	50	0.1	0	1	0.1	0.3
4	0	0		0	0.0	0.0
					$\Sigma = 2.9$	$\Sigma = 4.3$

$$G = \frac{\sum_{x=0}^k l(x) b(x) x}{\sum_{x=0}^k l(x) b(x)} = \frac{4.3}{2.9} = \mathbf{1.483 \text{ years}}$$

What would happen if species didn't reproduce until 2?

# Approximating $r$

- Use the relationship between generation time and Net reproductive rate to get an approximate value of  $r$

$$N_G = N_0 e^{rG}$$

$$\frac{N_G}{N_0} = e^{rG} \quad \text{as } R_0 \approx \frac{N_G}{N_0}$$

$$R_0 \approx e^{rG}$$

$$\ln(R_0) \approx rG$$

$$r \approx \frac{\ln(R_0)}{G}$$

# Euler Equation

- This method is only an approximation of  $r$
  - Euler Equation (“oiler”) used to derive exact values from lifetables:
  - $1 = \sum_{x=0}^k e^{-rx} l(x)b(x)$
1. Start with the estimate of  $r$
  2. calculate out the  $\sum_{x=0}^k e^{-rx} l(x)b(x)$  from the tables
  3. See if it sums to 1.0
  4. If it is too high, plug in a larger value for  $r$  (as we are using a negative exponential).
  5. If too small, put in a smaller value.

# Euler Equation

$x$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$l(x) b(x)$	$l(x) b(x) x$	$e^{-rx} l(x) b(x)$
0	500	1.0	0.8	0	0.0	0.0	0.0
1	400	0.8	0.5	2	1.6	1.6	0.78
2	200	0.4	0.25	3	1.2	2.4	0.285
3	50	0.1	0	1	0.1	0.3	0.012
4	0	0		0	0.0	0.0	0.0
					$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.077$

$$r \approx \frac{\ln(R_0)}{G} \approx \frac{\ln(2.9)}{1.483} \approx 0.718$$

# Euler Equation

*try  $r \approx 0.75$*

$x$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$l(x) b(x)$	$l(x) b(x) x$	$e^{-rx} l(x) b(x)$
0	500	1.0	0.8	0	0.0	0.0	0.0
1	400	0.8	0.5	2	1.6	1.6	0.756
2	200	0.4	0.25	3	1.2	2.4	0.268
3	50	0.1	0	1	0.1	0.3	0.0105
4	0	0		0	0.0	0.0	0.0
					$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.035$

*still too high ....*

# Euler Equation

*trial and error* –  $r = 0.776$

$x$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$l(x) b(x)$	$l(x) b(x) x$	$e^{-rx} l(x) b(x)$
0	500	1.0	0.8	0	0.0	0.0	0.0
1	400	0.8	0.5	2	1.6	1.6	0.736
2	200	0.4	0.25	3	1.2	2.4	0.254
3	50	0.1	0	1	0.1	0.3	0.010
4	0	0		0	0.0	0.0	0.0
					$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.0$

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

Can project future population size!

# Distribution within Age-classes

- In addition to forecasting future population sizes, we can determine the distribution of those individuals within each age class ( $i$ )
- Use age class notation
  - Number of individuals in time ( $t$ ) in age class  $i$  is  $n_i(t)$ .
  - This can be expressed as a vector:

$$n(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$



# Distribution within Age-classes

- Relating this back to the life table

$$\bullet \quad n(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix} = \begin{pmatrix} 500 \\ 400 \\ 200 \\ 50 \end{pmatrix}$$

<i>i</i>	<i>x</i>	<i>S</i> ( <i>x</i> )	<i>l</i> ( <i>x</i> )	<i>g</i> ( <i>x</i> )	<i>b</i> ( <i>x</i> )	<i>l</i> ( <i>x</i> ) <i>b</i> ( <i>x</i> )	<i>l</i> ( <i>x</i> ) <i>b</i> ( <i>x</i> ) <i>x</i>	$e^{-rx} l(x) b(x)$
	0	500	1.0	0.8	0	0.0	0.0	0.0
1	1	400	0.8	0.5	2	1.6	1.6	0.736
2	2	200	0.4	0.25	3	1.2	2.4	0.254
3	3	50	0.1	0	1	0.1	0.3	0.010
4	4	0	0		0	0.0	0.0	0.0
						$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.0$

# Predicting Future Age Structure

- To predict the age structure of a population from one time period  $n(t)$  to the next  $n(t+1)$ , we need to determine two factors:
- Survival Probability for each age class ( $P_i$ )
  - Chance that an individual in age class  $i$  survives to age class  $i+1$
- Fertility of each age class ( $F_i$ )
  - Average number of offspring produced by an individual in age class  $i$

