Lecture 1

An Introduction to Life History Theory

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Outline

1. General course info
2. Introduction to life history
   - Life history problems
   - Modeling

Course Info

- Life History Theory, October 2012 - January 2013.
- Language:
  - Slides in English.
  - Lecture and exam in Hebrew.
- Dr. Ido Filin, `ifilin@univ.haifa.ac.il`
- Office hours: Thursday 14:15-16:00,

  Room 241, Multipurpose build.
- Time: Thursdays, 16:30 - 18:00.
- Place: Computer room 576, main building.
- Exam: no exam, final project.

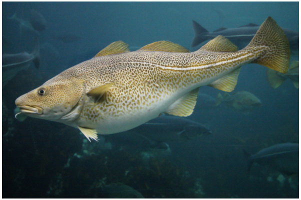
Course Info

- Life History Theory, October 2012 - January 2013.
- חובת הגשת תרגילים.
- הגשה עד תאריך שבדף התרגיל.
- ציון סופי: 40% תרגילים, 60% עבודה סופית .
- All of the course material will be available on the Highlearn system.
- **Reading:** selected pages from the literature listed in the syllabus, and possibly from other sources.
  Available through HighLearn.

Outline

Example: offspring size and number

- Basic life history (reproductive) traits.
- Fundamental tradeoff: Produce many small or few large offspring.
- Exhibit great deal of inter- and intra-specific variation.
- Plasticity and intra-individual variation.
- Life history theory studies this variation.

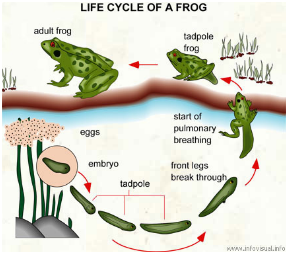


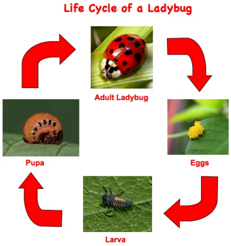
Prologue: life history and its subject of inquiry

- Life history mostly deals with the level of the whole organism.
- But also depends on knowledge and mechanistic models on intra-organismal processes.
- And on models from population ecology and population genetics.
- Has implications at the level of the population and community.

Organism = Life cycle

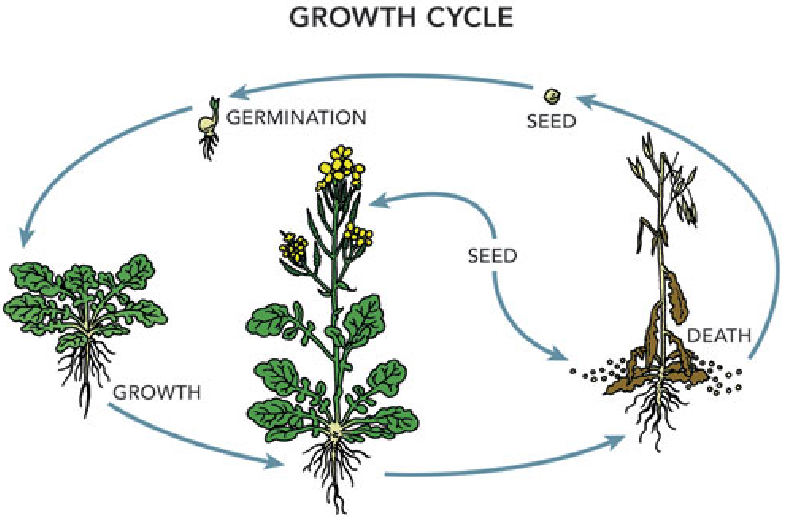
- The whole organism is the entire life-cycle.
- Spatial and temporal wholeness.
- A butterfly is neither the caterpillar nor the imago.
  A butterfly is the entire lifecycle
  (that includes caterpillar and imago as stages within it).
- Traits, phenotypic values, behavior, etc. are not fixed, but change through lifetime.





An example: what if I were an annual plant . . .

The timeline of an annual plant lifecycle.



An example: what if I were an annual plant . . .

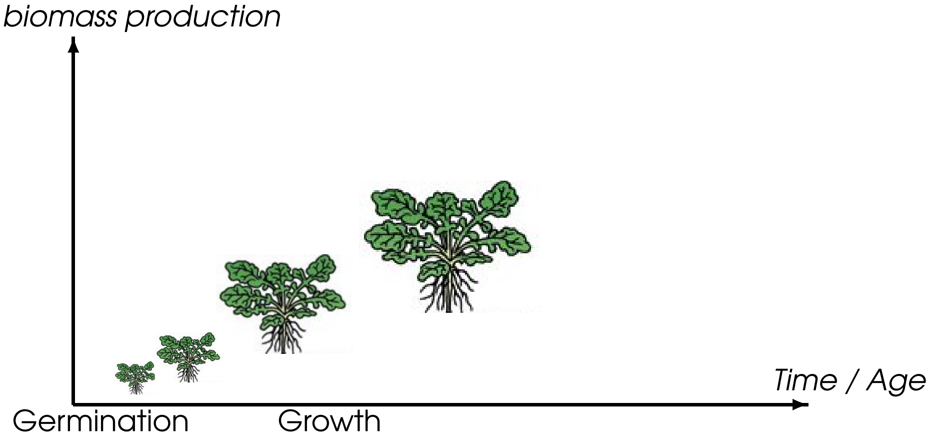
The timeline of an annual plant lifecycle.

