BIOL 410 Population and Community Ecology

Age structured populations
Sampling population density
Predicting Age Structure

\[
n_1(t + 1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t) \\
n_2(t + 1) = P_1 n_1(t) \\
n_3(t + 1) = P_2 n_2(t) \\
n_4(t + 1) = P_3 n_3(t)
\]
Leslie Matrix

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

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

Columns: age class at time $t$
Rows: age class at time $t+1$
Fertility rates
Survival probability
Leslie Matrix

<table>
<thead>
<tr>
<th>$x$</th>
<th>$i$</th>
<th>$l(x)$</th>
<th>$b(x)$</th>
<th>$P_i$</th>
<th>$F_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1.0</td>
<td>0.8</td>
<td>2</td>
<td>0.80</td>
<td>1.60</td>
</tr>
<tr>
<td>2</td>
<td>1.0</td>
<td>0.5</td>
<td>2</td>
<td>0.50</td>
<td>1.50</td>
</tr>
<tr>
<td>3</td>
<td>1.0</td>
<td>0.25</td>
<td>2</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>4</td>
<td>1.0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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

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

\[ n(t + 1) = A \, n(t) \]

\[
\begin{bmatrix}
F_1 & F_2 & F_3 & F_4 \\
P_1 & 0 & 0 & 0 \\
0 & P_2 & 0 & 0 \\
0 & 0 & P_3 & 0
\end{bmatrix}
\begin{pmatrix}
n_1 \\
n_2 \\
n_3 \\
n_4
\end{pmatrix}
\]
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:

\[
\begin{align*}
\text{Age Class}_i \\
1 & n_1 & F_1=1.6 & P_1=0.8 \\
2 & n_2 & F_2=1.5 & P_2=0.5 \\
3 & n_3 & F_3=0.25 & P_3=0.25 \\
4 & n_4 & F_4=0 & \\
\end{align*}
\]

\[
\begin{align*}
\mathbf{n}(t+1) &= \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} \times \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix} = \begin{pmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{pmatrix} \times \begin{pmatrix} 200 \\ 0 \\ 0 \\ 0 \end{pmatrix}
\end{align*}
\]
Examples of Using Leslie Matrix

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

\[
n(t + 1) = \begin{bmatrix} 1.6(200) + 1.5(0) + 0.25(0) + 0(0) \\ 0.8(200) + 0(0) + 0(0) + 0(0) \\ 0(200) + 0.5(0) + 0(0) + 0(0) \\ 0(200) + 0(0) + 0.25(0) + 0(0) \end{bmatrix} = \begin{bmatrix} 320 \\ 160 \\ 0 \\ 0 \end{bmatrix}
\]
# Age structured growth - one time step

\[ A \leftarrow \text{matrix}(c(1.6,1.5,0.25,0,0.8,0,0,0,0.5,0,0,0,0,0,0.25,0), \text{nrow}=4, \text{byrow}=\text{TRUE}) \]

\[
\begin{array}{cccc}
  [1,] & 1.6 & 1.5 & 0.25 & 0 \\
  [2,] & 0.8 & 0.0 & 0.00 & 0 \\
  [3,] & 0.0 & 0.5 & 0.00 & 0 \\
  [4,] & 0.0 & 0.0 & 0.25 & 0 \\
\end{array}
\]

\[
\begin{array}{c}
  \text{N0} \leftarrow \text{matrix}(c(200,0,0,0), \text{ncol}=1) \\
\end{array}
\]

\[
\begin{array}{c}
  [,1] \\
  [1,] & 200 \\
  [2,] & 0 \\
  [3,] & 0 \\
  [4,] & 0 \\
\end{array}
\]

\[
\begin{array}{c}
  \text{N1} \leftarrow A \%\% \text{N0} \\
\end{array}
\]

\[
\begin{array}{c}
  [,1] \\
  [1,] & 320 \\
  [2,] & 160 \\
  [3,] & 0 \\
  [4,] & 0 \\
\end{array}
\]
Leslie Matrix

\[
A \leftarrow \text{matrix}(c(1.6, 1.5, 0.25, 0.8, 0, 0, 0, 0.5, 0, 0, 0, 0.25, 0), \text{nrow}=4, \text{byrow}=\text{TRUE}) \\
N\emptyset \leftarrow \text{matrix}(c(200, 0, 0, 0), \text{ncol}=1)
\]

years \leftarrow 6 \\
\text{N.projections} \leftarrow \text{matrix}(\emptyset, \text{nrow}=\text{nrow}(A), \text{ncol}=\text{years} + 1) \\
\text{N.projections}[,1] \leftarrow N\emptyset \\

