Life-history modeling of marine mammal population using *Leslie* matrices

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Is this population increasing or decreasing?
Did a change in birth rates or death rates cause a decline?

Steller sea lion from the National Marine Mammal Lab, http://nmml.afsc.noaa.gov/
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??

Or adult female mortality from boat strikes and entanglement?

Is it calving rates?

Photo: Florida Fish and Wildlife Conservation Commission/NOAA
The most common analyses in conservation biology using life-history modeling are

• What is the population rate of growth (or decline)?
• What is the best way to recover the population? = what vital rate is most responsive?
• What is driving the population declines?
• How fast will the population go extinct?
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.
An STAGE-structured life-history model translates numbers in a stage THIS year to numbers in stage NEXT year.


Northern Right Whale life-history model
0.30 female pups per mature female

Survival to NEXT year
<table>
<thead>
<tr>
<th></th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>pup</td>
<td>100</td>
<td>60</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td></td>
<td>=200*0.3</td>
<td>= 450 x 0.3</td>
</tr>
<tr>
<td>Age 1</td>
<td>800</td>
<td>80</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>=100 x 80%</td>
<td>= 60 x 80%</td>
</tr>
<tr>
<td>Age 2</td>
<td>500</td>
<td>720</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>=800 x 90%</td>
<td>= 80 x 90%</td>
</tr>
<tr>
<td>Age 3</td>
<td>300</td>
<td>450</td>
<td>648</td>
</tr>
<tr>
<td></td>
<td></td>
<td>=500 x 90%</td>
<td>= 720 x 90%</td>
</tr>
<tr>
<td>Age 4+</td>
<td>200</td>
<td>450</td>
<td>810</td>
</tr>
<tr>
<td></td>
<td></td>
<td>=300 x 90% + 200 x 90%</td>
<td>= 450 x 90% + 450 x 90%</td>
</tr>
</tbody>
</table>
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

\[ \lambda > 1 \]

\[ \lambda < 1 \]

After a few years the proportion of animals in each age class stabilizes (it doesn’t take long)

Stable age-structure
How life-history models help answer: Is this population increasing or decreasing?

3-4 year study on reproduction and survival

Life-span of your marine mammal of interest might be long

Stable age-structure

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

Long-term rate of population increase (or decrease)
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- 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.

<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>
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<td>0</td>
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<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>

This YEAR

Pups
Age 1
Age 2
Age 3
Age 4+

Next YEAR

pup → 1 → 2 → 3 → 4+

80% 90% 90% 90% 90%
The Leslie matrix has 2 parts: fecundity and survival

- 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>This YEAR</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td></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>
<tr>
<td>Next YEAR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Let’s project the population forward with matrix algebra

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
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).
- Termed $\lambda = \text{maximum eigenvalue of the Leslie matrix}$
- If I were able to estimate the Leslie matrix, I could easily estimate the long-term rate of increase
Long-term population age-distribution

- A unperturbed populations go to a stable age-distribution.
- If I were able to estimate the 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.
Germany
Age-distribution in 1950

US age distribution 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

WWI & 1918/19 flu pandemic

Great Depression

WWII
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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

Ringed Seals Age Distribution (York 1993)

- Age of animals caught
- Cumulative fraction of animals
Where do reproductive estimates come from?

- Long-term cohort 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
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• The most analyses in conservation biology using Leslie matrices
  – Trend (increasing or decreasing)
  – Sensitivity analysis
  – Historical analysis
Sensitivities (and elasticities)

Definition

- The relative change in $\lambda$ when specific vital rates are increased by a small amount (sensitivity)?
- The relative change in $\lambda$ when specific vital rates are changed by a small percentage (elasticity)?
How much does $\lambda$ change when one (or a combo) of the elements is changed?

- **Sensitivity**: $A_{ij} + \text{a tiny amount}$
- **Elasticity**: $A_{ij} \times \text{a tiny percentage}$

You calculate sensitivities or elasticities directly from the Leslie matrix.

$$
\begin{bmatrix}
0 & 0 & 0 & 0 & 0 & .3 \\
.8 & 0 & 0 & 0 & 0 & 0 \\
0 & .9 & 0 & 0 & 0 & 0 \\
0 & 0 & .9 & 0 & 0 & 0 \\
0 & 0 & 0 & .9 & .9
\end{bmatrix}
$$
Why is the Northern Right Whale not recovering? Protected in 1935 by League of Nations resolution.

Photoindentification

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
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What cause 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 each age and sex expect to die

+ 

Number of animals of each age and sex from photoidentification catalog

Compare to number that did die
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 to convert a cartoon of a life-history model to a Leslie matrix
• What’s λ?
• What’s a stable age-structure
• What are sensitivities? And elasticities?
• Why would you want to estimate a Leslie matrix for your population of interest?