# Predicting Future Age Structure

- To calculate  $P_i$  and  $F_i$  some assumptions need to be made about when individuals reproduce and die!
- Birth-pulse model
  - Individuals give birth to all offspring on the day they enter a new age class
  - Population is censused immediately after breeding (postbreeding census)

# Survival Probability ( $P_i$ ) for age classes

- Survival Probability ( $P_i$ ) - the probability that an individual in age class  $i$  survives to age class  $i+1$ .
- number of individuals  $\mathbf{n}_{t+1}$  that will be in the next time step ( $\mathbf{t} + \mathbf{1}$ ) is a function of the number of individuals  $\mathbf{n}_i$  in the previous time step ( $\mathbf{t}$ ) and the survival probability for that time step  $\mathbf{P}_i$

$$\mathbf{n}_{t+1}(\mathbf{t} + \mathbf{1}) = \mathbf{P}_i \mathbf{n}_i(\mathbf{t})$$

- This works for all age classes except  $i=1$ . Individuals in the first age class depend on the fertility of individuals in all the age classes

# Predicting Future Age Structure

- Calculating Survival Probability  $P_i = \frac{l(i)}{l(i-1)}$

$x$	$i$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$P_i$	$l(x) b(x)$	$l(x) b(x) x$	$e^{-rx} l(x) b(x)$
0		500	1.0	0.8	0		0.0	0.0	0.0
1	1	400	0.8	0.5	2	0.80	1.6	1.6	0.736
2	2	200	0.4	0.25	3	0.50	1.2	2.4	0.254
3	3	50	0.1	0	1	0.25	0.1	0.3	0.010
4	4	0	0		0	0	0.0	0.0	0.0
							$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.0$

# Fertility ( $F_i$ ) for age classes

- Fertility ( $F_i$ ) -average number of offspring produced per female in age class  $i$ , adjusted by the survival probability for that age class

$$F_i = b(i)P_i$$

- The number of individuals in age class 1 at time  $t+1$  is the sum of the fertility of all age classes in the previous time.

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

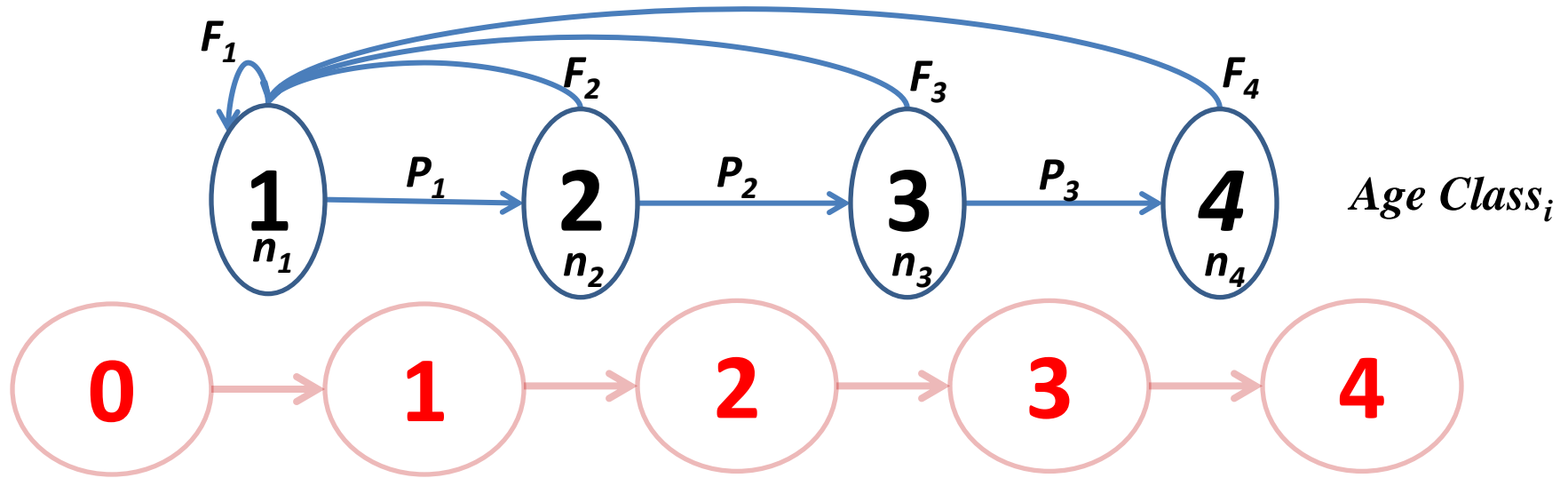
# Predicting Future Age Structure

- Calculating Fertility

$$F_i = b(i)P_i$$

$x$	$i$	$S(x)$	$l(x)$	$g(x)$	$b(x)$	$P_i$	$F_i$	$l(x) b(x)$	$l(x) b(x) x$	$e^{-rx}l(x)b(x)$
0		500	1.0	0.8	0			0.0	0.0	0.0
1	1	400	0.8	0.5	2	0.80	1.60	1.6	1.6	0.736
2	2	200	0.4	0.25	3	0.50	1.50	1.2	2.4	0.254
3	3	50	0.1	0	1	0.25	0.25	0.1	0.3	0.010
4	4	0	0		0	0	0	0.0	0.0	0.0
								$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.0$