\text{for(year in 1:years){} \\
  \text{N.projections}[,,\text{year}+1] \leftarrow A \cdot \text{N.projections}[,,\text{year}] \\
}\]

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</tr>
</thead>
<tbody>
<tr>
<td>[1,]</td>
<td>200</td>
<td>320</td>
<td>752</td>
<td>1607.2</td>
<td>3505.92</td>
<td>7613.312</td>
<td>16549.12</td>
</tr>
<tr>
<td>[2,]</td>
<td>0</td>
<td>160</td>
<td>256</td>
<td>601.6</td>
<td>1285.76</td>
<td>2804.736</td>
<td>6090.65</td>
</tr>
<tr>
<td>[3,]</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>128</td>
<td>300.8</td>
<td>642.88</td>
<td>1402.368</td>
</tr>
<tr>
<td>[4,]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>32</td>
<td>75.2</td>
<td>160.72</td>
</tr>
</tbody>
</table>
Leslie Matrix

\[
A \leftarrow \text{matrix}(c(1.6, 1.5, 0.25, 0, 0.8, 0, 0, 0, 0.5, 0, 0, 0, 0, 0.25, 0), \text{nrow}=4, \text{byrow=}\text{TRUE})
\]
\[
N_0 \leftarrow \text{matrix}(c(200, 0, 0, 0), \text{ncol}=1)
\]

\[
\text{years} \leftarrow 6
\]
\[
\text{N.projections} \leftarrow \text{matrix}(0, \text{nrow}=\text{nrow}(A), \text{ncol} = \text{years} + 1)
\]
\[
\text{N.projections}[,,1] \leftarrow N_0
\]

\[
\text{for(year in 1:years)}\{
    \text{N.projections}[,,\text{year+1}] \leftarrow A \times \text{N.projections}[,,\text{year}]
\}
\]
Leslie Matrix (different starting structure)

\[
A <- \text{matrix}(c(1.6, 1.5, 0.25, 0, 0.8, 0, 0, 0, 0, 0, 0.5, 0, 0, 0, 0.25, 0), \text{nrow}=4, \text{byrow}=\text{TRUE})
\]

\[
N0 <- \text{matrix}(c(50, 50, 50, 50), \text{nrow}=1)
\]

years <- 6
N.projections1 <- \text{matrix}(0, \text{nrow}=\text{nrow}(A), \text{ncol} = \text{years} + 1)
N.projections1[,1] <- N0

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

![Graph showing population projections over different years.]
Age distribution

\[ n(0) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200 \]

\[ n(0) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200 \]

- 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

\[ n(0) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200 \]

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<tbody>
<tr>
<td>[1,]</td>
<td>200.00</td>
<td>320.00</td>
<td>752.00</td>
<td>1607.20</td>
<td>3505.92</td>
<td>7613.31</td>
<td>16549.12</td>
</tr>
<tr>
<td>[2,]</td>
<td>0.00</td>
<td>160.00</td>
<td>256.00</td>
<td>601.60</td>
<td>1285.76</td>
<td>2804.74</td>
<td>6090.65</td>
</tr>
<tr>
<td>[3,]</td>
<td>0.00</td>
<td>0.00</td>
<td>80.00</td>
<td>128.00</td>
<td>300.80</td>
<td>642.88</td>
<td>1402.37</td>
</tr>
<tr>
<td>[4,]</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>20.00</td>
<td>32.00</td>
<td>75.20</td>
<td>160.72</td>
</tr>
<tr>
<td>N</td>
<td>200.00</td>
<td>480.00</td>
<td>1088.00</td>
<td>2356.80</td>
<td>5124.48</td>
<td>11136.13</td>
<td>24202.86</td>
</tr>
</tbody>
</table>

\[ c(x) = \begin{bmatrix} 1.00 \\ 0.00 \\ 0.00 \\ 0.00 \end{bmatrix} \]

\[ n(0) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200 \]

