BIOL 410 Population and Community Ecology

Age structured populations

Sampling population density

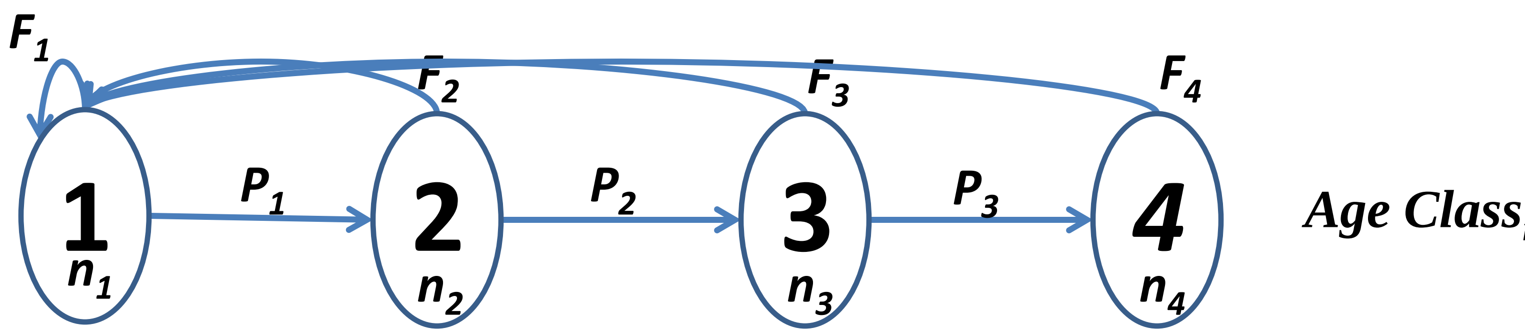
Predicting Age Structure

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
								$\Sigma = 2.9$	$\Sigma = 4.3$	$\Sigma = 1.0$

$$n_1(t+1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$
$$n_2(t+1) = P_1 n_1(t)$$
$$n_3(t+1) = P_2 n_2(t)$$
$$n_4(t+1) = P_3 n_3(t)$$

Leslie Matrix

Representing Growth in matrix of *k x k* age classes



Columns: age class at time t

Rows: age class at time t +1

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

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.

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

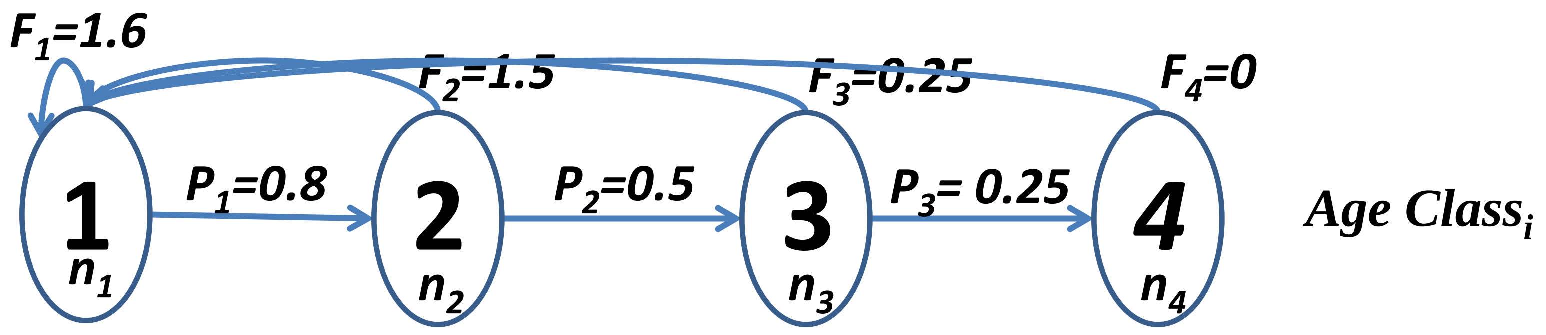
$$n(t+1) = \begin{bmatrix} \boldsymbol{F_1} & \boldsymbol{F_2} & \boldsymbol{F_3} & \boldsymbol{F_4} \\ \boldsymbol{P_1} & 0 & 0 & 0 \\ 0 & \boldsymbol{P_2} & 0 & 0 \\ 0 & 0 & \boldsymbol{P_3} & 0 \end{bmatrix} \boldsymbol{x} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}$$

Matrix algebra

- Product of a square matrix and a column matrix (vector) is a column matrix
- Useful for solving linear equations

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:



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

Examples of Using Leslie Matrix

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

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

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

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]
}
```

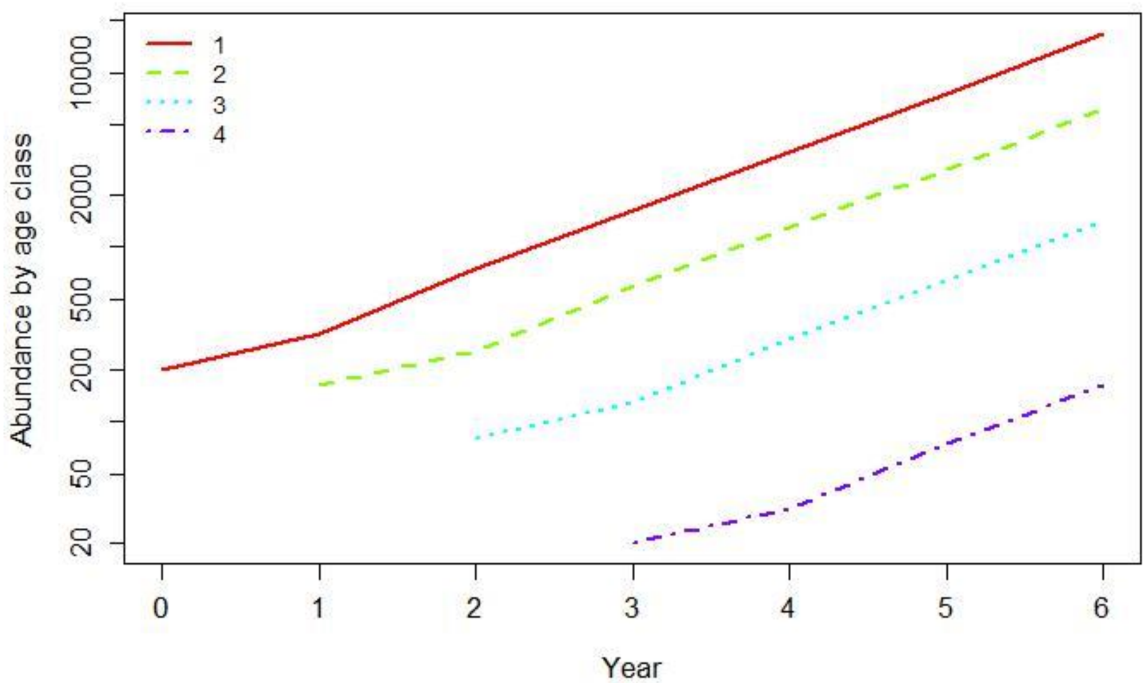
Year

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

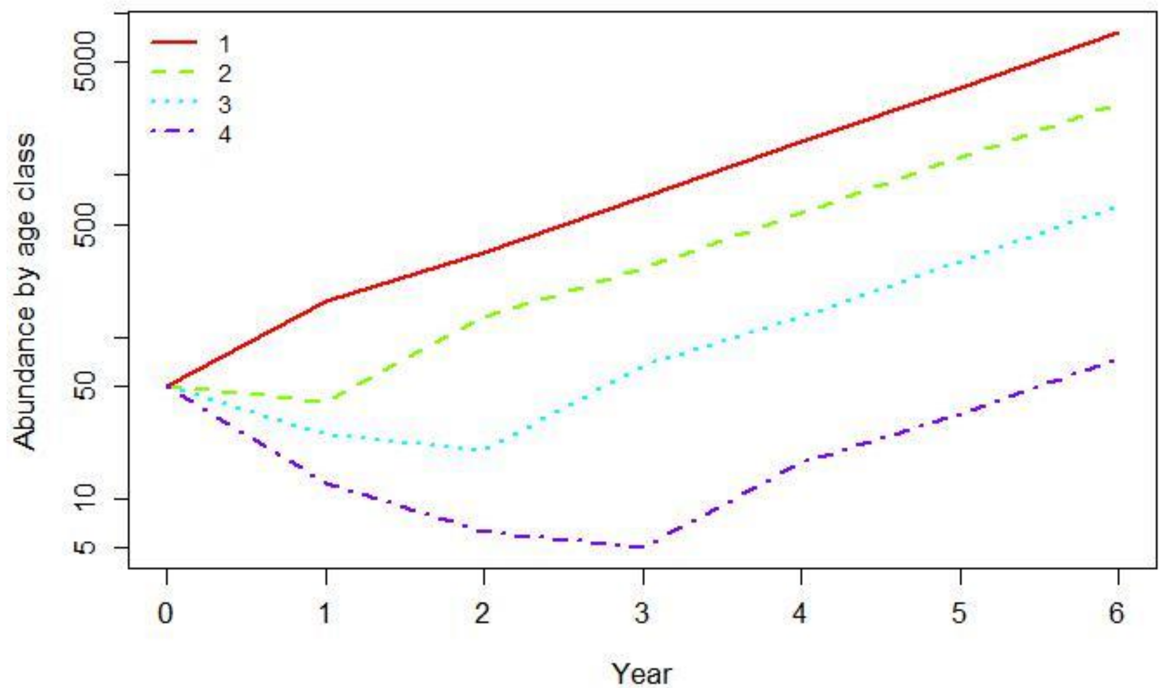
Leslie Matrix

