• Week 10: Life History Variation.

• Lecture summary:
  • Components of life histories.
  • Reproductive effort & value.
  • Trade-offs.
  • $r$- and $K$-selection
  • Habitat classification.
  • Clutch size.

Male & female guppies

http://www.guppies.com/
2. Components of life histories:

- 1. Growth:
  - Balance between the benefits and costs of large and small sized individuals (Figs. 14.1 & 4.16).

- 2. Development:
  - Can be varied independently of growth.

- 3. Fecundity:
  - Rapid development can lead to early reproduction and so timing is important (length of pre-reproductive period).
  - Duration and frequency of reproduction is also important (semelparity and iteroparity).
3. Components of life histories (continued/...):

- **4. Offspring size:**
  - Variation in parental investment in individual offspring.

- **5. Number of offspring:**
  - Variation in numbers.

- **6. Parental care:**
  - Variation in how much parents look after offspring.
4. Components of life histories (continued/…):

• 7. Survivorship:
  • Variation in mortality, affected by:

• 8. Energy storage:
  • Valuable for irregularly supplied resources.

• 9. Dispersal in space and time:
  • Like migration and diapause to escape periods of resource shortage.
5. Reproductive value:

- “The proportion of the available resource input that is allocated to reproduction over a defined period of time.”
  - For example, the allocation of energy or dry weight to different parts at various stages of development (Fig. 14.3).
- “Natural selection favors those individuals that make the greatest proportionate contribution to the future of the population to which they belong.”
  - Life histories are evolutionary attempts to maximize fecundity and survival and these can be compared as a single “currency:”
    - Reproductive value as a measure of fitness (such as intrinsic rate of natural increase $r$, or basic reproductive rate $R_o$).
6. Reproductive value:

• (i) Reproductive value at a stage or age is the sum of the current reproductive output and the future reproductive value.

• (ii) Future reproductive value includes both future survival and expected fecundity.

• (iii) Future contribution of an individual is determined relative to the contribution of others.

• (iv) Life history favored by natural selection will be the one with the highest sum of contemporary output and future output (Fig. 14.4).
7. Trade-offs:

- Life histories are balances of costs and benefits in which one characteristic can result in increased benefits that are associated with decreased benefits from another characteristic:
  - Fig. 14.5.
  - Includes the cost of reproduction:
    - Fig. 4.22.
8. *r* and *K* selection:

- After MacArthur & Wilson (1967) based on parameters of the logistic equation:
  - *r*-selected individuals favored for the ability to reproduce rapidly (high *r*-values) in *r*-selecting habitats (more unstable).
  - *K*-selected individuals are favored for the ability to make a large proportional contribution to a population which remains at its carrying capacity (*K*) in *K*-selecting habitats (more stable).
- These are extremes of a continuum:
  - Although Stephen Stearns objects vigorously to most of the concept of *r*- and *K*-selection!
9. Characteristics of *r*- and *K*-selected individuals:

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>K</em>-selected individuals</th>
<th><em>r</em>-selected individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Habitat stability</td>
<td>predictable, stable</td>
<td>unpredictable, unstable</td>
</tr>
<tr>
<td>2. Individual size</td>
<td>larger size</td>
<td>smaller size</td>
</tr>
<tr>
<td>3. Timing of reproduction</td>
<td>later</td>
<td>earlier maturity</td>
</tr>
<tr>
<td>4. Parity</td>
<td>iteroparity</td>
<td>semelparity</td>
</tr>
<tr>
<td>5. Reproductive allocation</td>
<td>lower</td>
<td>higher</td>
</tr>
<tr>
<td>6. Number of offspring</td>
<td>fewer offspring</td>
<td>many offspring</td>
</tr>
<tr>
<td>7. Size of offspring</td>
<td>larger offspring</td>
<td>smaller offspring</td>
</tr>
<tr>
<td>8. Parental care</td>
<td>parental care</td>
<td>no parental care</td>
</tr>
<tr>
<td>9. Survivorship investment</td>
<td>high investment</td>
<td>little investment</td>
</tr>
</tbody>
</table>

- see [Fig. 14.20](#) & [Table 4.7](#).
10. Habitat classification 1:

- T.R.E. Southwood (1977) - habitat is the **templet** (template) to which individuals fit their life histories.

