Life-history modeling of marine mammal populations:
*Lecture 2: Age- and stage-structured models*

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Did a change in birth rates or death rates cause a decline?

Northern Right Whales are highly endangered (ca. 300 left). Despite protection, they are not recovering. Why??

Is it calving rates?

Or adult female mortality from boat strikes and entanglement?

Photo: Florida Fish and Wildlife Conservation Commission/NOAA
Is this population increasing or decreasing?

Life-span of your marine mammal of interest

Length of your study period = 4 yrs

20,30,100 years
The most common approach for these types of analyses is life-history modeling with Leslie matrices.
Today’s lecture topics:

• What is a life-history model?

• Most important attributes of a life-history model
  – Long-term rate of increase, $\lambda$
  – Stable age-distribution

• The Leslie matrix version of a life-history model

• How do you determine a population’s Leslie matrix?

• Two types of common analyses using Leslie matrices
  – Sensitivity analysis
  – Historical analysis
An age-structured life-history model translates numbers THIS year to numbers NEXT year.
A stage-structured life-history model translates numbers in a stage THIS year to numbers in stage NEXT year.

Northern Right Whale life-history model

A generic pinniped life-history model

Life-history models are often female only

0.30 female pups per mature female

Survival to NEXT year

80% 90% 90% 90%
<table>
<thead>
<tr>
<th>Year</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>pup</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 1</td>
<td>800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 2</td>
<td>500</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 3</td>
<td>300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 4+</td>
<td>200</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Total # = 1900 1760 1713
After awhile, the population starts to grow (or decline) exponentially at some rate $\lambda$ (think of it like % change)
Some real population trajectories for long-lived species

Real data

Exponential growth

Northern fur seals

$\lambda < 1$

$\lambda > 1$

California sea lions

$\lambda > 1$

Northern Resident Killer Whales up to 2000

$\lambda > 1$

African Elephants

$\lambda > 1$

Whooping Cranes

$\lambda > 1$

Wandering Albatross

$\lambda < 1$
After a few years the proportion of animals in each age class stabilizes (it doesn’t take long)
How do life-history models help answer “Is this population increasing or decreasing?”

Life-span of your marine mammal of interest might be long (30+ yrs)

3-4 year study on reproduction and survival

Stable age-structure

\( \lambda \) long-term rate of population increase (or decrease)

40 yrs
Today’s lecture topics:

• What is a life-history model
• Most important attributes of a life-history model
  – Long-term rate of increase, $\lambda$
  – Stable age-distribution
• The **Leslie matrix** version of a life-history model
• How do you determine a population’s Leslie matrix?
• Two types of common analyses using Leslie matrices
  – Sensitivity analysis
  – Historical analysis (forensics)
A Leslie matrix is a mathematical way of writing the life-history cartoon.

This YEAR

<table>
<thead>
<tr>
<th></th>
<th>Pups</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pups</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>Age 1</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 2</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 3</td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 4+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Next YEAR

- 80% from pup to 1
- 90% from 1 to 2
- 90% from 2 to 3
- 90% from 3 to 4+
- 90% from 4+ to 1

0.30
The Leslie matrix

- Translates numbers this year (top) to next year (bottom)
- Top row is natality
- Other rows are survivorship

<table>
<thead>
<tr>
<th></th>
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<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4+</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>This YEAR</strong></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td><strong>Next YEAR</strong></td>
<td>0.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0.9</td>
</tr>
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</table>
Let’s project the population forward with matrix algebra

<table>
<thead>
<tr>
<th></th>
<th>Pups</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4+</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEXT year</td>
<td>60</td>
<td>80</td>
<td>720</td>
<td>450</td>
<td>450</td>
</tr>
<tr>
<td>THIS year</td>
<td>100</td>
<td>800</td>
<td>500</td>
<td>300</td>
<td>200</td>
</tr>
</tbody>
</table>

Green is pups next year by females age j in this year
Red is number of age j animals this year that survive to age j+1 next year
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<tbody>
<tr>
<td>pup</td>
<td>100</td>
<td>60</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>(=200 \times 0.3)</td>
<td>(=450 \times 0.3)</td>
<td></td>
</tr>
<tr>
<td>Age 1</td>
<td>800</td>
<td>80</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>(=100 \times 80%)</td>
<td>(=60 \times 80%)</td>
<td></td>
</tr>
<tr>
<td>Age 2</td>
<td>500</td>
<td>720</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>(=800 \times 90%)</td>
<td>(=80 \times 90%)</td>
<td></td>
</tr>
<tr>
<td>Age 3</td>
<td>300</td>
<td>450</td>
<td>648</td>
</tr>
<tr>
<td></td>
<td>(=500 \times 90%)</td>
<td>(=720 \times 90%)</td>
<td></td>
</tr>
<tr>
<td>Age 4+</td>
<td>200</td>
<td>450</td>
<td>810</td>
</tr>
<tr>
<td></td>
<td>(=300 \times 90%)</td>
<td>(=450 \times 90%)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(+200 \times 90%)</td>
<td>(+450 \times 90%)</td>
<td></td>
</tr>
<tr>
<td>Total #</td>
<td>1900</td>
<td>1760</td>
<td>1713</td>
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After awhile, the population starts to grow (or decline) **exponentially** at some rate $\lambda$. 