```
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)

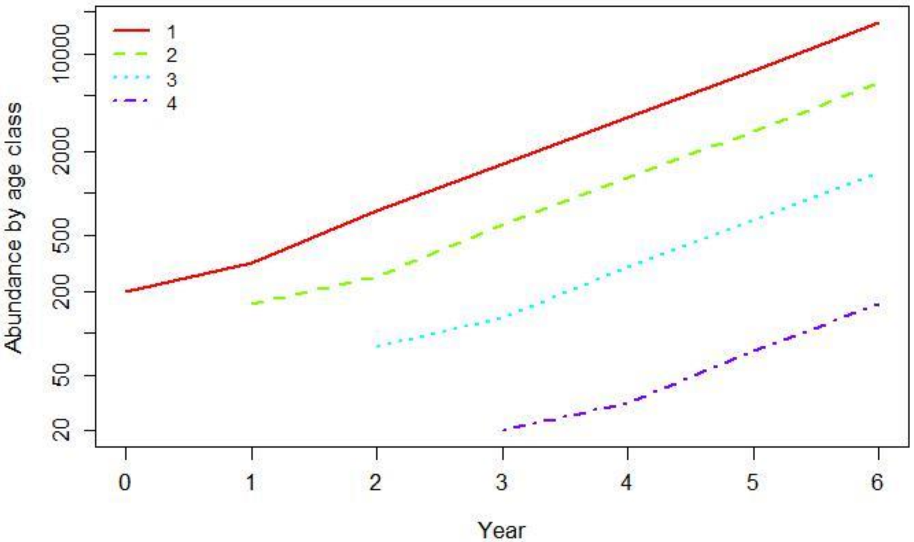
```
A <- matrix(c(1.6,1.5,0.25,0,0.8,0,0,0,0,0.5,0,0,0,0,0.25,0), nrow=4, byrow=TRUE)
N0 <- matrix(c(50,50,50,50),ncol=1)

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]
}
```

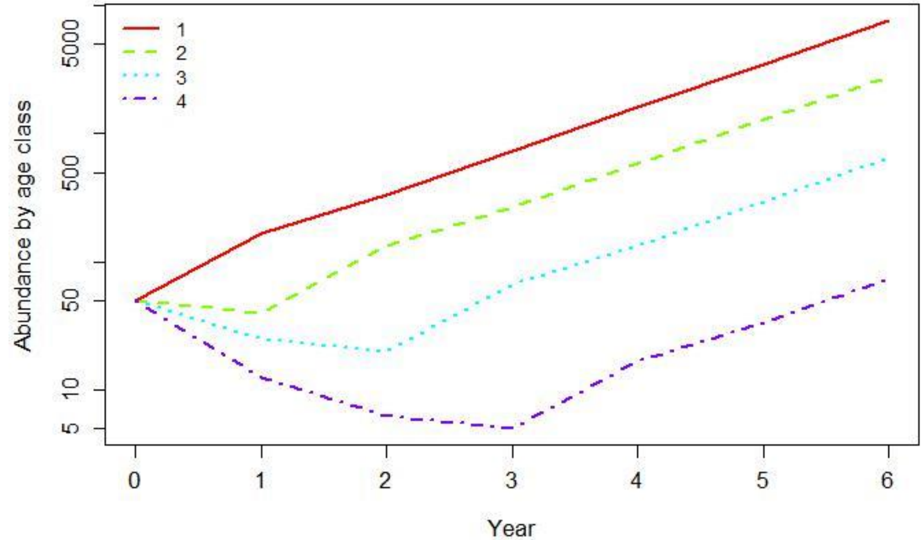


Age distribution

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

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





- 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

$$n(\mathbf{0}) = \begin{bmatrix} \color{red}{200} \\ \color{yellowgreen}{0} \\ \color{deepskyblue}{0} \\ \color{purple}{0} \end{bmatrix} = 200$$

	[,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

c(x)

$$n(\mathbf{0}) = \begin{bmatrix} \color{red}{50} \\ \color{yellowgreen}{50} \\ \color{deepskyblue}{50} \\ \color{purple}{50} \end{bmatrix} = 200$$

	[,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

c(x)

