Mortality and natality data for a cohort of Belding's ground squirrel, *Citellus beldingi* (after Zammuto and Sherman 1986, Can. J. Zool. 64 602-605). Squirrels were censused once per year in mid-summer, shortly after weaning; $m_x$ is the average number of female young just weaned by a female of age $x$.

<table>
<thead>
<tr>
<th>Age class $x$</th>
<th>Number alive $N_x$</th>
<th>Annual Survival $S_x$</th>
<th>Cumulative survival $I_x$</th>
<th>Expected life $e_x$</th>
<th>Fecundity $m_x$</th>
<th>Realized fecundity $l_x m_x$</th>
<th>Reproductive value $V_x$</th>
<th>Cohort size at SAD $C_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>238</td>
<td></td>
<td></td>
<td></td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>93</td>
<td></td>
<td></td>
<td></td>
<td>1.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>49</td>
<td></td>
<td></td>
<td></td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td>2.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td>3.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>6</td>
<td>0</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

1. Fill in the life table.

2. What proportion of squirrels live to be 2 years old?

3. Of those squirrels that live to be 1 year old, what proportion survive to the 2nd year?

4. What is the expected future lifespan of a 1 year old squirrel?

5. Calculate $R_0$. Write it with the correct units. If there are 100 squirrels in mid-summer this year, how many would you expect to find in mid-summer next year? How many the year after?

6. Write the correct general equation for calculating reproductive value $V_x$ for a post-breeding model.

7. If you were managing this population of squirrels and a users group wanted to harvest as many squirrels as possible on a sustained yield basis, which age class would you recommend that they exploit? Explain.
**BIO 21/51/120: EXAMPLE OF LIFE TABLE CALCULATIONS**

Cohort life table for little brown bat *Myotis lucifugus* (based on annual pre-breeding censuses)

<table>
<thead>
<tr>
<th>x</th>
<th>N_x</th>
<th>S_x</th>
<th>l_x</th>
<th>e_x</th>
<th>m_x</th>
<th>l_x m_x</th>
<th>V_x</th>
<th>C_x</th>
<th>(\lambda) l_x</th>
<th>l_x m_x x</th>
<th>(v_x)</th>
<th>(v_{x+1})</th>
<th>(v_{x+2})</th>
<th>(v_{x+3})</th>
<th>(v_{x+4})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1'</td>
<td>320</td>
<td>0.4</td>
<td>1</td>
<td>0.82</td>
<td>0</td>
<td>0</td>
<td>1.1</td>
<td>0.563</td>
<td>0.968</td>
<td>0</td>
<td>0.4</td>
<td>0.42</td>
<td>0.28</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>128</td>
<td>0.7</td>
<td>0.4</td>
<td>1.05</td>
<td>1</td>
<td>0.4</td>
<td>2.75</td>
<td>0.218</td>
<td>0.375</td>
<td>0.80</td>
<td>1.05</td>
<td>0.7</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>90</td>
<td>0.5</td>
<td>0.28</td>
<td>0.5</td>
<td>1.5</td>
<td>0.42</td>
<td>2.5</td>
<td>0.148</td>
<td>0.254</td>
<td>1.26</td>
<td>1.5</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>45</td>
<td>0.14</td>
<td>0</td>
<td>2</td>
<td>0.28</td>
<td>2</td>
<td>0.071</td>
<td>0.123</td>
<td>1.12</td>
<td>2</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\Sigma)</td>
<td></td>
<td>1.10</td>
<td>1.00</td>
<td>1.718</td>
<td>3.18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The value of \(x\) in the first row of the table is the approximate age at the time of sampling of the youngest individuals that are recognized (with a pre-breeding census, the table starts with \(x = 1\); with a post-breeding census, the table starts with \(x = 0\)).

