Leslie matrices for marine mammals and conservation biology

Eli Holmes
National Marine Fisheries Service
The most common analyses in conservation biology using life-history modeling are

- What is the population rate of decline?
- To what vital rate is the population growth rate most responsive?
- How fast will the population go extinct?
- What happened to the population in the past?
Leslie matrices for marine mammals and conservation biology

• Life-history models and Leslie matrices
• Most important attributes of Leslie matrix models
  – Long-term rate of increase, $\lambda$
  – Stable age-distribution
• How do you estimate a Leslie matrix?
• Two types of common analyses using Leslie matrices
  – Sensitivity analysis
  – Historical analysis
A life-history model translates numbers THIS year to numbers NEXT year

- Heterozygous: 1 wk
- Heterozygous: 1 yr + 1 wk
- Heterozygous: 2 yr + 1 wk
- Heterozygous: 3 yr + 1 wk
- Heterozygous: 4+ yr + 1 wk

average number of newborns NEXT year

Survival of age i this to age i+1 NEXT year
Let’s make this into a generic female pinniped model

- Start reproducing at age 4
- On average 60% of females have a pup every year
- 50:50 sex ratio of newborns
- Lower juvenile survivorship
- High adult survivorship
\[ s1 = .8; \ s2,3,4 = .9; \ f3 = .3 \]

<table>
<thead>
<tr>
<th></th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
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</thead>
<tbody>
<tr>
<td>pup</td>
<td>100</td>
<td>60</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(=200\cdot.3)</td>
<td></td>
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<tr>
<td>Age 1</td>
<td>800</td>
<td>80</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>(=100\cdot.8)</td>
<td>(=800\cdot.9)</td>
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<tr>
<td>Age 2</td>
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<td>720</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>(=500\cdot.9)</td>
<td>(=300\cdot.9+200\cdot.9)</td>
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<tr>
<td>Age 3</td>
<td>300</td>
<td>450</td>
<td>648</td>
</tr>
<tr>
<td>Age 4</td>
<td>200</td>
<td>450</td>
<td>810</td>
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</tbody>
</table>
Write the model as a **Leslie Matrix**

- Translates numbers this year to next year
- Top row is fecundity
- Other rows are survivorship

<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>
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<td>0</td>
<td>0</td>
<td>0.3</td>
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<tr>
<td>Age 1</td>
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<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>
Let’s project the population forward with matrix algebra

\[
\begin{bmatrix}
60 \\
80 \\
720 \\
450 \\
450
\end{bmatrix}
\times
\begin{bmatrix}
0 & 0 & 0 & 0 & 0.3 \\
0.8 & 0 & 0 & 0 & 0 \\
0 & 0.9 & 0 & 0 & 0 \\
0 & 0 & 0.9 & 0 & 0 \\
0 & 0 & 0 & 0.9 & 0.9
\end{bmatrix}
\times
\begin{bmatrix}
100 \\
800 \\
500 \\
300 \\
200
\end{bmatrix}
\]

**Red** is pups next year by females age j in this year

**Blue** is number of age j animals this year that survive to age j+1 next year
So the life-history cartoon is also a picture of a Leslie matrix.
After awhile, the population starts to grow (or decline) exponentially.
Some real population trajectories for long-lived species

Long-term population growth rate

• Termed $\lambda$
• The $\lambda = \text{maximum eigenvalue of the Leslie matrix}$
• What’s an eigenvalue?
• Take-home messages
  – A life-history model goes to a steady exponential rate of increase (or decrease).
  – Max. eigenvalue of the Leslie matrix is the long-term growth rate
  – If I were able to estimate the Leslie matrix, I could easily estimate the long-term rate of increase
average number of newborns NEXT year

Survival of age $i$ this to age $i+1$ NEXT year
After a few years the proportion of animals in each age class stabilizes (it doesn’t take long)
Long-term population age-distribution

• The stable age-distribution = dominant eigenvector of the Leslie matrix

• Take-home messages
  – A life-history model goes to a stable age-distribution.
  – If I were able to estimate the Leslie matrix, I could easily estimate the long-term stable age-distribution.
  – I could compare my population’s actual age-distribution to the stable one.
Leslie matrices, marine mammals and conservation biology

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The Leslie matrix has 2 parts: fecundity and survival.

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<tr>
<td>0</td>
<td>0</td>
<td>0.9</td>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
<td></td>
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Leslie matrix model
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)

- number of animals
- age of animals caught
- Cumulative fraction of animals

age

0 10 20 30 40 50

0 0.2 0.4 0.6 0.8 1.0 1.2
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
Average number of newborns born next year

X fraction of females at age i that are mature
X fraction of mature females that are impregnated
X fraction of impregnated females that survive to the next year
X fraction of early term pregnancies that make it to late-term and birth
X fraction of newborns that survive to census date

= average number of newborns born NEXT year to females age i THIS year
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Sensitivities (and elasticities)

Definition

• What is the relative change in $\lambda$ when specific vital rates are increased by a small amount (sensitivity)?
• What is 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**: $A_{ij} +$ a tiny amount
- **Elasticity**: $A_{ij} \times$ a tiny percentage

You calculate sensitivities or elasticities directly from the Leslie matrix.
A famous example of elasticities affecting management of a long-live species
Leslie matrices, marine mammals and conservation biology

- Leslie matrix
- How to convert a cartoon of a life-history model to a Leslie matrix
- What’s $\lambda$?
- 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?
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Analyzing impacts from the past in a long-lived species

Length of your study period

Life-span of your marine mammal of interest

20,30,100 years
Predicted age-distribution in 2050 in Germany

Federal Statistical Office Germany
Actual age-distribution in 1950 in Germany
30% of drafted men were killed in WWII

Draft age (18-30) in 1939-1945

Federal Statistical Office Germany
Families don’t have kids during wartime

Born in 1914-18

Born in 1939-45

Federal Statistical Office Germany
The age-structure of a long-lived animal is a record of the history the population has experienced.

Men who served in WWII

Men who served in WWI

WWI

The Great Depression

WWII
B. Southern

\[ y = 0.001e^{0.0057x} \]

\[ R^2 = 0.3548 \]
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?