Finite Rate of Change

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

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

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

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

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

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

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

$$\lambda = \frac{n(t)}{n(t-1)} \qquad r = ln\,\lambda$$

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

	[,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*

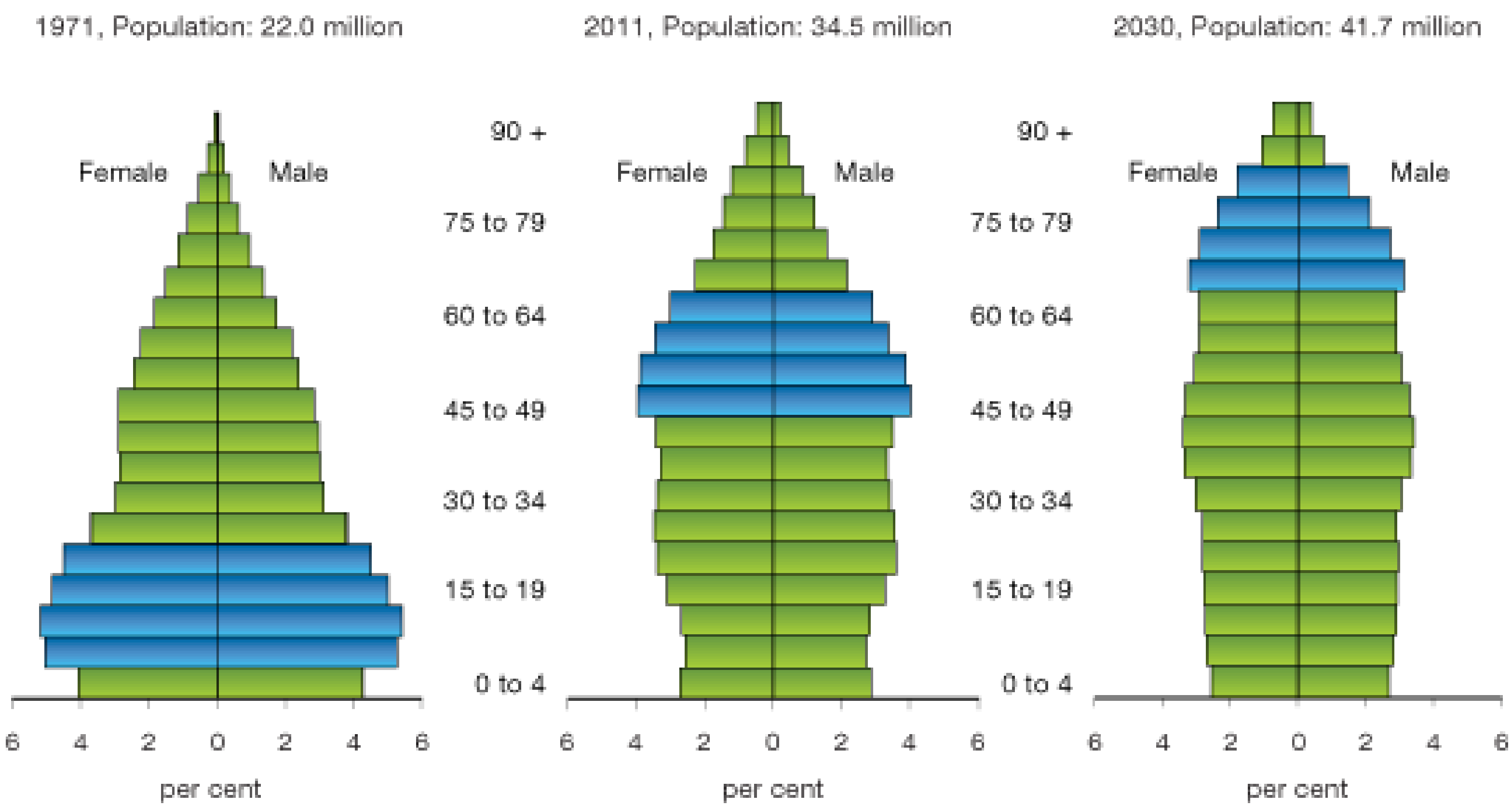
Cohort vs Static Life Tables

- 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

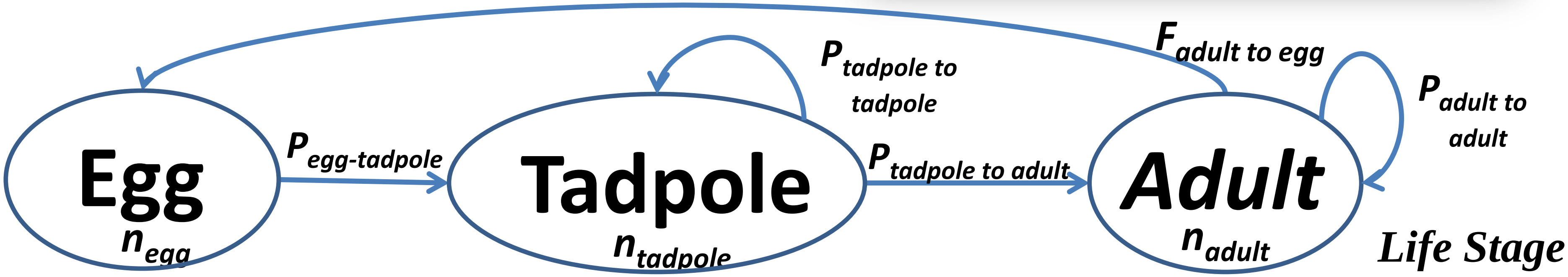


State structured matrix model

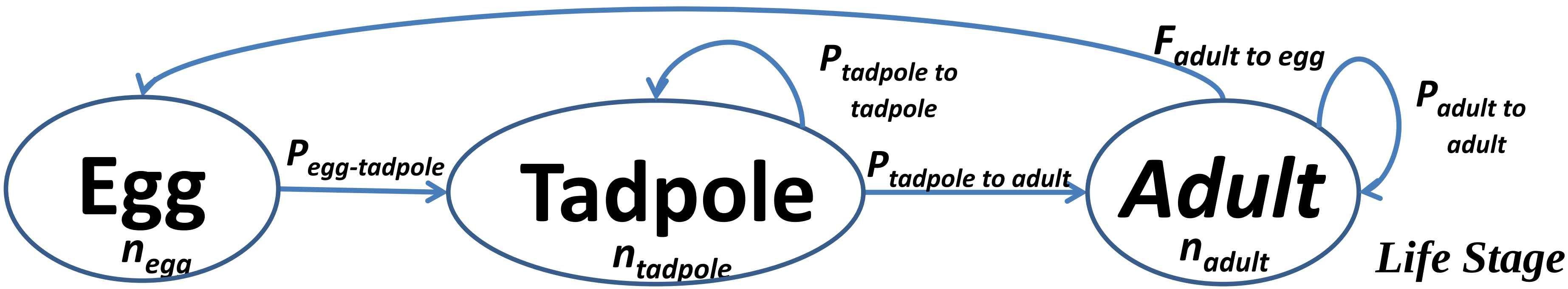
Life Stage, rather than Age, Models (Lefkovitch Matrices)

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

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



Stage structured model



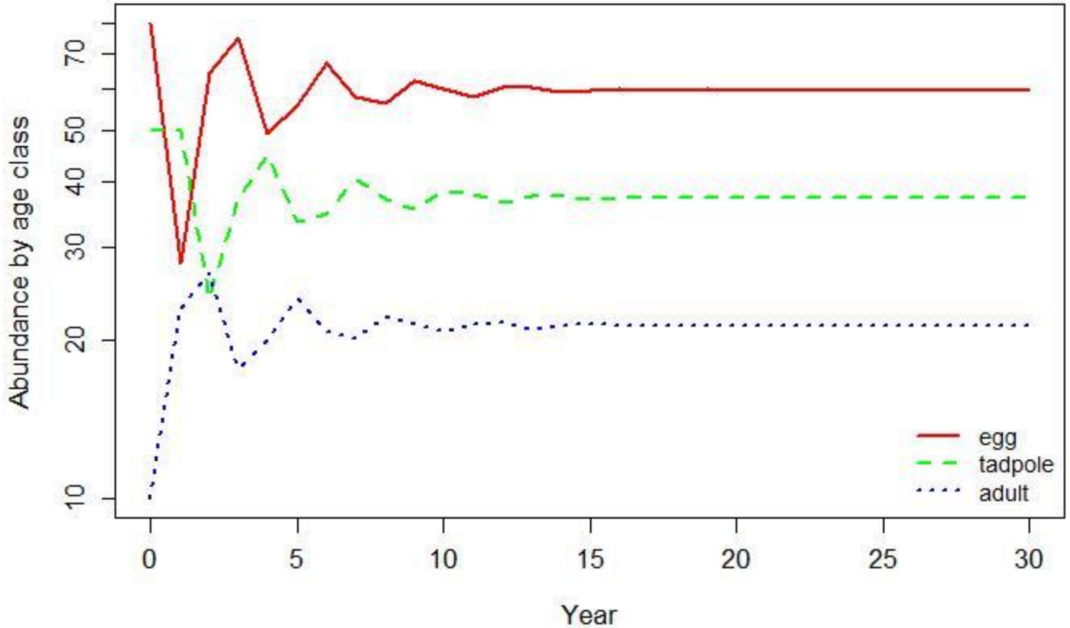

```r
# Stage structured growth: frog 1
A <- matrix(c(0,0,2.8,0.5,0.2,0,0,0.4,0.3), nrow=3, byrow=TRUE)
N0 <- matrix(c(80,50,10),ncol=1)
```

A =

```
     [,1] [,2] [,3]
[1,]  0.0  0.0  2.8
[2,]  0.5  0.2  0.0
[3,]  0.0  0.4  0.3
```

Stage structured model

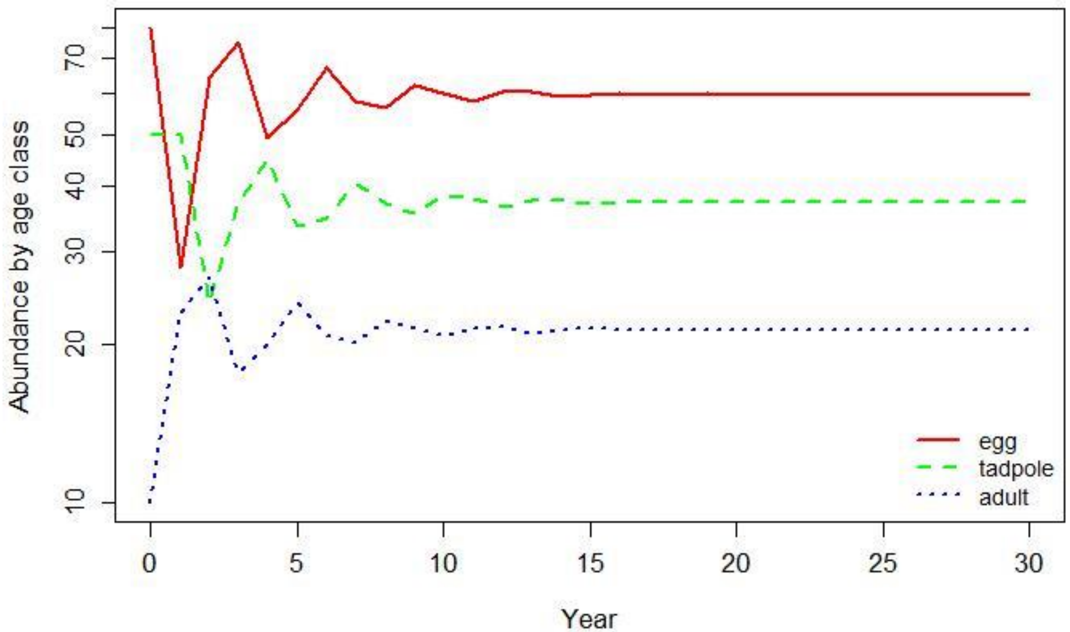
```
# Stage structured growth: frog 1
A <- matrix(c(0,0,2.8,0.5,0.2,0,0,0.4,0.3), nrow=3, byrow=TRUE)
N0 <- matrix(c(80,50,10),ncol=1)

years <- 30
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]
}
```



