UNIT 2. TESTING HYPOTHESES IN BEHAVIORAL ECOLOGY

SOURCES
required: Chapter 2 in Krebs & Davies (1993)
remedial: Halliday (1994:133-139); "Homemaking" in The Trials of Life video series
supplemental: Dugatkin (2001 chapter 8); Blumstein & Fernandez-Juricic (2010:chapt 3)

PARTS OF THIS LECTURE OUTLINE
1. The comparative approach
2. The optimality approach
3. Evaluation- comparative vs. optimality approaches

1. COMPARATIVE APPROACH

1.1 **Behavioral variation among >1 species** (*Krebs & Davies 1993:25-29)*

1.1.1.alternative hypotheses about adaptations(CID; "video")
1.1.2 **C**: convergence (different ancestors, similar environment, similar derived traits)
1.1.3 **I**: inertia (no change; ancestral traits similar to derived traits)
1.1.4 **D**: divergence (similar ancestors, different environment, different derived traits)

TIP: For those of you familiar with evolutionary theory, this viewpoint is now referred to as "deep evolution", meaning that these processes happened a very long time ago. Hypotheses like this are tested using the fossil record or genetic markers. See the tutorial if you need a refresher on these concepts. The jargon has precise meaning in a scientific context. We will be using this jargon throughout this course.

1.2 **Variation within 1 species** (*Krebs & Davies 1993:42-43)*

1.2.1. alternative functional hypotheses (LMN; "snapshot")
1.2.2. **L**: less fit (proportion of genotype A declines relative to B)
1.2.3. **M**: more fit (proportion of genotype A increases relative to B)
1.2.4. **N**: no change in proportion of genotypes (at adaptive peak or neutral)

TIP: For evolutionary theory geeks, this viewpoint is "shallow evolution", meaning that we can measure variation in phenotypes and genotypes in existing populations. In last lecture, the concept of "fitness" was foreshadowed. This precise meaning is often the biggest "stumbling block" for students taking this course. As soon as you begin to understand we are talking about the shifting proportions of genotypes within the gene pool of a population, then the rest of it will make more sense. I like to think about the analogy of a child's see-saw. Imagine genotype A on one seat and genotype B on the other seat. When A gets a little push off the ground (the environmental influence), then B drops. However, this balance can easily shift when B gets a push and rises, then A drops. The balance may shift back and forth several times as the environment changes (e.g. climate change).This is why we say fitness cannot be measured in an individual separate from the population. Fitness is a property of a genotype within the gene pool of a population.

1.3 **Example: Among >1 species:**

1.3.1. **divergence** of grassland species from forest ancestors
1.3.2. weaver birds *(Crook 1964 cited in Krebs & Davies 1993:27 Fig. 2.1)*
- forest: insectivorous; territorial pairs; cryptic solitary nests; camouflaged
- grassland: seed-eaters; food patches change; flocks; colonies; bright males

1.3.3. primates *(Crook & Gartlan 1966; cited in Krebs & Davies 1993:33 Table 2.2)*
- forest: eat scarce insects; solitary foragers; pairs; active at night/dusk
- forest/grass edge: eat patchy fruit/leaves; small groups; multi-male; day active
- grassland/savannah: omnivore; medium-large groups; single-male groups; day

1.3.4. ungulates *(Jarman 1974; cited in Krebs & Davies 1993:28 Table 2.1)*
- forest: small-bodied; picky browsers; pairs; hiders
- forest/grass edge: medium-sized; browse/graze; small groups; hide/flee
- grassland/savannah: big-bodied; graze; large herds; flee

1.4 **Example: Within 1 species**

1.4.1. eggshell removers vs. non-removers in Black-headed Gulls *(Tinbergen cited in Krebs & Davies 1993:42-43)*
1.4.2. in the past, some gulls removed eggshells, others did not ("bad house-keepers")
1.4.3. predators were more likely to destroy eggs next to eggshells ("white flag" saying "eat me")

1.4.4. those that removed eggshells raised more chicks than non-removers (differential fitness)
1.4.5. hypothesis

- eggshell removal functions in reducing predation on chicks (informal wording)
- high proportion of "remover" genotypes is an adaptive peak (formal wording)

1.5 **Take-home message: Comparative approach**

1.5.1. examine similarities and differences to develop alternative hypotheses
1.5.2. may be applied between several species (evolution) or within one species (function)
1.5.3. examples

