S2 Appendix. Leslie Matrix and definitions of lambda and $r$

The basic building blocks of life history theory are $x$, $l_x$, and $m_x$, where $x$ is the age in years since hatching, $l_x$ is the average probability of surviving to age $x$, and $m_x$ is the average number of offspring of a female of age $x$. We usually treat age $x$ as a discrete variable in that measurements are taken at discrete times, like the ten-year census of the US population or the passages of salmonids across a weir on their spawning run.

A life history table lists $x$, $l_x$, and $m_x$ for each age $x$. A life history table for a hypothetical iteroparous population that experiences a 50% mortality rate each year and has females that are fertile only in ages 2 and 3 might look like:

<table>
<thead>
<tr>
<th>$x$</th>
<th>$l_x$</th>
<th>$m_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>.5</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>.25</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>.125</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Fishery biologists summarize the complicated life history of salmonids by representing the total age of the fish as a combination of stream age (years spent in the stream before smolting) and lake age (years spent in the lake after smolting). This distinction between stream age and lake age is made because the conditions for growth and survival are usually very different between these environments.

A more dynamic approach to studying life histories uses difference equations and their Leslie Matrix formulation. [See, for example, Caswell (2001)]. Consider a species whose maximum life span is $M$ years, whose females lay their eggs once a year, roughly on the same day, whose eggs hatch soon thereafter, and who are
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censused just before they lay their eggs. Let $x$ denote the age in years of an individual starting at hatch ($x = 0$). We call the collection of all (female) individuals with age between $x$ and $x+1$ “age class $x$.” Let $n_x(t)$ denote the size of age class $x$ at time $t$. Using life history parameters $l_x$ and $m_x$, let $s_x = l_{x+1}/l_x$ be the probability of surviving from age $x$ to age $x+1$. The following system of difference equations keeps track of each age class over time:

$$
n_1(t+1) = m_1 n_1(t) + m_2 n_2(t) + m_3 n_3(t) + \ldots + m_M n_M(t)
$$

$$
n_2(t+1) = s_1 n_1(t)
$$

$$
n_3(t+1) = s_2 n_2(t)
$$

$$
n_4(t+1) = s_3 n_3(t), \text{ and so on.}
$$

The first equation keeps track of newborns from each age class of females; the rest keep track of survivors from one age class to the next.

In matrix form, this system becomes, for the $M = 4$ case:

$$
\begin{pmatrix}
  n_1(t+1) \\
  n_2(t+1) \\
  n_3(t+1) \\
  n_4(t+1)
\end{pmatrix} =
\begin{pmatrix}
  m_1 & m_2 & m_3 & m_4 \\
  s_1 & 0 & 0 & 0 \\
  0 & s_2 & 0 & 0 \\
  0 & 0 & s_3 & 0
\end{pmatrix}
\begin{pmatrix}
  n_1(t) \\
  n_2(t) \\
  n_3(t) \\
  n_4(t)
\end{pmatrix}
$$

or in vector notation $\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t)$. The matrix $\mathbf{A}$ is called a Leslie matrix. If we iterate this process starting from an initial population distribution $\mathbf{n}(0)$: $\mathbf{n}(1) = \mathbf{A} \mathbf{n}(0)$, $\mathbf{n}(2) = \mathbf{A} \mathbf{n}(1)$, $\mathbf{n}(3) = \mathbf{A} \mathbf{n}(2)$, and so on. Eventually each $\mathbf{n}(t+1)$ will be a constant multiple of the previous $\mathbf{n}(t)$, so that the relative size of each age class becomes constant. This multiplier, usually denoted by $\lambda$, is called the dominant eigenvalue of matrix $\mathbf{A}$. It gives the long run growth rate of the population. The corresponding vector $\mathbf{n}$ of relative sizes of the age classes is called the corresponding eigenvector. To be precise, $\lambda$ is an eigenvalue for matrix $\mathbf{A}$ and $n$-tuple $\mathbf{n}$ is a corresponding eigenvector if $\mathbf{A} \mathbf{n} = \lambda \mathbf{n}$. Any multiple of an eigenvector is
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an eigenvector; we often normalize by dividing each entry $n_i$ of $n$ by the sum of the
$n_k$'s; in this case we do get an eigenvector whose entries are the long run
proportional size of each age class. By a bit of algebra (Wikipedia: “Euler-Lotka
equation”), one can relate $\lambda$ to the basic $l_x$ and $m_x$ parameters in a Leslie matrix via
Euler’s Formula:

$$\lambda^1 \frac{m_1 l_1}{\lambda^1} + \lambda^2 \frac{m_2 l_2}{\lambda^2} + \ldots + \lambda^T \frac{m_T l_T}{\lambda^T} = 1$$  \hspace{1cm} (B.01)

We usually replace the annual growth multiplier $\lambda$ by its instantaneous
counterpart: the so-called “intrinsic growth rate” $r$, where $e^r = \lambda$ or $r = \ln \lambda$. In this
case, Euler’s Formula becomes:

$$\frac{m_1 l_1}{e^{r_1}} + \frac{m_2 l_2}{e^{r_2}} + \ldots + \frac{m_T l_T}{e^{r_T}} = 1.$$  \hspace{1cm} (B.02)