Dynamic link between stage classes

Stage structured model

```
# Stage structured growth: frog 1
A <- matrix(c(0,0,2.8,0.5,0.2,0,0,0.4,0.3), nrow=3, byrow=TRUE)
N0 <- matrix(c(80,50,10),ncol=1)

years <- 30
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]
}
```

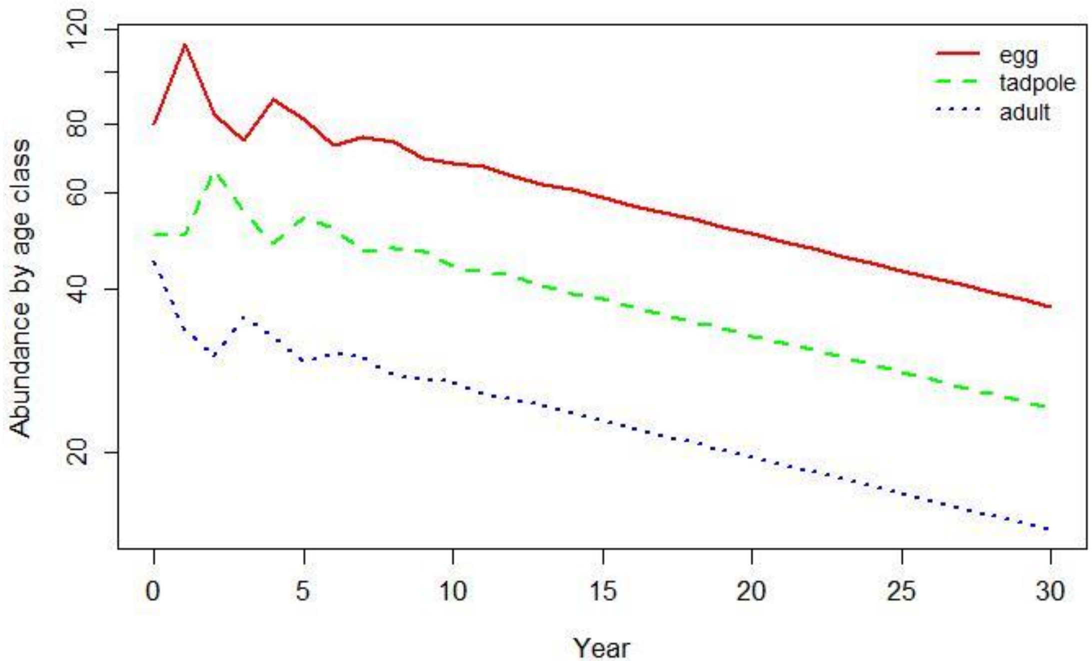


What does this suggest about r?

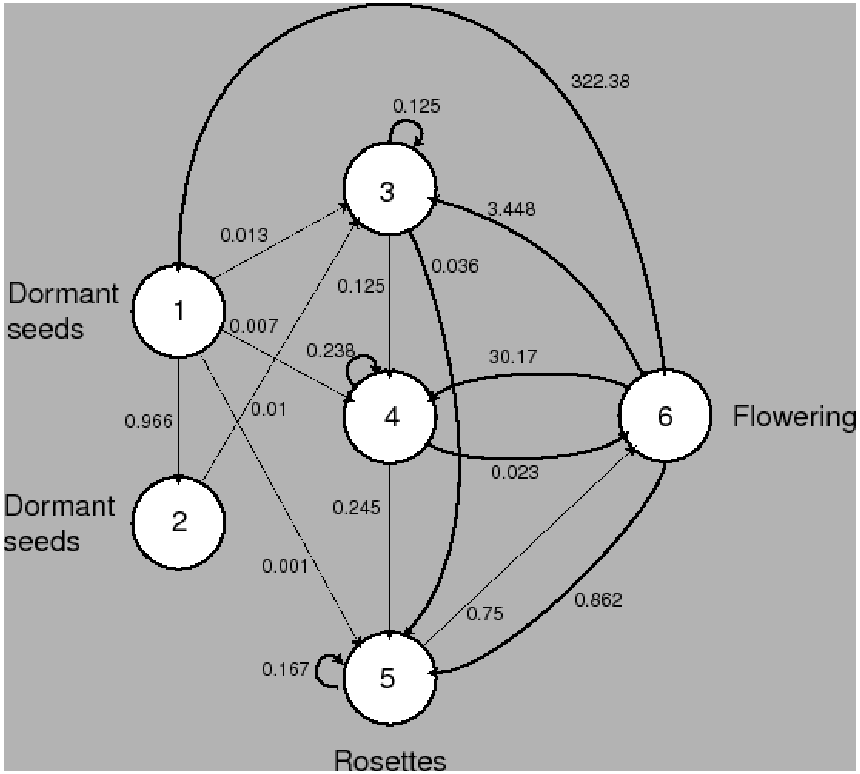
What does this suggest about perturbation at t = 0?

Stage structured model

```
A <- matrix(c(0,0,2.5,0.5,0.2,0,0,0.4,0.3), nrow=3, byrow=TRUE)
N0 <- matrix(c(80,50,45),ncol=1)

years <- 30
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]
}
```



Life history complexity



$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 322.38 \\ 0.966 & 0 & 0 & 0 & 0 & 0 \\ 0.013 & 0.010 & 0.125 & 0 & 0 & 3.448 \\ 0.007 & 0 & 0.125 & 0.238 & 0 & 30.170 \\ 0.001 & 0 & 0.036 & 0.245 & 0.167 & 0.862 \\ 0 & 0 & 0 & 0.023 & 0.750 & 0 \end{pmatrix}$$

wild teasel

H Caswell.
Matrix Population Models: Construction, Analysis, and Interpretation.
Sinauer Associates, Sunderland, MA, 2nd edition, 2001.

Population sampling

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

$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

$$N_t = \frac{K}{1 + [(K - N_0)/N_0]e^{-rt}}$$

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

Population sampling

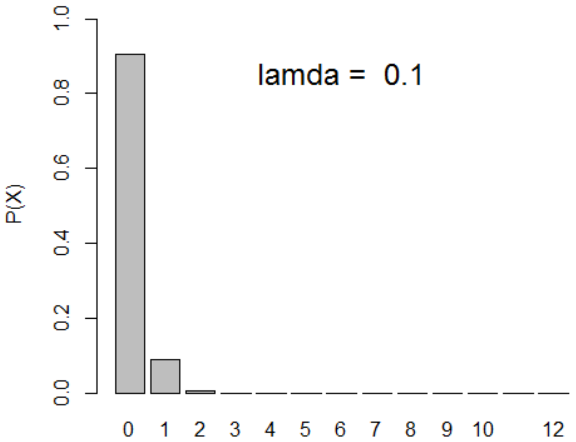
Estimating N

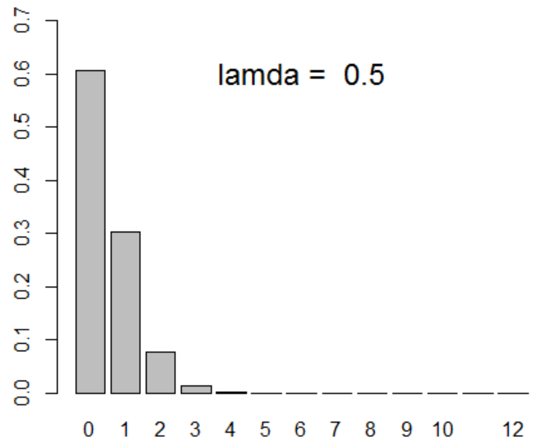
N is always estimated (sampled)

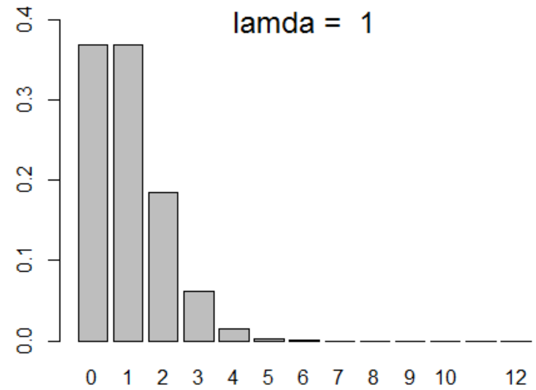
- Distribution not a point estimate
  - Measure of central tendency (mean)
  - Measure of variation (standard deviation)

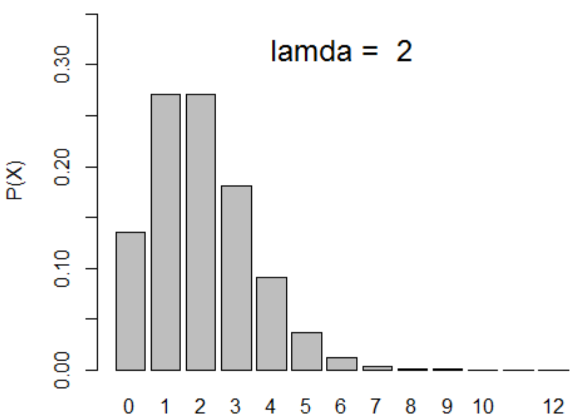
- Accuracy
  - The distance of the measured value from the “true” value
- Precisions
  - The degree of aggregation of the measured values
  - Confidence intervals
- Bias
  - A consistent directional disparity between the measured value and the true value.