- **(A) Present reproduction and growth** combine to determine comparative fitness in different habitats:
  
  - **Figs. 4.24, 4.25a.**
  
  - 1) **High-CR habitats** (high cost of reproduction habitats):
    
    - **Growth-sensitive**, reduced growth from present reproduction reduces future reproduction.
    
    - High reproduction/low growth = low reproduction/high growth. Caused by:
      
      - (a) intense competition that favors growth.
      
      - (b) high mortality of small individuals from abiotic conditions or predation.
11. Habitat classification 2:

- 2) **Low-CR habitats**:
  - Future reproduction is little affected by present growth - **growth insensitive**.
  - Caused by:
    - (a) indiscriminate mortality.
    - (b) competition-free, benign habitat.
    - (c) largest individuals may be vulnerable to mortality.

- **Fig. 4.26.**
12. Habitat classification 3:

• (B) **Newly born offspring** can also be used to classify habitats:
  • **Fig. 4.25b.**
  • For a given reproductive allocation, larger offspring can only be produced if there are fewer of them.

• (C) **Offspring size-sensitive habitats:**
  • Reproductive value of individual offspring rises with size.
  • Competition among offspring or high mortality of small individuals.
13. Habitat classification 4:

• (D) **Offspring size-insensitive habitats:**
  • Indiscriminate mortality in benign environments with abundant resources and selection against large offspring size.
  • Together, growth and offspring size combine to give 4 habitat classifications as in Fig. 4.25c.

• **Table 4.6** shows that guppies shift offspring sizes and reproductive allocation in response to selection by different predators.
14. Clutch size:

- How many eggs should a bird lay?
  - “Lack clutch size”:
    - Balance between number produced and their survival leading to a maximum number of offspring surviving to maturity.
  - Fig. 14.19a.

- Lack’s predictions were not borne out by experiment, because:
  - (1) inadequate assessment of offspring fitness:
    - subsequent survival of added eggs not measured.
    - so Lack may be correct?
  - (2) cost of reproduction (Fig 14.19b):
    - not considered
    - impact of present reproduction on future reproduction in iteroparous species.
Figure 14.1 (3\textsuperscript{rd}): Fecundity and body size.
Figure 4.16 (4th): Predicted sizes of male damselflies agrees with actual sizes.
Figure 14.3 (3rd): Allocation of energy in 2 annual plants (see Fig 4.17 4th ed.).
Figure 14.4 (3rd): Reproductive value changes with age in (a) *Phlox* and (b) squirrels (see Fig 4.18 4th ed.)
Figure 14.5 (3rd): Life history trade-offs in fruit flies (a, c) and Douglas fir trees (b) (see Fig. 4.19, 4th ed.).
Figure 4.22 (4th): Cost of reproduction in ragwort (*Senecio jacobaea*).
Figure 14.20 (3rd):
(see Fig. 4.30, 4th ed.)

Conformity with $r/K$
scheme in plants
Table 4.7 (4th): Cattail life history variation.

Table 14.2: Life-history traits of two *Typha* (cattail) species, along with properties of the habitats in which they grow. ‘$s^2 / \bar{x}$’ refers to the variance : mean ratio, a measure of variability. The cattails conform to the $r / K$ scheme. (After McNaughton, 1975.)