- among >1 species: weaver birds, ungulates, primates,
- within 1 species: "remover" & "non-remover" genotypes in Black-headed gulls

Part 1	**Study Questions for Chat & Quiz 2 "Testing hypotheses: comparative approach"**
1.1.1	Comparing >1 species, name 3 alternative hypotheses re. evolutionary history (CID)?
1.1.2	Comparing genotypes within 1 species, name 3 alternative hypotheses re. function (LMN)?
1.2	Describe 1 hypothesis re: evolutionary history, based on a comparative study of your choice? (TIP: weaverbirds, primates, ungulates)
1.3	Using the comparative approach, how was an hypothesis about function tested in 1 species? (TIP: gulls)
1.4	Which study best helps you remember the concept of the comparative approach? (explain)

2. OPTIMALITY APPROACH

2.1 **A predictive model**: quantitative test of whether behavior is adaptive *(Krebs & Davies 1993:42-47)*

2.1.1. specify currency trade-offs in terms of fitness costs and fitness benefits
2.1.2. predict the optimum trade-off: maximize cost:benefit ratio
2.1.3. measure whether the animals make decisions as predicted

TIP: It is easy to miss the point that the authors are making in this chapter. They are basically saying the "old way" was the comparative method. The "new way" is optimality theory. Why? Because the comparative approach is good for coming up with hypotheses, but the optimality approach is better at testing them. Being British academics, the authors value testing hypotheses (deductive reasoning) over generating hypotheses (inductive reasoning). This is a good illustration of how a scientific field has been shaped by the people in it. It may also be why the examples in this textbook may sometimes appear too academic for those of us who try to apply the principles to management of real animals and landscapes. If this is bothering you, jump ahead and read the last chapter and lecture outline to put it in perspective.

2.2 **Options for choice of "currency" to test predictions about fitness of genotypes based on optimality theory**

Time-scale	**Currency**	**Pros**	**Cons**
short-term	energy costs/benefits	relatively easy to measure	assumption that "energy=fitness" is rarely tested
medium-term	seasonal reproduction	measurable	may vary over lifetime (good & bad years)
long-term	lifetime reproduction	best match to theory	hardest to measure

TIP: Compare this table to our discussion of space & time scales in Unit 1. Hopefully, it will now make more sense why I emphasized those scales in Unit 1. Basically, the theory is based on the long-term scale. But since we rarely can measure lifetime reproduction (except maybe for fruitflies), we measure energy as a "currency" in the short term. The analogy of "currency" works because energy is something we can count, like dollars (or Euros, or Yen, or Pesos), and it is a "stand-in for the gold standard". In this analogy, the "gold standard" would be fitness of genotypes in a population. For more examples of how "fitness currency" has been measured, jump ahead to read Table 3.1 in Krebs & Davies 1993:75.

2.3 **Example: Crows crack whelks** *(Zach 1979 cited in Krebs & Davies 1993:44-46 Fig. 2.8)*

2.3.1.specified currency trade-offs in optimal foraging

- benefit- calories gained by eating whelk
- cost- calories lost by flying high to drop whelk

2.3.2. predicted optimal decisions (Benefit:Cost ratio)

- H1: choose larger whelks (more gain per effort)
- H2: choose minimum effective drop height (5.2 m = least cost per shell)

2.3.3. measured behavior supported predictions

- H1: average size chosen > size offered
- H2: average height of drop = 5.2 (success on first drop)

2.4 Take-home message: Optimality approach

2.4.1. independent calculations of costs & benefits => testable prediction
2.4.2. reject hypothesis if behavior does not match prediction
2.4.3. example: crows - whelk size and height for dropping whelks

Part 2	**Study Questions for Chat & Quiz 2 "Testing hypotheses: optimality approach"**
2.1.1	In your own words, what is the concept of an "optimality model", in the sense used to test an hypothesis about the function of a behavioral trait?
2.1.2	Why are optimality models used for hypotheses re. function rather than evolutionary history?
2.2	Why do behavioral ecologists measure "currency" in optimality models in terms of calories, when lifetime fitness is theoretically better?
2.3	What was a study where the optimality approach was used in behavioral ecology? (explain)
2.4	Critique the assumptions about currency for an optimality model of your choice?