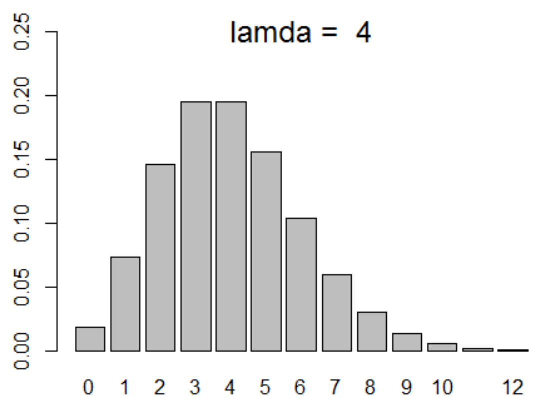
Normal vs. Poisson











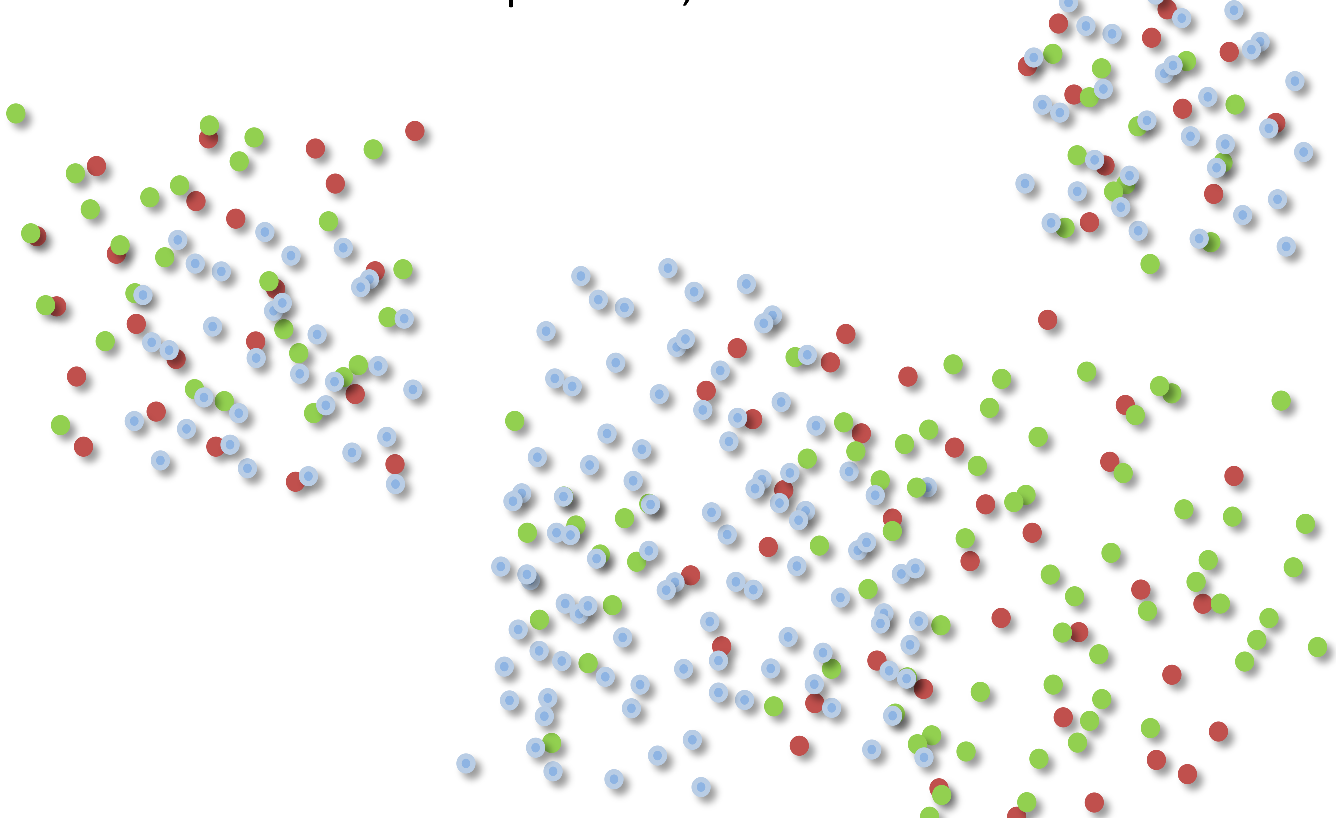

```
# Poisson distribution
x <- c(0:12)
lamda <- 8 # 0.1, 0.5, 1,2,3,8
p <- dpois(x,lamda)
barplot(p,axes = TRUE,
        names.arg = x,
        ylim=c(0,max(p)+0.1),
        ylab = "P(X)"
        )
mtext(paste("lamda = ",lamda),side=3,
      outer=FALSE,line=-3,cex=1.5)
```

Population sampling strategies

Number
Density

- Random sampling
- Stratified random sampling
- Stratified sampling
- Systematic sampling

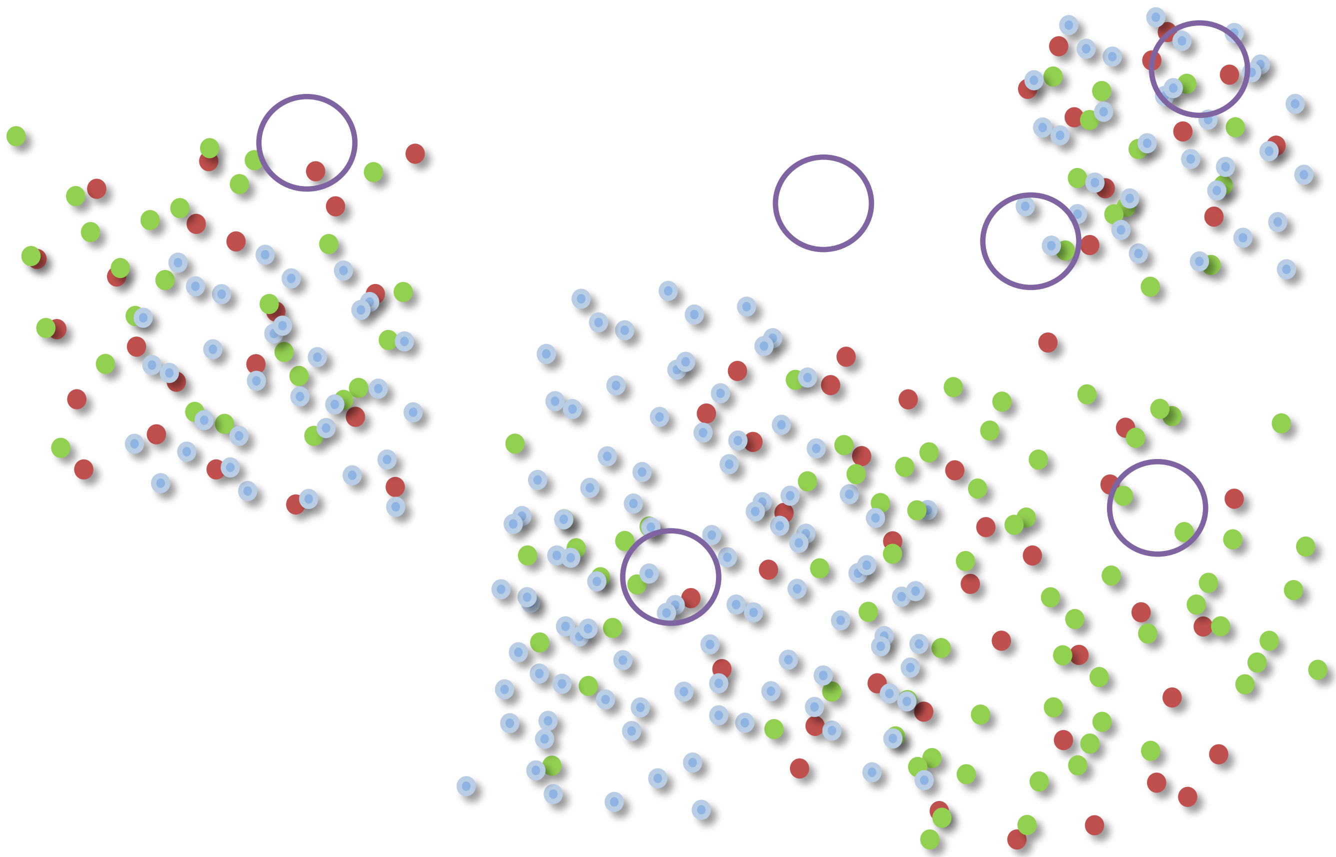
- Objective: high accuracy, least bias, greatest precision, lowest cost