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</tr>
</thead>
<tbody>
<tr>
<td>[1,]</td>
<td>50.00</td>
<td>167.50</td>
<td>334.25</td>
<td>740.80</td>
<td>1603.13</td>
<td>3487.39</td>
<td>7577.67</td>
</tr>
<tr>
<td>[2,]</td>
<td>50.00</td>
<td>40.00</td>
<td>134.00</td>
<td>267.40</td>
<td>592.64</td>
<td>1282.50</td>
<td>2789.91</td>
</tr>
<tr>
<td>[3,]</td>
<td>50.00</td>
<td>25.00</td>
<td>20.00</td>
<td>67.00</td>
<td>133.70</td>
<td>296.32</td>
<td>641.25</td>
</tr>
<tr>
<td>[4,]</td>
<td>50.00</td>
<td>12.50</td>
<td>6.25</td>
<td>5.00</td>
<td>16.75</td>
<td>33.43</td>
<td>74.08</td>
</tr>
<tr>
<td>N</td>
<td>200.00</td>
<td>245.00</td>
<td>494.50</td>
<td>1080.20</td>
<td>2346.22</td>
<td>5099.64</td>
<td>11082.91</td>
</tr>
</tbody>
</table>

\[ c(x) = \begin{bmatrix} 0.25 \\ 0.25 \\ 0.25 \end{bmatrix} \]
Finite Rate of Change

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

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

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

• \( n(1) = \begin{bmatrix} 320 \\ 160 \\ 0 \\ 0 \end{bmatrix} = 480 \)

\[
\lambda = \frac{480}{200} = 2.4
\]

\[
r = ln \lambda = ln2.4 = 0.875
\]
Stable age distribution

\[ n(0) = \begin{bmatrix} 200 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 200 \]

\[ n(0) = \begin{bmatrix} 50 \\ 50 \\ 50 \\ 50 \end{bmatrix} = 200 \]

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

\[ r = \ln \lambda \]
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

1971, Population: 22.0 million
2011, Population: 34.5 million
2030, Population: 41.7 million
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

\[
\begin{bmatrix}
  e_{gg} & t_{tadpole} & a_{adult} \\
  0 & 0 & F_{a-e} \\
  P_{e-t} & P_{t-t} & 0 \\
  0 & P_{t-a} & P_{a-a}
\end{bmatrix}
\]
# 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)
Stage structured model

# Stage structured growth: frog 1

\[
A \leftarrow \text{matrix}(c(0,0,2.8,0.5,0.2,0,0,0.4,0.3), \text{nrow}=3, \text{byrow}=\text{TRUE})
\]

\[
N0 \leftarrow \text{matrix}(c(80,50,10), \text{ncol}=1)
\]

\[
\text{years} \leftarrow 30
\]

\[
\text{N.projections1} \leftarrow \text{matrix}(0, \text{nrow} = \text{ncol}(A), \text{ncol} = \text{years} + 1)
\]

\[
\text{N.projections1}[1:1] \leftarrow N0
\]

\[
\text{for}(\text{year in 1:years}){
\quad \text{N.projections1}[\text{year+1}] \leftarrow A \times N.projections1[\text{year}]
\}
\]

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

\[
\begin{bmatrix}
0 & 0 & 2.5 \\
0 & 0.5 & 0.2 \\
2.5 & 0.5 & 0.2 \\
\end{bmatrix}
\]

\[
N_0 = \begin{bmatrix} 80 \\ 50 \\ 45 \end{bmatrix}
\]

\[
\text{years} = 30
\]

\[
\text{N.projections1} = \begin{bmatrix} 0 \\ & & \end{bmatrix}
\]

\[
\text{N.projections1}[,1] = N_0
\]

\[
\text{for(year in 1:years)}{
\quad \text{N.projections1}[,year+1] = A \times N.projections1[,year]
}\]

![Graph showing abundance by age class over years](image-url)
Life history complexity

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

Population sampling

\[ N_t = N_0 e^{rt} \]

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

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

\[ n(t + 1) = A \, n(t) \]
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

```r
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

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

Objective: high accuracy, least bias, greatest precision, lowest cost
Population sampling strategies

- 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

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

• Stratified sampling
  • Assumed underlying ecological structure (grouping)
  • Aggregate sampling by strata
  • Systematic sampling within strata
Population sampling strategies

- Systematic sampling
  - Known or unknown ecological structure

Number Density
Do you require high precision N estimates

Yes

Indices for relative density

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

No

Quadrat counts

Spatial distribution / distance methods

Yes

Is the population dispersion random

Yes

Line transects

Is density low?

No

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 quadrat 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

\[ \hat{D} = \frac{n}{2La} \]

\(\hat{D}\) = 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

\[ \frac{N}{\pi \sum(r_i^2)} = \text{trees/m}^2 \]