# Predicting Future Age Structure



$$n_1(t + 1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$

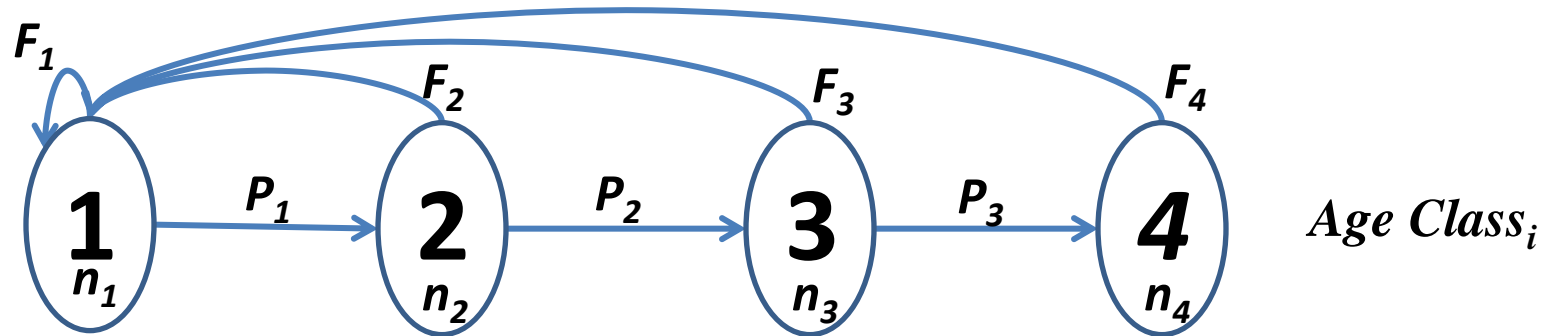
$$n_2(t + 1) = P_1 n_1(t)$$

$$n_3(t + 1) = P_2 n_2(t)$$

$$n_4(t + 1) = P_3 n_3(t)$$



# Predicting Future Age Structure



$$n_1(t + 1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$

$$n_2(t + 1) = P_1 n_1(t)$$

$$n_3(t + 1) = P_2 n_2(t)$$

$$n_4(t + 1) = P_3 n_3(t)$$

What else would be needed if this is stage instead of age based?

# Predicting Age Structure

$$n_1(t+1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$

$$n_2(t+1) = P_1 n_1(t)$$

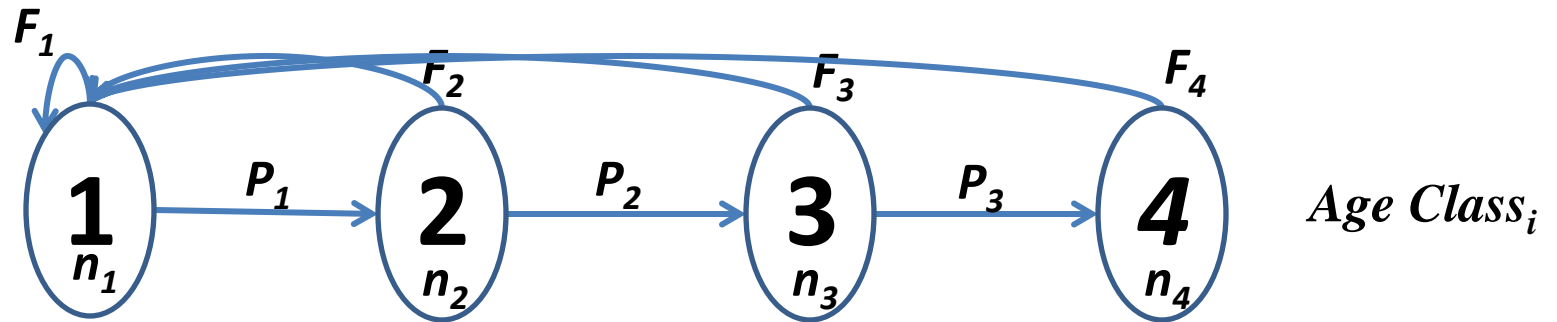
$$n_3(t+1) = P_2 n_2(t)$$

$$n_4(t+1) = P_3 n_3(t)$$

- Cumbersome with life-table data
- Use matrix formulation
  - Leslie matrix (age structured population)
  - Lefkovich matrix (stage structured population)