- \(N_x\): Number in cohort surviving to age \(x\) (measured; e.g., from marked individuals).
- \(S_x\): Annual probability of survival = Probability that an individual of age \(x\) will survive to age \(x+1\).
  \[ S_x = \frac{N_{x+1}}{N_x} \quad \text{eq. 1} \]
  \[ 0.40 = \frac{128}{320} \]
- \(l_x\): Cumulative Survivorship = Proportion of individuals in age class 0 that survive to age class \(x\). Note that \(l_0 = 1.0\) by definition.
  \[ l_x = l_{x-1} \cdot S_{x-1}; \quad \text{eq. 2} \]
  \[ 0.4 = 1 \cdot 0.4 \quad \text{i.e., } l_1 = l_0 \cdot P_0 \]
  \[ 0.28 = 0.4 \cdot 0.7 \]
- \(e_x\): Expected life = Expectation of future life given survival to age \(x\).
  \[ e_x = \left( \sum_{i=x+1}^{\infty} l_i \right) \cdot \frac{1}{l_x} \quad \text{eq. 3} \]
  \[ 1.05 = \frac{(0.28 + 0.14)}{0.4} \]
- \(m_x\): Fecundity at age \(x\) (average number of female offspring produced during the next year that survive to the time of the next census; e.g., average number of female bats produced last summer that survived to the next spring; measured in nature). Note that this is sometimes denoted as \(b_x\) in life table models. Note that we define \(m_x\) differently in a post-breeding model.
- \(l_x m_x\): Realized fecundity = \(l_x \cdot m_x\) \quad \text{eq. 4}
  \[ = \text{Probability of survival to age } x \cdot \text{Fecundity given survival.} \]
  \[ = \text{Female offspring in year } x \text{ per initial female of age } 1 \]
  \[ 0.42 = 0.28 \cdot 1.5 \text{ females } / \text{female} \]
- \(R_0\): Net reproductive rate (per capita progeny / lifetime, individuals \(\cdot\) individual\(^{-1}\) \(\cdot\) lifetime\(^{-1}\)) = Average number of offspring produced by an average newborn offspring during its entire lifetime. Also equals the reproductive value for age class 0 (\(RV_0\)).
  \[ R_0 = \sum_{x=0}^{\infty} l_x m_x \quad \text{eq. 5} \]
  \[ = 1.10 \]


\( G \) = Generation time (units = time step of life table; in this case, years)  
\( = \frac{\sum x \cdot m_x \cdot x}{R_0} \)  
\( \text{eq. 6} \)

2.89 = \frac{3.18}{1.10}.

\( r \) = Intrinsic rate of increase (individuals \( \cdot \) individual\(^{-1} \) \( \cdot \) year\(^{-1} \))  
\( = \frac{\ln R_0}{G} \)  
\( \text{eq. 7} \) An exact solution requires iteration with Euler’s equation.

0.033 = \ln 1.10 / 2.89

\( \lambda \) = Finite rate of increase. (pronounced lambda)  
\( = e^r \)  
\( \text{eq. 8} \)

1.034 = \( e^{0.033} \)

\( V_x \) = Reproductive value\(^*\)  
\( = \text{Age-specific expectation of future offspring (females of age 1 / female of age } x) \)  
\( = \text{Expected reproduction during the remainder of its life for an organism of age } x \)

\( = m_x + \sum_{i=x+1}^{\infty} \left( \frac{i}{l_x} \cdot m_i \right) \)  
\( \text{eq. 9} \) Note that columns in the table labelled \( v_0, v_1, \) etc., show values used in the summation for each \( V_x \)

2.75 = \( 1 + .28 / .4 \cdot 1.5 + .14 / .4 \cdot 2 \)  
\( = 1 + 1.05 + 0.7 \)

\( \) This equation can be different in alternative life table models. Derive it as Eq 10 for a post-breeding census model.

\( C_x \) = Cohort size at stable age distribution  
\( = \text{Proportion of total population of age } x \text{ at stable age distribution} \)

\( = \frac{\lambda^{-x} \cdot l_x}{\sum_{x=0}^{\infty} (\lambda^{-x} \cdot l_x)} \)  
\( \text{eq. 11} \)

0.563 = \frac{1}{1.718}

0.218 = \frac{0.375}{1.718}

Given current population size, \( N_0 \), future population size at time \( t \) can be projected using \( r \) or \( \lambda \) assuming that (1) mortality and natality schedules remain the same and (2) the population is at a stable age distribution.

\( N'_t = N_0 \cdot e^{r \cdot t} \)  
\( \text{eq. 12} \)

e.g., if \( N_0 = 100 \), and \( r = 0.033 \), \( N'_t = 139 \)

\( N'_t = \lambda^t \cdot N_0 \)  
\( \text{eq. 13} \)

e.g., if \( N_0 = 100 \), and \( \lambda = 1.034 \), \( N'_t = 139 \)