3. EVALUATION- COMPARATIVE VS. OPTIMALITY APPROACHES

3.1 **Advantages of comparative approach** *(Krebs & Davies 1993:36-37)*

3.1.1. correlates differences in behaviour with differences in ecology (or similarities)
3.1.2. develop hypotheses in one taxon to be tested in another taxon (or population)
3.1.3. good for long time-scales that are hard to measure (e.g. speciation, lifetime fitness)
3.1.4. multivariate statistics can be used to get around the major criticisms (Box 2.1)

3.2 **Critique of comparative approach** (correlation is not causation) *(Krebs & Davies 1993:29-31,41, 45-47)*

3.2.1. failure to test alternative hypotheses (e.g. predation vs. sexual competition)
3.2.2. confounding variables- linked traits (e.g. body size & brain size)
3.2.3. different solutions to the same problem (e.g. antlers & horns)
3.2.4. complex & gradual variation => intuitive categories (e.g. 5 grades of primates)
3.2.5. similarities may be due to phylogenetic inertia, not ecology (e.g. apes are folivores)

3.3 **Advantages of optimality approach** *(Krebs & Davies 1993:45-47,73-74)*

3.3.1. specify costs and benefits separately before examining trade-offs
- benefits of maintaining camouflage of nest (re. eggshell removal)
- cost of leaving vulnerable chicks

3.3.2. test alternative hypotheses based on a quantitative model
3.3.3. general enough to apply to various currencies (e.g. fitness, energy, time)
3.3.4. explains why a trait may persist despite costs, due to over-riding benefits

3.4 **Critique of optimality approach** *(Krebs & Davies 1993:29,74-75)*

3.4.1. adaptationist reasoning is illogical
- a species exists, therefore it is perfectly adapted (extinction happens when environments change!)
- animals are designed to maximize net benefit (who was the designer?)
- fitness trade-offs at the time the trait evolved may have been different

3.4.2. unrealistic assumptions
- no change in costs and benefits over evolutionary time
- variation in the trait is highly heritable
- energy/time are reliable currency to measure lifetime fitness of genotypes

TIP: In this chapter, the authors are not even in their treatment of the comparative vs. the optimality approaches. They are making a transition from comparative to optimality in the next chapter. The information at the end of the next chapter is actually better at explaining that there are disadvantages to the optimality approach as well. I choose to put both the pros and cons together for both approaches in this lecture outline, because it is more balanced. If you are feeling lost, jump to read ahead at (Krebs & Davies 1993:74-75). Also, reread the section on "Adaptationist Storytelling". What they say there *applies to both comparative and optimality approaches. No points earned for storytelling in this course!*

3.5 **Take-home message:** pros and cons of the two approaches

	Pros	**Cons**
comparative	intuitive, inductive (develop hypotheses)	methodological problems (species are not independent)
optimal	quantitative, deductive (test hypotheses)	unrealistic assumptions about energy=fitness

Part 3	**Study Questions for Chat & Quiz 2 "Testing hypotheses: comparative vs. optimality approaches"**
3.1	Advantages of the comparative approach in behavioral ecology, what are they?
3.2	Disadvantages of the comparative approach in behavioral ecology, what are they?
3.3	Advantages of the optimality approach in behavioral ecology, what are they?
3.4	Disadvantages of the optimality approach in behavioral ecology, what are they?
3.5	What is your conceptual map of the pros and cons of comparative vs. optimality approaches?

SUMMARY

1. The comparative approach

1.1. generate hypotheses re. behavioral adaptations based on similarities and differences
1.2. applied to comparisons within species and between species
1.3 e.g. within: egg removal in gulls; between: weaver birds, ungulates, primates

2.The optimality approach

2.1. generate/test hypotheses re. behavioral adaptations based on costs & benefits
2.2 e.g. shell-cracking behavior of crows

3. Evaluation- comparative vs. optimality approaches

3.1. comparative: more intuitive based on observed variation; criticized for loose methods
3.2. optimality: based on what would be predicted in an "ideal, unchanging world"

Summary	**Study Questions for Chat & Quiz 2 "Testing Hypotheses"**
4.1	What were 3 take-home messages re. testing hypotheses in behavioral ecology?
4.2	How do comparative and optimality approaches relate to evolutionary history and function?

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