Population sampling strategies

Number
Density

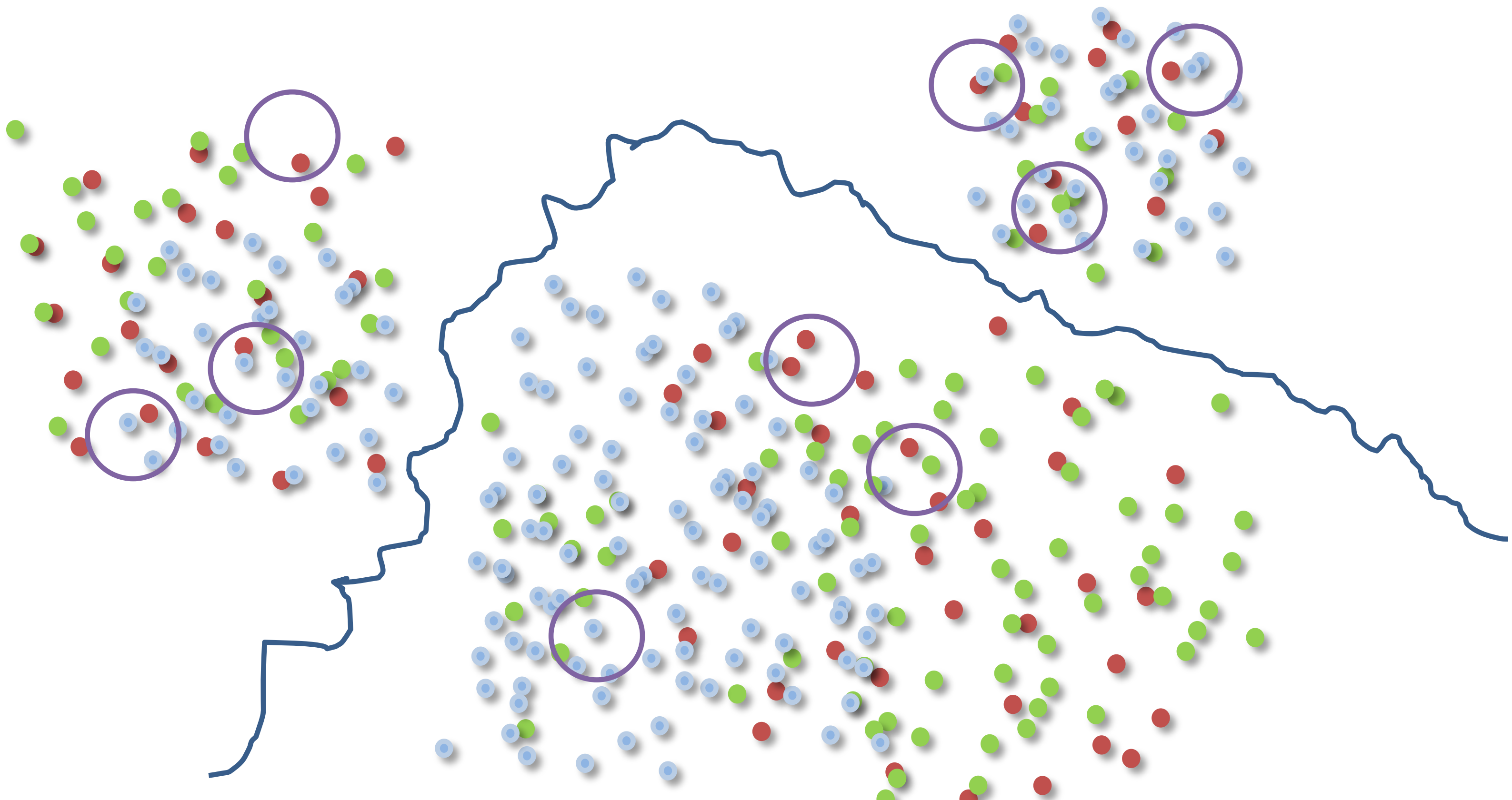
- Random sampling
  - Minimizes the amount our estimate of N is confounded by **unknown** or **unmeasured** variables
  - Minimize bias (unknown, accessibility, judgement)
  - Unknown (unknowable) environmental heterogeneity



Population sampling strategies

Number
Density

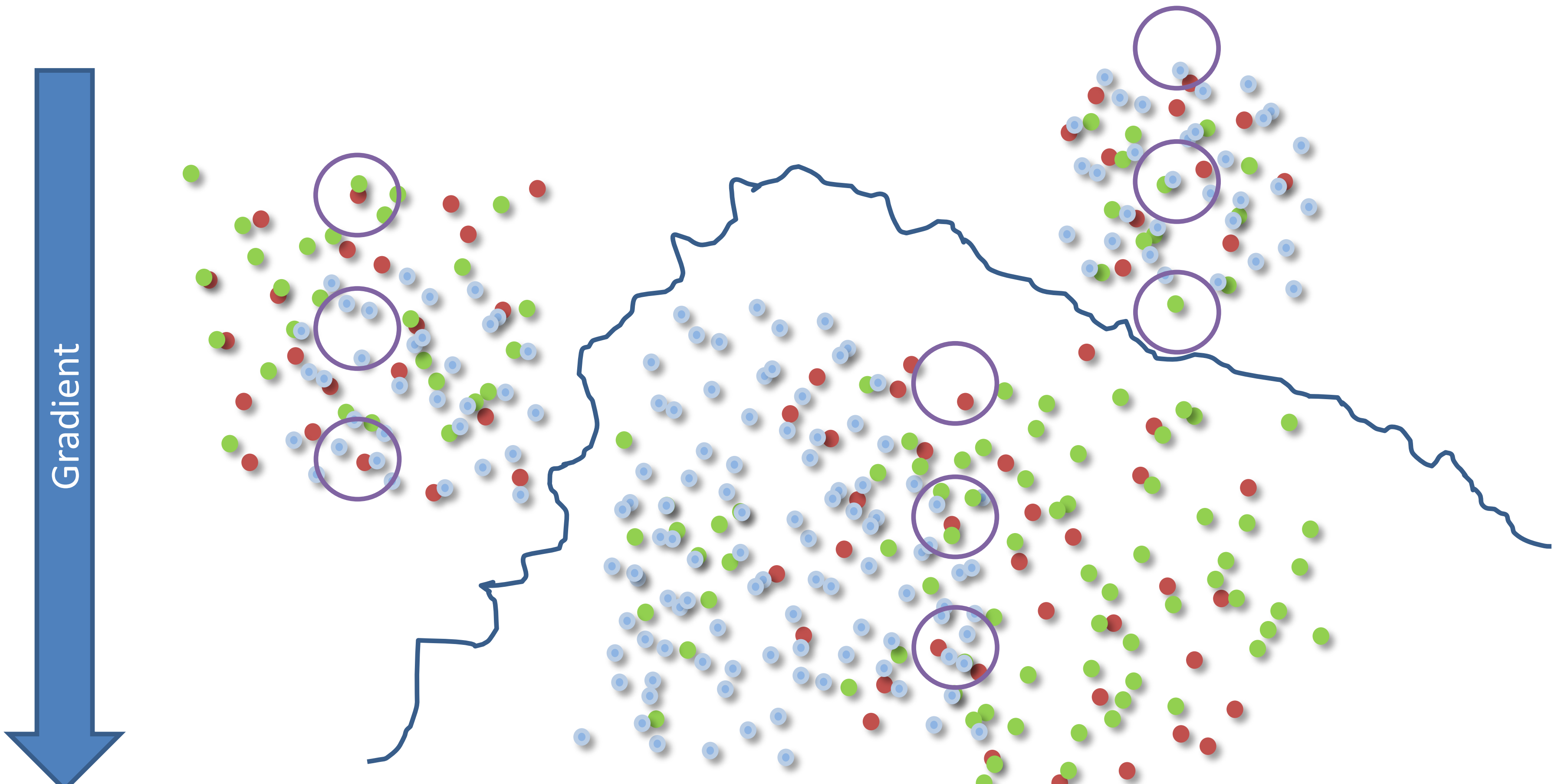
- Stratified random sampling
  - Assumed underlying ecological structure (grouping, subpopulations)
  - Aggregate sampling by strata
  - Random sampling within strata
    - Unknown structure within strata



