Leslie Matrix = Population Projection Matrix

Contains age-specific fecundity and survival rates.

For example, with 3 age classes (ages 0-2, females only) the Leslie matrix would take the form:

\[
\begin{bmatrix}
F_0 & F_1 & F_2 \\
S_0 & 0 & 0 \\
0 & S_1 & 0
\end{bmatrix}
\]

\(F_x\) = age-specific fecundity (modified to take survival between census periods into account)

\(S_x\) = age-specific survival rate (denoted \(P\) by many authors, including Gottelli in your handout)

- Note that this is an annual survival rate \((s_x)\), not survival from birth \((l_x)\)

The equation for \(F_x\) depends on where the annual census occurs relative to the breeding season:

(Overhead - diagrams from Donovan & Weldon)

1. Pre-birth pulse sampling (young-of-year not present): \(F_x = S_0 \, m_x\)
   (account for survival of offspring from end of breeding season to the next census period)

2. Post-birth pulse sampling: \(F_x = S_x \, m_{x+1}\)
   (account for survival of parents from end of one breeding season to beginning of next breeding season)

3. Birth-flow fertility: more complicated situation

4. \(F_x\) is used to calculate the number of recruits (young) in the next generation

Leslie Matrix \((A)\) replaces \(\lambda\) in the shift from a simple exponential growth curve to an age-structured population growth model (note, this is still exponential after shifting)

\[N_{t+1} = N_t \lambda\]
\[N_t = N_0 \lambda^t\]
Assumes population is at the stable age distribution. Stable age distribution arises inevitably, if $l_k$ and $m_k$ curves are constant. If there is variation in survival or reproduction thorough time (good years and bad years), then population will not perfectly match stable age distribution.

Deviations so that a high proportion of the population is in main reproductive years: ↑ the current growth rate

Deviations so that high proportion of population is currently young or old: usually ↓ the current growth rate (though it might cause subsequent ↑, too).

To account for the impact of the population's age structure on it's growth rate:

$$N_{t+1} = A \cdot N_t$$

So what does $A \cdot N_t$ mean?

<table>
<thead>
<tr>
<th>$F_0$</th>
<th>$F_1$</th>
<th>$F_2$</th>
<th>$N_0$</th>
<th>$N_1$</th>
<th>$N_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_0$</td>
<td>0</td>
<td>0</td>
<td>$N_0$</td>
<td>$N_1$</td>
<td>$N_2$</td>
</tr>
<tr>
<td>0</td>
<td>$S_1$</td>
<td>0</td>
<td>$N_0$</td>
<td>$N_1$</td>
<td>$N_2$</td>
</tr>
</tbody>
</table>

$N_0$ $t+1$ = $(N_0 t \cdot F_0) + (N_1 t \cdot F_1) + (N_2 t \cdot F_2)$

$N_1$ $t+1$ = $(N_0 t \cdot S_0) + (N_1 t \cdot 0) + (N_2 t \cdot 0)$

$N_2$ $t+1$ = $(N_d t \cdot 0) + (N_1 t \cdot S_1 t) + (N_2 t \cdot 0)$

And since $N_2$ is the oldest observed in the data set, they all die, and we don't need any more math to track it.
For many real analyses, individuals are aged only as juveniles, subadults and adults.

(1) In this case, we are assuming that adults of all ages have the same survival rate. In other words, we are assuming that the $l_x$ curve is linear (on log Y scale) for the adult ages.

![Graph showing log (N_x) vs age (x) with slopes for different age classes]

Constant $s_x$ for adults is commonly true for birds. E.g. Northern Spotted Owls

(Ohead: Hopkins et al. Table 1 p 33, Fig 1 p. 32, Reid et al. Fig 2 p.62)

In this case, we are not tracking each age class separately once they reach adulthood, with respect to data on survival.

(2) Often, the data variation in fecundity among adults of different ages is weaker than the data on annual survival → data constraints force pooling of $m_x$ data across all adult ages.

(Ohead: Hopkins et al Fig 3, p 35: $m_x$ data: note error bars, note $\sigma$ among years, compared to $s_x$ data)

(3) End up with a model based on 2 or 3 age classes. 2 age classes: juvenile & adult.

Three age-classes:
juvenile (dependent on parents),
subadult (independent but low probability of breeding),
adult (independent and of breeding age)

How do we modify the Leslie matrix to deal with this type of data constraint (lumped adult age classes)?

"Extended" Leslie Matrix
Now (time = t)           Next time step (t+1)

\[
\begin{pmatrix}
F_j & F_s & F_a \\
S_j & 0 & 0 \\
0 & S_s & S_a
\end{pmatrix}
\begin{pmatrix}
N_j \\
N_s \\
N_a
\end{pmatrix} =
\begin{pmatrix}
N_j \\
N_s \\
N_a
\end{pmatrix}
\]

only change is here

What effect on \(N(t+1)\) vector?

\[
N_{jt+1} = (N_j t^* F_j) + (N_s t^* F_s) + (N_a t^* F_a)
\]

\[
N_{st+1} = (N_j t^* S_j) + (N_s t^* 0) + (N_a t^* 0)
\]

\[
N_{at+1} = (N_j t^* 0) + (N_s t^* S_s t) + (N_a t^* S_a t)
\]

Only change is here: \(Na(t+1)\) is affected by recruitment of subadults (as before) but also by survival of adults present at time \(t\)… these survivors are older now, but they are still in the same age class (adult)