Methods

Behavioral ecology

The study of the ultimate reasons for behavior:

its function

(= fitness consequences in an ecological context)

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

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

	Comparative method	**Experiments**	**Modelling**
Advantages	real natural selection	well-controlled	proof of optimality
Disadvantages	confound-ing factors	artificial situation	abstract & hard to validate

Krebs & Davies Chapters 1&2

- What evidence is there that genes influence behavior?

Modelling in Biology

Why
How
What

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

What models can do:

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

mostly this

this is much harder

What models can do:

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:

- What is my question?
- What are the hypotheses? (at least 2!!)

1. Can models make non-obvious predictions? **Model represents hypothesis**

or

2. Is modelling the best way to distinguish between predictions? **Model represents world / test**

Models representing hypotheses

Are used if predictions of hypotheses are not obvious; predictions can't be derived empirically.

Examples:

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

Models representing hypotheses

Main problem:

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

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.

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

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

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.

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 $F_{g+1} = O_{own} * 0.5 + O_{r1} * r_1 + O_{r2} * r_2$ ...

We derive the prediction that animals help each other when

$$c_{own} < b_r * r$$

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.

Example - an optimal foraging model:

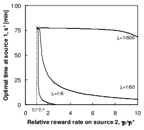
We hypothesize that animals behave to maximise the amount of food collected per time, and that they can recruit at a central place.

We derive that the average long term intake is

[redacted]

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.



analytical	**computational**
All conclusions are derived analytically -	Conclusions are derived by plugging in values and computing results -
Results general	Results specific to values used
This is only possible for few parameters and interactions.	Many parameters and interactions can be present.
Applicability to real world mostly dependent on clever abstraction.	Applicability to real world mostly dependent on clever choice of studied values.

Individual-based modeling

A particular form of computational models…

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

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

- Careful parameter estimation
- Thorough investigation of insect system
- Sensitivity analysis

- No real optimality testing (only between specific alternatives)
- insects may be operating under different constraints / parameters

- May (2004): Uses and Abuses of Mathematics in Biology. (Science 303: 790-793)
- 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): emphazise that, and how, models can be tested (Anim Behav 59: 665-676)
- Gould & Lewontin (1979): critique of adaptationism (Proc R Soc London B 205: 581-598)