Lecture 3

Fitness in Constant Environments and Trade-offs

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Outline

Age schedules of survival and reproduction

- In their most narrow sense, life-history traits relate directly to schedules of survival and reproduction.

- If a denotes age ($0 \leqslant a < \infty$), the basic life history traits are:
  1. Age-dependent survival, l_a or $l(a)$.
  2. Age-dependent reproduction / birth rate, b_a or $b(a)$.

- Note that l_a and b_a are not just single values (scalars), but are in fact functions.

- What is optimized is the entire schedule – i.e., curves / functions of age.

Age schedules of survival and reproduction

- However, often the shape of l_a or b_a can be summarized using one or few variables, with some assumptions about functional forms and parameters.
- Then, it is those few variables that serve as the life-history traits, and are subsequently optimized.
- For example, in our annual plant example, we in fact optimize a step-like function of reproduction, where the timing of the step from zero to maximum reproduction is controlled by a scalar variable, τ.

Age schedules of survival and reproduction

- Sometimes, however, it is required to directly optimize the l_a and b_a functions themselves, and then we have a **dynamic optimization** problem – what is optimized is an entire function or curve.

- Other traits that do not directly affect fitness (body size, mass of fat reserves, social status, secondary sexual traits, etc.) may still be optimized as life-history traits through their influence on survival or reproduction schedules.

Fitness in a constant environment

In constant environments the most commonly used fitness measures are:

The **net reproductive rate**, R_0

$$R_0 = \sum_a l_a b_a \quad or \quad \int_0^\infty l(a)b(a)da$$

Or ...

The **instantaneous rate of increase**, r, which is the solution of the equation

$$\sum_a l_a b_a e^{-ra} = 1 \quad or \quad \int_0^\infty l(a)b(a)e^{-ra}da = 1$$

This last equation is often called **Euler's equation**.

Fitness in a constant environment

- R_0 is usually said to be an appropriate fitness measure only at ecological equilibrium, i.e., when population size or density does not change much from generation to generation.
- However, in constant environments we anyhow expect equilibrium to be reached quickly and maintained thereafter – so r and R_0 may be used interchangeably.
- Certain typical changes in survival schedules, l_a, and reproduction schedules, b_a, result in predictable changes in fitness, R_0 or r.
- For example, earlier switch to reproduction without any associated change in survival curve, would increase both R_0 and r.
- Uniform proportional increase in survival would increase R_0 by the same factor.

Fitness in a constant environment

- Obviously, the ultimate lifecycle would be to survive indefinitely and reproduce at maximum possible rate from age 0: $l_a = 1$ (for all a), and b_a = maximum possible value (for all a).
- This of course does not occur in nature.
- Because we have **trade-offs** – if you increase reproduction you often sacrifice survival, and *vice versa*.
- Similarly, if you increase performance (reproduction or survival) in one age, it is usually on the expense of performance in a later age.
- Some ages are more "valuable", from natural selection / life-history point of view. $\longrightarrow$ Senescence at old age.

Outline

Introduction to trade-offs

- Usually modeled as a negative relation or negative correlation between two (or more) traits.
- In experiments and natural observations, we compare how the two traits covary or are expressed in
  - Different individuals of the same population or species.
  - Different species or lineages.
  - Same or similar individuals at different times or circumstances.
- An increase in one comes on the expense of the other.
- Through examination of trade-offs, we can learn about the typical life-history traits that are commonly modeled and observed.

Survival vs. reproduction

- Reproductive investment or behavior is often associated with survival cost.
- More resources invested in offspring means less resources for parents (e.g., to survive winters).
- More intense reproductive activity may attract enemies – e.g., mating calls in frogs, or more intense and risky foraging in birds with larger broods.
- This trade-off may also relate to survival of offspring, rather than parent – but I address this under the offspring size-number trade-off.
- The survival-reproduction trade-off may be significant only during bad (low-resource) years.

Current vs. future reproduction

- If resources for reproduction are limited, then reproducing more today is on the expense of reproduction tomorrow.
- More flowers this year, means less flowers next year.
- Mast years in trees.
- A separation between **capital breeders** and **income breeders** should be made here.
- Clearly, we expect a stronger trade-off for capital breeders.

Growth vs. reproduction

- Time and resources devoted to growth of somatic tissues, does not contribute directly to reproduction and therefore, is on the expense of current reproduction.
- But may contribute to future reproduction.
- Larger females usually lay more eggs, reproduce more often, and are more attractive to males.
- Larger males may gain more copulations.
- Larger body size may also enhance foraging performance and survival.
- Relevant for determining age at maturity or metamorphosis and first reproduction.

Offspring size vs. number

- Usually offspring of larger size or better quality that perform better (e.g., have higher survival) require more maternal investment per offspring.
- This is of course on the expense of producing more offspring.
- Those two traits show great variation among lineages.
- But also a lot of plasticity between or within individuals.

Other trade-offs

- Current reproduction vs. condition: related somewhat to the trade-offs between current reproduction and survival or future reproduction;
  e.g., a trade-off between nursing or gonads mass and mass of fat reserves.
- Behavioral trade-offs: e.g., the energy-predation trade-off.
- Growth vs. development / differentiation / defense in plants.