Beginning of growing season: a seed germinates and the plant begins to growth vegetatively.

An example: what if I were an annual plant . . .

The timeline of an annual plant lifecycle.

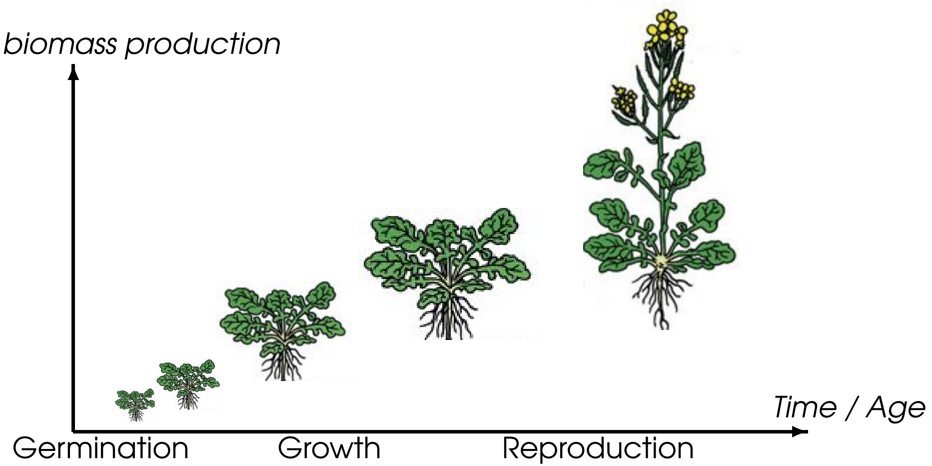
Vegetative growth: as the plant grows, its biomass production rate increases – this biomass production translates to further vegetative growth, which further increases biomass production rate.



An example: what if I were an annual plant . . .

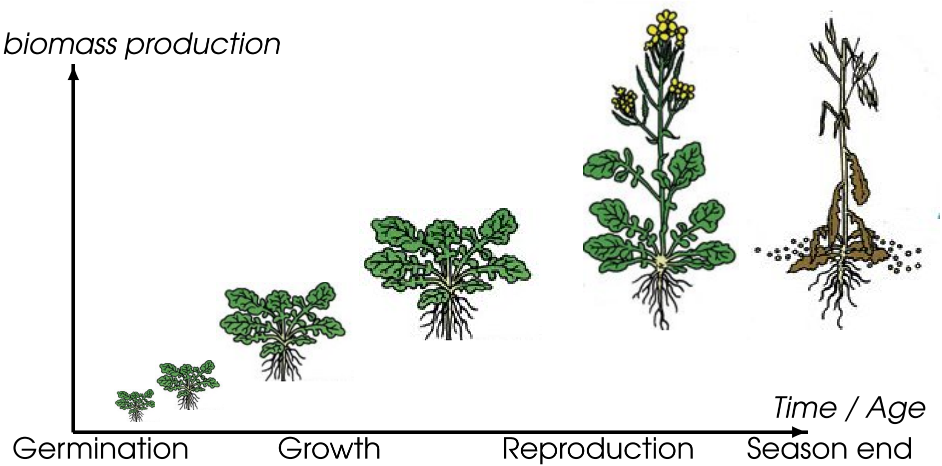
The timeline of an annual plant lifecycle.

Switch to reproduction: at some time within the season, vegetative growth ceases and the plant switches to investing in reproduction –producing flowers and seeds.