# Leslie Matrix

Representing Growth in matrix of  $k \times k$  age classes



Columns: age class at time t

Rows: age class at time t + 1

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

Fertility rates

Survival probability

# Leslie Matrix

$x$	$i$	$l(x)$	$b(x)$	$P_i$	$F_i$
0		1.0	0		
1	1	0.8	2	0.80	1.60
2	2	0.4	3	0.50	1.50
3	3	0.1	1	0.25	0.25
4	4	0	0	0	0

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

$$A = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.80 & 0 & 0 & 0 \\ 0 & 0.50 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

# Leslie Matrix

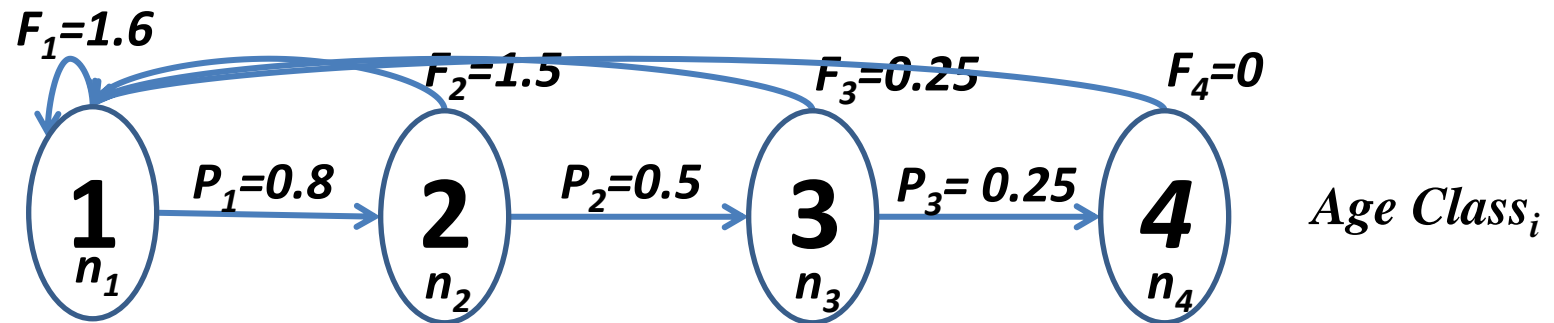
- Forecasting future age structure ( $n$  at time  $t+1$ ) based current population structure ( $n$  at time  $t$ ) using Fertility and Survival Probability from the Leslie Matrix.

$$n(t + 1) = A n(t)$$

$$n(t + 1) = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} x \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}$$

# Examples of Using Leslie Matrix

- Start with a cohort of 200 individuals in age-class 1 with the Fertility and Survival probabilities in our example:



$$n(t+1) = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} x \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} x \begin{pmatrix} 200 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

# Examples of Using Leslie Matrix

$$n(t+1) = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} x \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix} x \begin{pmatrix} 200 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

$$n(t+1) = \begin{bmatrix} 1.6(200) + & 1.5(0) + & 0.25(0) + & 0(0) \\ 0.8(200) + & 0(0) + & 0(0) + & 0(0) \\ 0(200) + & 0.5(0) + & 0(0) + & 0(0) \\ 0(200) + & 0(0) + & 0.25(0) + & 0(0) \end{bmatrix}$$

$$n(t+1) = \begin{bmatrix} 320 \\ 160 \\ 0 \\ 0 \end{bmatrix}$$

# Leslie Matrix

# Age structured growth - one time step

```
A <- matrix(c(1.6,1.5,0.25,0,0.8,0,0,0,0,0.5,0,0,0,0,0.25,0), nrow=4, byrow=TRUE)
```

	[,1]	[,2]	[,3]	[,4]
[1,]	1.6	1.5	0.25	0
[2,]	0.8	0.0	0.00	0
[3,]	0.0	0.5	0.00	0
[4,]	0.0	0.0	0.25	0

```
N0 <- matrix(c(200,0,0,0),ncol=1)
```

	[,1]
[1,]	200
[2,]	0
[3,]	0
[4,]	0

```
N1 <- A %*% N0
```

	[,1]
[1,]	320
[2,]	160
[3,]	0
[4,]	0



# Leslie Matrix

```
A <- matrix(c(1.6,1.5,0.25,0,0.8,0,0,0,0,0.5,0,0,0,0,0.25,0), nrow=4, byrow=TRUE)
N0 <- matrix(c(200,0,0,0),ncol=1)

years <- 6
N.projections <- matrix(0,nrow=nrow(A),ncol = years +1)
N.projections[,1]<- N0

for(year in 1:years){
  N.projections[,year+1]<- A %*% N.projections[,year]
}
```

		Year						
Age class		[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
	[1,]	200	320	752	1607.2	3505.92	7613.312	16549.12
	[2,]	0	160	256	601.6	1285.76	2804.736	6090.65
	[3,]	0	0	80	128	300.8	642.88	1402.368
	[4,]	0	0	0	20	32	75.2	160.72