Population sampling strategies

Number
Density

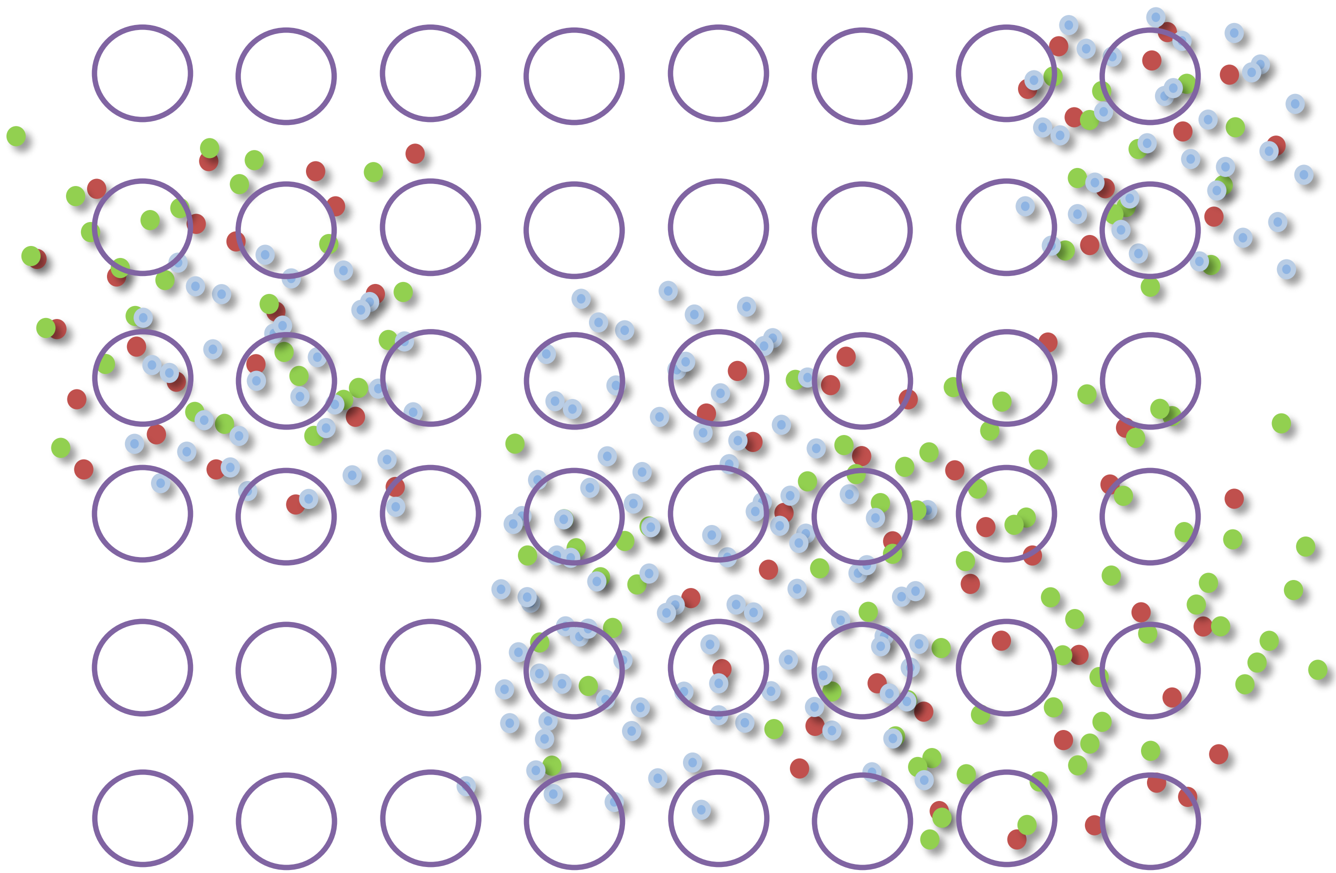
- Stratified sampling
  - Assumed underlying ecological structure (grouping)
  - Aggregate sampling by strata
  - Systematic sampling within strata

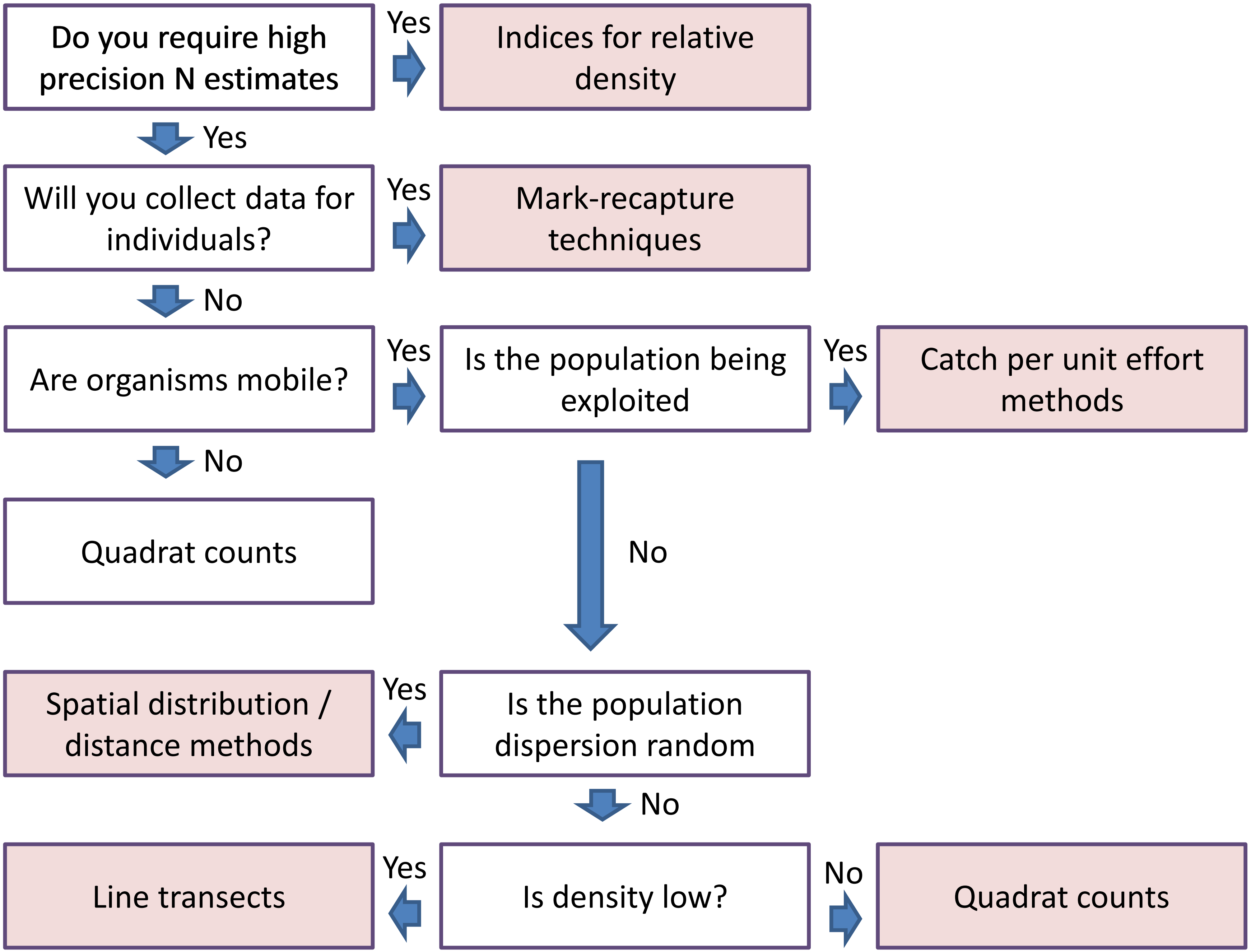


Population sampling strategies

Number
Density

- Systematic sampling
  - Known or unknown ecological structure



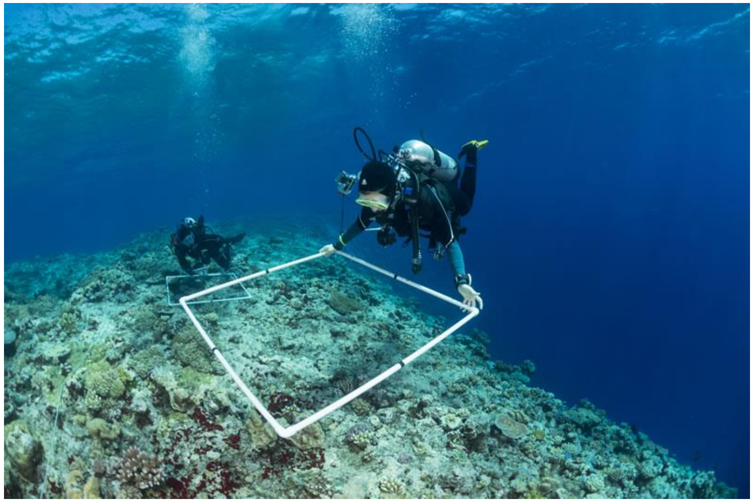

Do you require high precision N estimates
Yes
Indices for relative density
Yes
Will you collect data for individuals?
Yes
Mark-recapture techniques
No
Are organisms mobile?
Yes
Is the population being exploited
Yes
Catch per unit effort methods
No
Quadrat counts
No
Spatial distribution / distance methods
Yes
Is the population dispersion random
No
Line transects
Yes
Is density low?
No
Quadrat counts