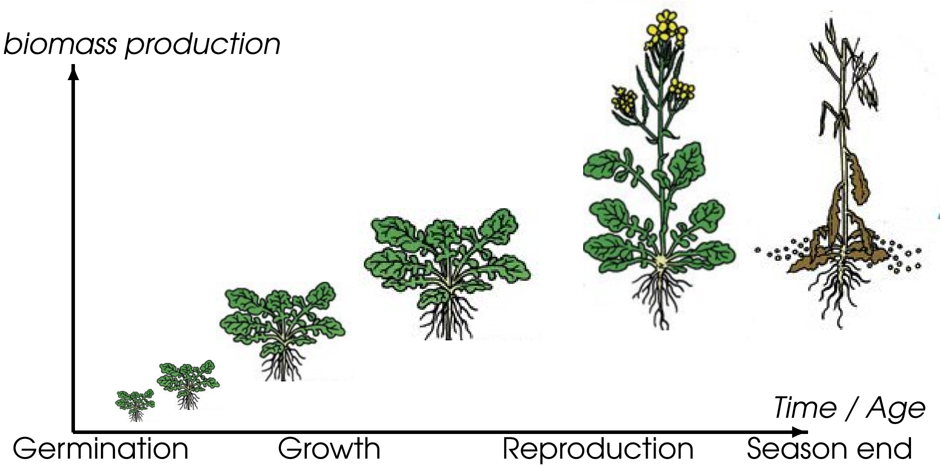
An example: what if I were an annual plant . . .

The timeline of an annual plant lifecycle.
End of season: death.



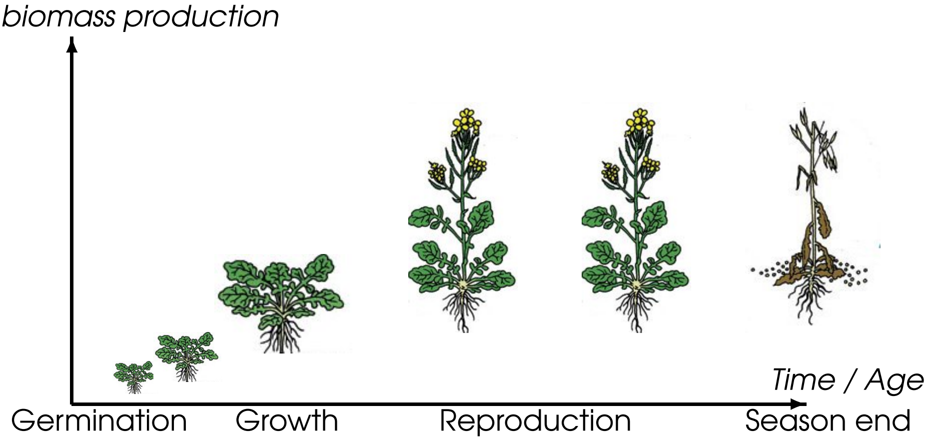
An example: what if I were an annual plant . . .

State-dependence: The rate of growth or reproduction depends on biomass production rate, which increases as the plant becomes larger.



An example: what if I were an annual plant . . .

Trade-off: Start reproducing earlier – slower reproduction but for longer time; or later – less time to reproduce but reproduction is faster. A trade-off between growth and reproduction



Life history traits

- In the most narrow sense, life history traits relate to schedules of reproduction and mortality.
    - Age-dependent reproduction.
    - Age-dependent survival.

- Closely related to "fitness" – the demographic impact of the individual.

- But nowadays also relate to a wider scope of organismal traits.
    - Behavior.
    - Physiology.
    - Morphology.
    - Secondary sexual traits.

  All of which can eventually affect organismal performance in terms of reproduction and survival.

Modeling in the natural sciences

This course is about mathematical modeling.

> *The **sciences** do not try to explain, they hardly even try to interpret, they mainly **make models**. By a model is meant a **mathematical construct** which, with the addition of certain verbal interpretations **describes observed phenomena**. The justification of such a mathematical construct is solely and precisely that it is **expected to work**.*
>
> *John von Neumann*

> *Essentially, all models are **wrong**, but some are **useful**.*
>
> *George Box*

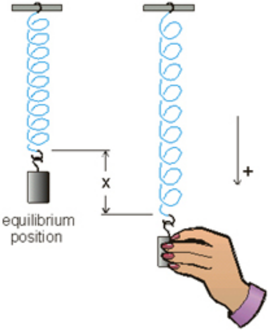
Modeling in the natural sciences

- Example: Classical Newtonian mechanics is **wrong**.
- It is only an **approximate** description of nature – there is always an error, unexplained phenomenon, or deviation from model-based prediction.
- Newtonian mechanics is not a very good description of nature for very high speeds, very large masses, or at the atomic or molecular scale.
- However, Newtonian mechanics is still **useful** for everyday life: building bridges, designing cars, launching satellites or playing "angry birds".
- As science progresses, we develop better approximations – in this case, relativity and quantum mechanics.
- But those are still only approximate descriptions – some difference remains between prediction and observation.

Modeling in the natural sciences

- Science deals with observed phenomena – nature, "reality"– not with truth (whatever truth is).
- Science tries to find general patterns in nature and to describe them – to bring together disparate observations under a unified conceptual framework.
- Sooner or later this process leads to a **mathematical model**.
- A mathematical construct that approximately describes (mimics) nature.
- A mathematical model is **useful** because:
  1. It is a **compact description** of a set of observed phenomena.
  2. Provides **quantitative** results that can be compared to observed values.
  3. Can **predict** future (not yet observed) occurrences of the natural phenomena it attempts to describe.