# Leslie Matrix

```
A <- matrix(c(1.6,1.5,0.25,0,0.8,0,0,0,0,0.5,0,0,0,0,0.25,0), nrow=4, byrow=TRUE)
```

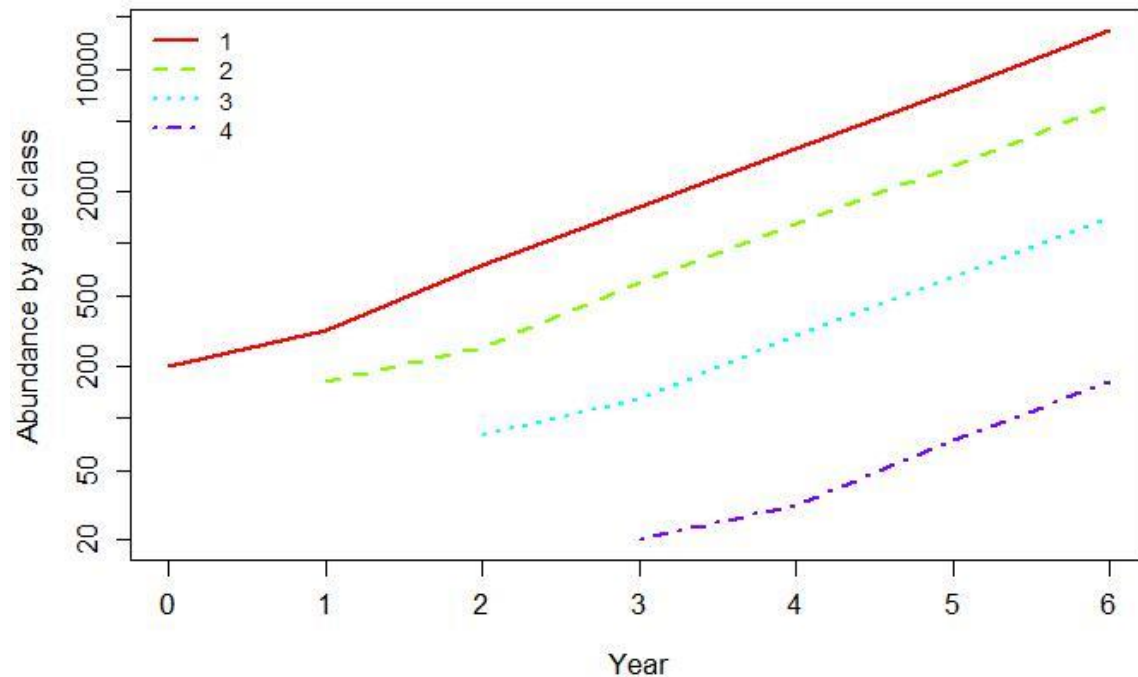
```
N0 <- matrix(c(200,0,0,0),ncol=1)
```

```
years <- 6
```

```
N.projections <- matrix(0,nrow=nrow(A),ncol = years +1)
```

```
N.projections[,1]<- N0
```

```
for(year in 1:years){  
  N.projections[,year+1]<- A %*% N.projections[,year]  
}
```



# Leslie Matrix (different starting structure)

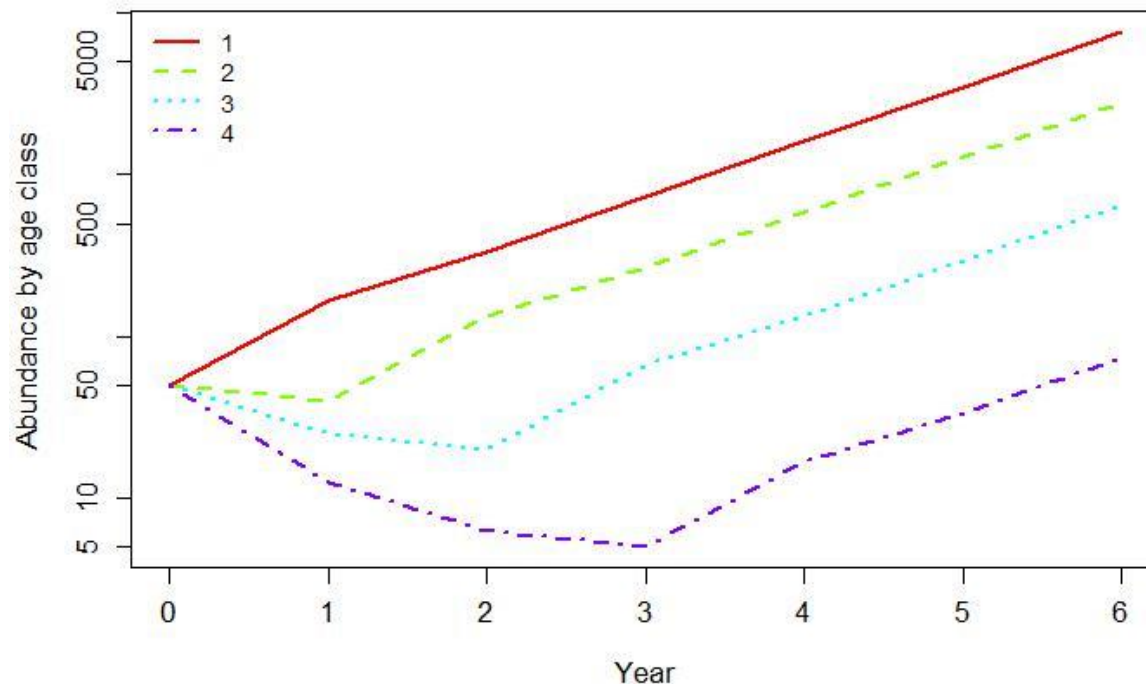
```
A <- matrix(c(1.6,1.5,0.25,0,0.8,0,0,0,0,0.5,0,0,0,0,0.25,0), nrow=4, byrow=TRUE)
N0 <- matrix(c(50,50,50,50),ncol=1)
```

```
years <- 6
```

```
N.projections1 <- matrix(0,nrow=nrow(A),ncol = years +1)
```

```
N.projections1[,1]<- N0
```