<table>
<thead>
<tr>
<th>Habitat property</th>
<th>Measured by</th>
<th>Growing season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Short</td>
</tr>
<tr>
<td>Climate variability</td>
<td>$s^2 / \bar{x}$ frost-free days per year</td>
<td>3.05</td>
</tr>
<tr>
<td>Competition</td>
<td>Biomass above ground (g m$^{-2}$)</td>
<td>404</td>
</tr>
<tr>
<td>Annual recolonization</td>
<td>Winter rhizome mortality (%)</td>
<td>74</td>
</tr>
<tr>
<td>Annual density variation</td>
<td>$s^2 / \bar{x}$ shoot numbers m$^{-2}$</td>
<td>2.75</td>
</tr>
<tr>
<td>Plant traits</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>T. angustifolia</em></td>
<td></td>
</tr>
<tr>
<td>Days before flowering</td>
<td>44</td>
<td>70</td>
</tr>
<tr>
<td>Mean foliage height (cm)</td>
<td>162</td>
<td>186</td>
</tr>
<tr>
<td>Mean genet weight (g)</td>
<td>12.64</td>
<td>14.34</td>
</tr>
<tr>
<td>Mean number of fruits per genet</td>
<td>41</td>
<td>8</td>
</tr>
<tr>
<td>Mean weights of fruits (g)</td>
<td>11.8</td>
<td>21.4</td>
</tr>
<tr>
<td>Mean total weight of fruits (g)</td>
<td>483</td>
<td>171</td>
</tr>
</tbody>
</table>
Figure 4.24 (4\textsuperscript{th}): (a, b) life history option sets, (c) fitness contours, (d) interaction.

More vertical fitness contours = lower cost of reproduction; More horizontal = higher cost.
Figure 4.25 (4th): Demographic classification of habitats by fitness contours: (a) cost of reproduction, (b) offspring size, (c) combined.
Figure 4.26 (4th): (a) Option sets and fitness contours, (b) distribution of dandelion biotypes, (c) reproductive allocations of dandelion biotypes.
### Table 4.6 (4th): Life history responses to selection in Trinidad guppies.

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<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td><strong>Crenicichla</strong></td>
<td><strong>Rivulus</strong></td>
</tr>
<tr>
<td>Male age at maturity (days)</td>
<td>51.8 <strong>P &lt; 0.01</strong></td>
<td>58.8</td>
</tr>
<tr>
<td>Male size at maturity (mg wet)</td>
<td>87.7 <strong>P &lt; 0.01</strong></td>
<td>99.7</td>
</tr>
<tr>
<td>Female age at first birth (days)</td>
<td>71.5 <strong>P &lt; 0.01</strong></td>
<td>81.9</td>
</tr>
<tr>
<td>Female size at first birth (mg wet)</td>
<td>218.0 <strong>P &lt; 0.01</strong></td>
<td>270.0</td>
</tr>
<tr>
<td>Size of litter 1</td>
<td>5.2 <strong>P &lt; 0.01</strong></td>
<td>3.2</td>
</tr>
<tr>
<td>Size of litter 2</td>
<td>10.9 NS</td>
<td>10.2</td>
</tr>
<tr>
<td>Size of litter 3</td>
<td>16.1 NS</td>
<td>16.0</td>
</tr>
<tr>
<td>Offspring weight (mg dry) litter 1</td>
<td>0.84 <strong>P &lt; 0.01</strong></td>
<td>0.99</td>
</tr>
<tr>
<td>Offspring weight litter 2</td>
<td>0.95 <strong>P &lt; 0.05</strong></td>
<td>1.05</td>
</tr>
<tr>
<td>Offspring weight litter 3</td>
<td>1.03 <strong>P &lt; 0.01</strong></td>
<td>1.17</td>
</tr>
<tr>
<td>Interlitter interval (days)</td>
<td>22.8 NS</td>
<td>25.0</td>
</tr>
<tr>
<td>Reproductive effort (%)</td>
<td>25.1 <strong>P &lt; 0.05</strong></td>
<td>19.2</td>
</tr>
</tbody>
</table>

NS, not significant.

Large fish predator: Large fish predator
Small fish predator: Small fish predator
Figure 14.19 (3rd): (a) ‘Lack clutch size’ prediction, (b) maximized net fitness predicts a smaller clutch (see Fig. 4.29, 4th ed.).