State variables: compact description of nature



Mass on a spring.

The state of the system is described by displacement from equilibrium point.

We denote it by x.
We measure x in units of length.
(mm, cm, inches, etc.)

The spring-mass system can be in
Extension state: $x > 0$.
Compression state: $x < 0$.
Equilibrium state: $x = 0$.

By comparing values of x we can compare different springs, or the state of the same spring in different times.
We can also look for rules in the way x changes over time
→ predict the state of the system in the future.

State variables: compact description of nature

- A **state variable** is that element of the mathematical model that relates to a **property of the natural system** that we are interested in.
- Usually, it relates to a property that changes, or at least may change, over time.
- Examples:
  - x – displacement of the mass-spring system.
  - State of matter: solid, liquid, gas.
  - p – allele frequency in a population.
  - Body mass of an animal.
- Can be continuous:
  - $x = 1$cm, -2.3mm, 10.9m.
  - $p = 0.5, 0.99, 0.01, 1, 0.$
- or discrete:
  - solid/liquid/gas.
  - extended/compressed/at equilibrium.

State variables: compact description of nature

Rarely does a single state variable fully captures the relevant properties of a natural system.

We usually require several. For example:

- A more complete description of the spring-mass system requires both displacement, x, and velocity, v.
- A thermodynamic system is described by volume, pressure and temperature.
- Allele frequencies of several alleles/loci/genes.

In life history theory:

- Age – reproduction and survival vary with age.
- Size – larger plants have higher rate of biomass production.
- Nutritional state – a starving animal has higher mortality risk than a well-fed one.
- etc.

Dynamics in discrete vs. continuous time

- We can measure time in **discrete steps**: day 0, day 1, day 2, ...; year 1999, year 2000, year 2001, ...
- Assume we know x_t, the value of the state variable at time-step t.
- The value at the next time-step is obtained by a **recursion relation**: $x_{t+1} = \ldots$
- or by a **difference equation**: $\Delta x = \ldots$
- The recursion relation and difference equation are related of course, because $\Delta x = x_{t+1} - x_t$ and $x_{t+1} = x_t + \Delta x$.
- We can repeatedly use the recursion or difference equation to obtain also $x_{t+2}, x_{t+3}, x_{t+4} \ldots$
- And also go backward in time to derive past values: $x_{t-1}, x_{t-2}, \ldots$

Dynamics in discrete vs. continuous time

- We can also measure time along a **continuous scale**: 21.3 sec since beginning of experiment; 1.7 years since birth, ...
- In such cases, a law of dynamics takes the form of a **differential equation**
- For example, Newton's second law of motion and law of gravitation.
- In mathematical form: $dx/dt = \ldots$
- It describes the time-derivative (= rate of change) of the state variable.
- By solving, we get the the time-trajectory $x(t)$.
- $x(t)$ = a function of time that provides the value of the state variable for every value of the time coordinate, t.

Extremum principles

- In many cases, the natural system would tend to change towards a maximum or minimum (collectively, extremum) of some quantity.
- In mechanics – minimum energy, minimum action.
- In thermodynamics – maximum entropy.
- In biology, evolution by natural selection can serve as an extremum principle.
- The “fitness” improves over the course of phenotypic evolution $\leftrightarrow$ Trait values would change over the course of evolution in the direction of increasing “fitness”.

Why extremum principles are useful?

Examples of applying extremum principle

We can predict the state of the system in the long-term, without the need to know the dynamics and the time-trajectory the system followed to get to that state.

Optimization

Sometimes we want to maximize or minimize some other invented quantity, which depends on the problem we are trying to solve.

- In economics – Maximize profit to cost ratio; Maximize profit from investment portfolios; Minimizing risk of bankruptcy;
- In engineering – maximize signal-to-noise ratio; minimize energy loss / dissipation;
- In biology – maximize "fitness" – the **optimal** trait value or the optimal phenotype is the one for which "fitness" is highest.

If evolution proceeds by natural selection we expect to **eventually** obtain the phenotype with the highest "fitness".

Optimization models and suboptimal observations

Usually, we do not observe the predicted optimal trait value in nature.

- Nature is complex – model may not include all causes of variability among individuals, populations, species, etc.
- Evolution takes time – We may not yet have reached the maximum value.
- Environments change – The optimal value in the (recent) past might have been different.
- Natural selection requires variation – Not enough genetic variation in the population to allow for evolution to optimal value.

Optimization models and suboptimal observations

Usually, we do not observe the predicted optimal trait value in nature.

Nonetheless optimization models are still **useful** because:

- They are based on a **valid biological rationale** – evolution by natural selection.
- They provide **quantitative predictions** that can be compared to prediction.
- They establish the **direction** that trait evolution should take.