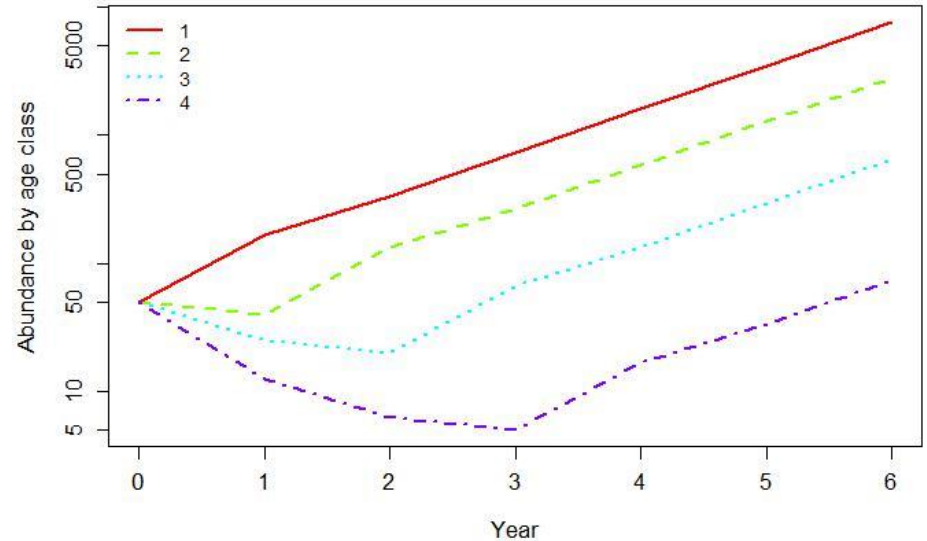
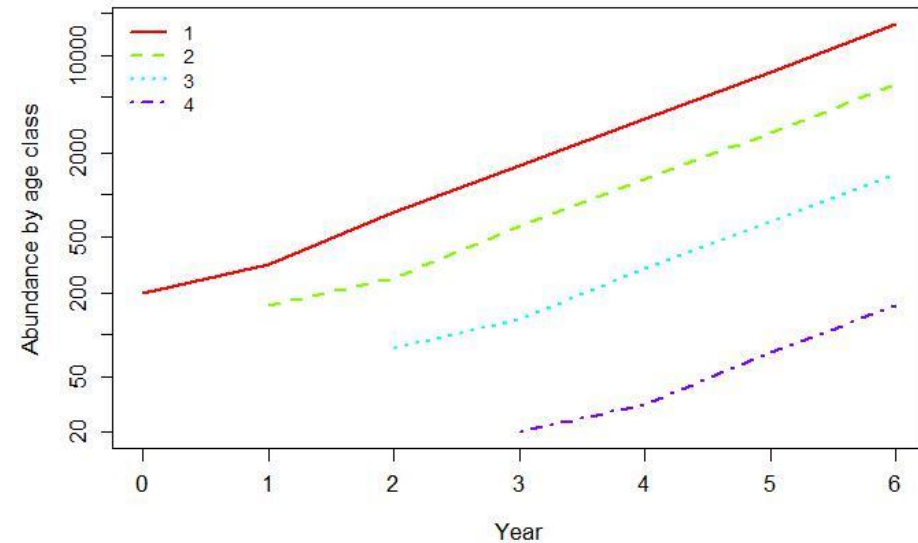
```
for(year in 1:years){
  N.projections1[,year+1]<- A %*% N.projections1[,year]
}
```



