## Behavioral ecology

The study of the ultimate reasons for behavior: its function (= fitness consequences in an ecological context)

### Behavioral ecology methods

**How do you measure/investigate the fitness consequences of a behavior?**

- Behavioral ecologists seldom do this directly.

**How do you measure/investigate the ‘function’ of a behavior?**

- Comparative studies
- Experimental manipulation (‘psudomutants’)
- Modeling

### Behavioral ecology methods

**Comparative studies**

- Compare expression of behavior in different species
- Correlate (or not) with ecological (or other) variables
- Problems: causal connection?
- Problem: indendent samples? - use phylogenetic contrasts method

**Experimental manipulation**

- Manipulate or prevent behavior and observe consequences
- Ideally: actually measure fitness
- Usually: measure a proxy
- Problem of behavioral flexibility (?)
- Problem of rare events
- Problem of natural conditions
**Modelling**

- Represent behavior in a mathematical or algorithmic formulation
- Compute or deduce optimum of a function given particular parameters
- Problem of abstraction
- Problem of validation
- Problem of ‘natural parameters’

**Comparison of methods**

<table>
<thead>
<tr>
<th>Comparative method</th>
<th>Experiments</th>
<th>Modelling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Advantages</td>
<td>real natural selection</td>
<td>proof of optimality</td>
</tr>
<tr>
<td>Disadvantages</td>
<td>confounding factors</td>
<td>artificial situation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>abstract &amp; hard to validate</td>
</tr>
</tbody>
</table>

**Reading for today**

**Krebs & Davies Chapters 1&2**

- What evidence is there that genes influence behavior?

**Modelling in Biology**

- Why
- How
- What

**Why model?**

**The purpose of models and the scientific process**

(I’m basically only talking about explanatory models)

**How science works:**

- Have two hypotheses about something
- Find out where these hypotheses make different predictions
- Develop a test that will show which prediction is true
- Discard the other hypothesis
### Why model?

**What models can do:**

- Help find sensible hypotheses
- Derive predictions from hypotheses
- Test predictions

**Why model?**

Essentially, modelling is a method to derive conclusions from certain assumptions.

1. If the assumptions reflect a hypothesis, the conclusions are the predictions of that hypothesis.
2. If we know the assumptions to reflect the world, then the model results can be compared to hypothesis predictions, and hypotheses thus tested.

### Ask yourself before modeling:

1. Can models make non-obvious predictions? **Model represents hypothesis**
2. Is modelling the best way to distinguish between predictions? **Model represents world / test**

### Models representing hypotheses

Main problem:

Show that the hypothesis' predictions are relevant, i.e. are the ones that will be empirically tested.

Examples:

- Non-trivial processes, e.g. optimal foraging
- Complex systems, many interactions: e.g., hypothesis about mechanism for collective behavior

### Models representing the real world

Are used if the test can't be performed in the real world; if the real system is too big or expensive or if non-existing conditions are to be tested.

Example:

- Hypothesis: the waggle dance is an adaptation to particular environments. Test: quantify performance in different environments.
# 2. Testing hypotheses

**Models representing the real world**

**Main problem:**
Show that the assumptions actually do represent the real world. (This is very hard!!)

**Historically...**

- Biology as a science is not very old (especially the quantitative bits)
- Most modeling until about the 1980s was about finding the optimal thing to do under certain conditions (optimal foraging, kin selection, reproductive skew theory)
  
  = studying ultimate causes, using analytical models to derive predictions

**What to model**

**Historically...**

- Then: with PCs came computational approaches not possible before and the study of mechanisms
- also: ‘adaptationism’ and optimal foraging theory was strongly criticised

Non-adaptive traits and constraints were studied, optimality tested

**Different modeling methods**

**Analytical vs. computational approaches**

**Analytical approach**

A system or hypothesis is represented in mathematical or logical terms.

From this representation, conclusions are derived analytically with mathematical or logical methods.

**Methods: analytical approach**

Example - kin selection:

We hypothesize that animals behave to maximise the frequency of their genes in the next generation, not their number of offspring.

We know that relatives have a likelihood of carrying our genes that depends on relatedness.

Thus $F_{g+1} = O_{\text{own}} \times 0.5 + O_{r1} \times r1 + O_{r2} \times r2 \ldots$

We derive the prediction that animals help each other when

$$c_{\text{own}} < b_i \times r$$
**Computational approach**

A system or hypothesis is represented in some way, usually in a computer. Conclusions are derived by computing output parameters from given input values. This could mean numerically solving an equation, or simulating a multi-step process.

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**Example - an optimal foraging model:**

We hypothesize that animals behave to maximise the amount of food collected per time, and that they can recruit at a central place.

We derive that the average long term intake is

\[ T_s P_s \gamma + T_s P_s G \gamma \]

and we want to find the time at the food patch \( s^* \) that maximises it.

By solving numerically, we can predict time spent at the food patch for any combination of \( T, \lambda, \) and \( \gamma \).

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**Different modeling methods**

<table>
<thead>
<tr>
<th>analytical</th>
<th>computational</th>
</tr>
</thead>
<tbody>
<tr>
<td>All conclusions are derived analytically -</td>
<td>Conclusions are derived by plugging in values and computing results -</td>
</tr>
<tr>
<td>Results general</td>
<td>Results specific to values used</td>
</tr>
<tr>
<td>This is only possible for few parameters and interactions.</td>
<td>Many parameters and interactions can be present.</td>
</tr>
<tr>
<td>Applicability to real world mostly dependent on clever abstraction.</td>
<td>Applicability to real world mostly dependent on clever choice of studied values.</td>
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**Individual-based modeling**

A particular form of computational models…

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**Questions**

The IBM answers

- which individual rules/algorithms produce which collective behaviors
- which collective behaviors are used by insects
- and which of a given set of behaviors are optimal for a given problem

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**Model advantages & disadvantages**

- Can analyse how collective behavior arises from individual rules
- Non-existent (in insects) algorithms & parameters can be tested
- No real optimality testing (only between specific alternatives)
- Insects may be operating under different constraints / parameters
Model advantages & disadvantages

- No real optimality testing (only between specific alternatives)
- Insects may be operating under different constraints/parameters
- Careful parameter estimation
- Thorough investigation of insect system
- Sensitivity analysis

Methods: individual-based models

- Peck (2004): simulations should be treated like experiments - variability is expected, statistics and replication necessary (TREE 19: 530-534)
- Fussmann & Blasius (2004): in complex systems, subtle differences in functions can lead to different results - this is almost untestable (Biol. Lett.)
- Judson (1994): The rise of the individual-based model in ecology (TREE 9: 9-14)
- Hutchinson & McNamara (2000): emphasise that, and how, models can be tested (Anim Behav 59: 665-676)

if you want to know more