Population density sampling

- Quadrat counts
- Line transects
- Distance metrics

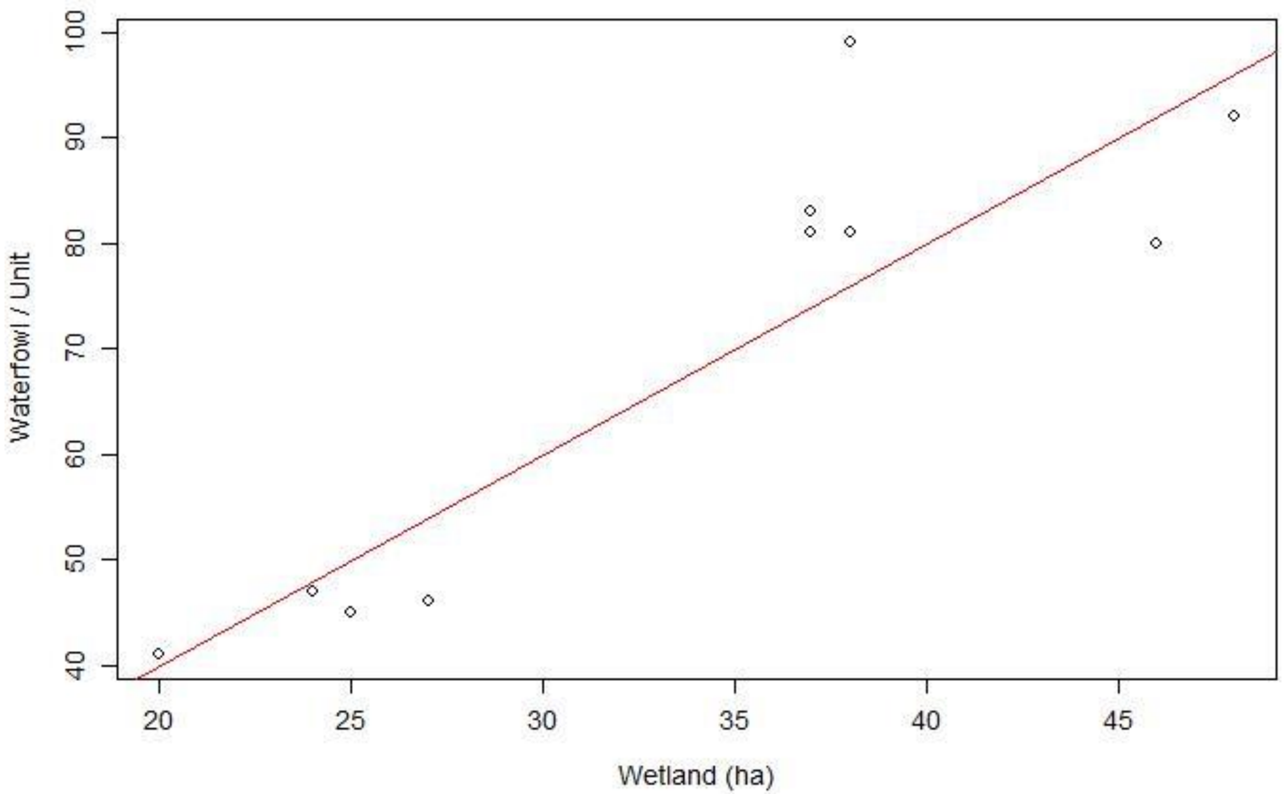
Quadrat counts

- Count plants/ animals in a known area
  - Simplest technique fore density estimation
  - Counts can be taken from units using any number of sample designs: random, stratified random, systematic..
  - Assumptions
    - All individuals in the quadrate are observed
    - Quadrat samples are representative of the study area as a whole
    - Individuals don’t move between quadrats during a sampling session



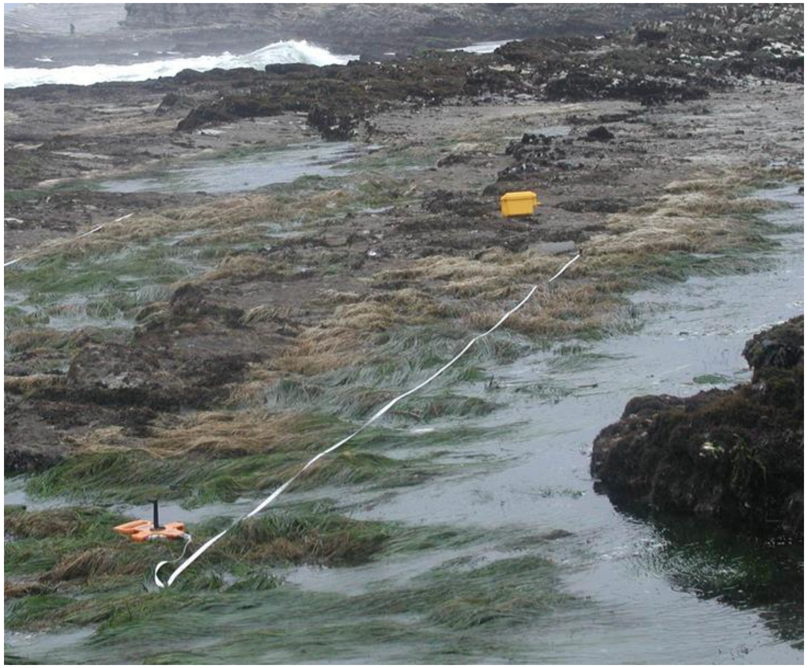
Quadrat counts

- Statistical extrapolation
  - Relate distribution of counts to a statistical distribution
  - Use count distribution not a continuous distribution
  - Devise a statistical model that estimates population size



Line transects

- Used to calculate density of animals in rectangular “quadrats”



Line transects

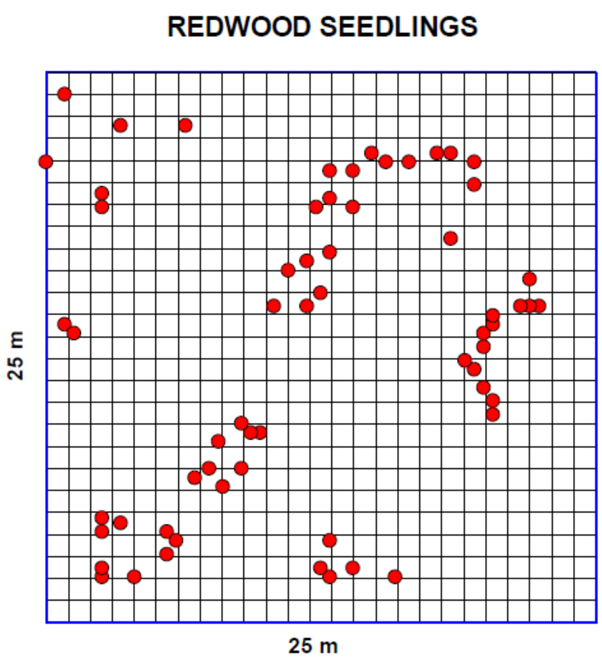
- Used to calculate density of animals in rectangular "quadrats"
  - If detectability 100% simple count
  - If detectability <100% then develop detection function to estimate density

$$\widehat{D} = \frac{n}{2La}$$

$\widehat{D}$ = density of animals per unit area
n = number of animals seen on transect
L = length of transect
a = detection constant (detection probability vs distance)

Distance methods

- Distance to individual from random point
- Distance to nearest neighbor



$$\widehat{N_2} = \frac{N}{\pi \sum (r_i{}^2)} = trees/m^2$$