# Age distribution

$$n(\mathbf{0}) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200$$

$$n(\mathbf{0}) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200$$



- Dynamics initially strongly influenced by starting population age distribution
- However, populations quickly approach a stable and stationary age distribution

# Stable Age Distribution

- If Survival and Fertility schedules stay constant, the *proportion of individuals in the population* at each age will stay constant (Stable Age Structure) even as the population as a whole increases.
- The proportion of the population within each age  $[c(x)]$  is the number in that age divided by the total population size.
- $$c(x) = \frac{e^{-rx}l(x)}{\sum_{x=0}^k e^{-rx}l(x)}$$

# Stable age distribution

$$n(\mathbf{0}) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200$$

	[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
[1,]	200.00	320.00	752.00	1607.20	3505.92	7613.31	16549.12
[2,]	0.00	160.00	256.00	601.60	1285.76	2804.74	6090.65
[3,]	0.00	0.00	80.00	128.00	300.80	642.88	1402.37
[4,]	0.00	0.00	0.00	20.00	32.00	75.20	160.72
N	200.00	480.00	1088.00	2356.80	5124.48	11136.13	24202.86
	1.00	0.67	0.69	0.68	0.68	0.68	0.68
	0.00	0.33	0.24	0.26	0.25	0.25	0.25
	0.00	0.00	0.07	0.05	0.06	0.06	0.06
	0.00	0.00	0.00	0.01	0.01	0.01	0.01

$$n(\mathbf{0}) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200$$

	[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
[1,]	50.00	167.50	334.25	740.80	1603.13	3487.39	7577.67
[2,]	50.00	40.00	134.00	267.40	592.64	1282.50	2789.91
[3,]	50.00	25.00	20.00	67.00	133.70	296.32	641.25
[4,]	50.00	12.50	6.25	5.00	16.75	33.43	74.08
N	200.00	245.00	494.50	1080.20	2346.22	5099.64	11082.91
	0.25	0.68	0.68	0.69	0.68	0.68	0.68
	0.25	0.16	0.27	0.25	0.25	0.25	0.25
	0.25	0.10	0.04	0.06	0.06	0.06	0.06
	0.25	0.05	0.01	0.00	0.01	0.01	0.01

# Finite Rate of Change

- Use population Change from  $n(t)$  to  $n(t+1)$  to calculate the finite rate of change ( $\lambda$ )

- $\lambda = \frac{n(t)}{n(t-1)}$

- $n(\mathbf{0}) = \begin{bmatrix} 200 \\ \textcolor{blue}{0} \\ \textcolor{red}{0} \\ \textcolor{green}{0} \end{bmatrix} = 200$

$$\lambda = \frac{480}{200} = 2.4$$

$$r = \ln \lambda = \ln 2.4 = 0.875$$

- $n(\mathbf{1}) = \begin{bmatrix} 320 \\ \textcolor{blue}{160} \\ \textcolor{red}{0} \\ \textcolor{green}{0} \end{bmatrix} = 480$

# Stable age distribution

$$n(\mathbf{0}) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200$$

	[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
[1,]	200.00	320.00	752.00	1607.20	3505.92	7613.31	16549.12
[2,]	0.00	160.00	256.00	601.60	1285.76	2804.74	6090.65
[3,]	0.00	0.00	80.00	128.00	300.80	642.88	1402.37
[4,]	0.00	0.00	0.00	20.00	32.00	75.20	160.72
N	200.00	480.00	1088.00	2356.80	5124.48	11136.13	24202.86
lambda		2.40	2.27	2.17	2.17	2.17	2.17
r		0.88	0.82	0.77	0.78	0.78	0.78

$$\lambda = \frac{n(t)}{n(t-1)}$$

$$r = \ln \lambda$$

$$n(\mathbf{0}) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200$$

	[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
[1,]	50.00	167.50	334.25	740.80	1603.13	3487.39	7577.67
[2,]	50.00	40.00	134.00	267.40	592.64	1282.50	2789.91
[3,]	50.00	25.00	20.00	67.00	133.70	296.32	641.25
[4,]	50.00	12.50	6.25	5.00	16.75	33.43	74.08
N	200.00	245.00	494.50	1080.20	2346.22	5099.64	11082.91
lambda		1.23	2.02	2.18	2.17	2.17	2.17
r		0.20	0.70	0.78	0.78	0.78	0.78