![Population over time](chart.png)
Review key things a life-history model (Leslie matrix) tell us:

Long-term population growth rate

- A Leslie matrix model goes to a steady exponential rate of increase (or decrease). This is called $\lambda$
- The $\lambda = \text{maximum eigenvalue of the Leslie matrix}$
- If I were able to estimate the Leslie matrix, I could easily estimate the long-term rate of increase
Long-term age-distribution

- A unperturbed populations go to a stable age-distribution.
- With a Leslie matrix, I could calculate stable age-distribution.
- I could compare my population’s actual age-distribution to the stable one.
A population that hasn’t experienced too many big mortality events or low birth rate events has a smooth age structure.
Versus Germany’s age-distribution in 1950
Age structure is a history of mortality and low birth rate events

Draft age (18-30) during WWI

Draft age (18-40) during WWII

was 18 at last yr of WWII

was 17 at last yr of WWII

WWI
1916/1917 famine
1918/19 flu pandemic

post-WWI
1920s hyperinflation
1933 30% unemploy.

WWII
Today’s lecture topics:

• Life-history models and Leslie matrices
• Most important attributes of Leslie matrix models
  – Long-term rate of increase, $\lambda$
  – Stable age-distribution
• The Leslie matrix version of a life-history model
• How do you estimate a Leslie matrix?
• Two types of common analyses using Leslie matrices
  – Sensitivity analysis
  – Historical analysis
Estimating survival from mark-capture-recapture studies

- Capture and mark individuals or id them (photo-id typically)
- Sight them (not actually recapture them) in subsequent years
- Use a **Cormack-Jolly-Seber Model** to analyze the data using some program like MARK or SURGE.
Estimating survival from age-structure
Where do reproductive estimates come from?

- Mark-resight studies – basically long-term field studies that follow individuals using marks or photo-id
- Opportunistic analysis of dead animals (examine the uterus) or analysis of a deliberate large sample of dead animals
Today’s lecture topics:

- Life-history models and Leslie matrices
- Most important attributes of Leslie matrix models
  - Long-term rate of increase, $\lambda$
  - Stable age-distribution
- The Leslie matrix version of a life-history model
- How do you estimate a Leslie matrix?
- The most analyses in conservation biology using Leslie matrices
  - Trend (increasing or decreasing)
  - Sensitivity analysis
  - Historical analysis
Sensitivity: How much does $\lambda$ change when one (or a combo) of the elements is changed?

Matrix element + a tiny amount = how much increase in $\lambda$

You can calculate sensitivities directly from the Leslie matrix (this week’s computer lab)
Why is the Northern Right Whale not recovering? Protected in 1935 by League of Nations resolution

Demography of the endangered North Atlantic right whale

Masami Fujiwara & Hal Caswell

Photoidentification

North Atlantic Right Whale Catalog
30,000+ pictures of 430+ individually identified individuals 1980-present

Program MARK: statistical analysis of resight data to estimate survivorships and fecundities

Expected ~200 yrs to extinction
-- Mortality of adult females is the main cause of decline
-- Saving 2 females per year leads to recovery
-- Ship strikes are the main anthropogenic cause of adult deaths

Management action: move shipping lanes to avoid areas of high right whale density
Second common type of analysis: historical changes in survival and fecundity
What caused the Southern and Northern Resident killer whales to decline?
Basic strategy for this analysis

Matrix model for southern and northern resident killer whales

+ Number of animals of each age and sex from photoidentification catalog

Number of each age and sex expect to die

Compare to number that did die
John K.B. Ford, Graeme M. Ellis, Peter F. Olesiuk, Fisheries & Oceans Canada, Linking prey and population dynamics: did food limitation cause recent declines of ‘resident’ killer whales (*Orcinus orca*) in British Columbia?
B.

$y = -2.7172x + 4.1462$

$R^2 = 0.7627$
Summary: basic questions to be able to answer

• What is a Leslie matrix?
• How do you convert a cartoon of a life-history model to a Leslie matrix?
• What is $\lambda$?
• What is a stable age-structure?
• What are sensitivities?
• Why would you want to estimate a Leslie matrix for your population of interest?
Computer lab: what caused Steller sea lion declines?