# Assumptions

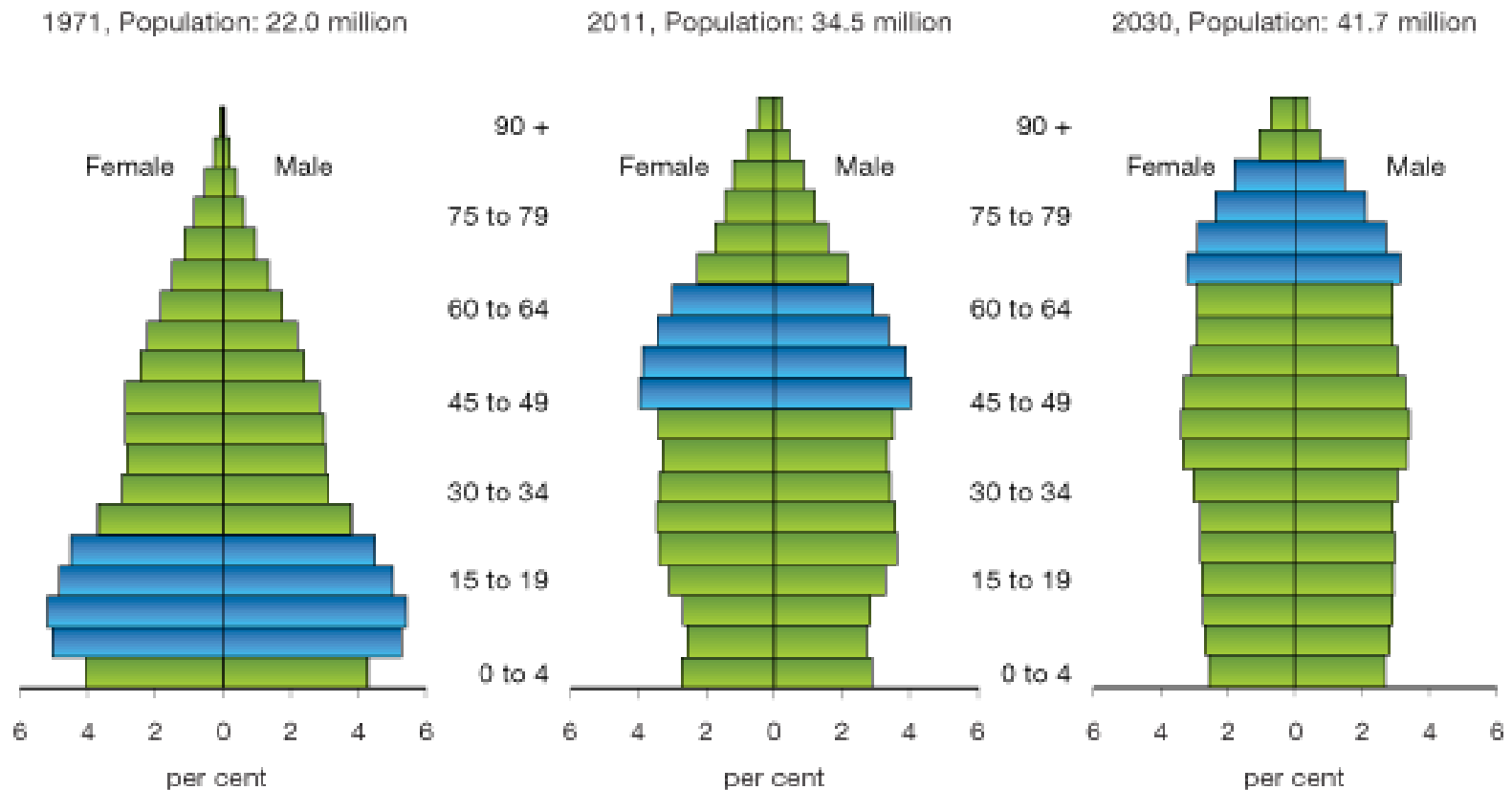
- Assumptions associated with Exponential Growth...
- Closed population
- No genetic structure
- No time lags
  
- Within Age-structured Populations
- Assume  $l(x)$  and  $b(x)$  schedules are constant
  - *no resource limitation*

# Cohort vs Static Life Tables

- **Cohort Life Tables** — follow an entire cohort from birth to death to determine age-specific survivorship and fecundity schedules.
- **Static Life Table** – cross section of the population at a given time interval. Used to calculate short-term mortality rates by comparing number of individuals within each consecutive age class.
- Also assumes population has reached a stable age structure

# Changes in Age structure of populations over time

## Changing age structure in Canadian Populations, and future projections



# State structured matrix model

## Life Stage, rather than Age, Models (Lefkovitch Matrices)

- Fecundity and survivorship may be based more on life stage than absolute age

$$\begin{array}{l}
 \text{egg} \\
 \text{tadpole} \\
 \text{adult}
 \end{array}
 \begin{bmatrix}
 \text{egg} & \text{tadpole} & \text{adult} \\
 0 & 0 & F_{a-e} \\
 P_{e-t} & P_{t-t} & 0 \\
 0 & P_{t-a} & P_{a-a}
 \end{bmatrix}$$

