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Selection, Adaptation, Fitness, and Species

Short Course @ Ilia State University
April 23, 2025

Four Sets of Questions

1. What is selection, and how does selection generate adaptations?
2. What is actually being selected?
3. In what sense is selection picking “fitter” organisms?
4. How does that create new species?

Part 1: Selection

What is selection, and how does selection generate adaptations?

A “Principle” of Selection

The “Lewontin conditions” (1970):

1. There is variation in the morphological, physiological, or behavioral traits of a species (the principle of variation)
2. Variation is at least partly heritable, such that individuals resemble their parents more than they resemble unrelated individuals, and, in particular, offpsring resemble their parents (the principle of heredity)
3. Different variants will leave behind a different number of descendants, either immediately or in future generations (the principle of differential fitness)

Genetic Drift

In the absence of selective pressures, traits will change in a random manner: **genetic drift**

- Neutral evolution (Kimura)
- Shifting balance theory (Wright)

Selection and Adaptation

But! The result of the Lewontin conditions just looks like “differential growth rates” of traits, not the generation of **adaptations,** which is what Darwin had set out to explain in the first place.

- Organisms have problems that they need to solve, that are “set” by their environmental interactions
- Organisms with better solutions do better at solving them

How do we identify the “solutions” and the “problems”? It seems strange to say that the landscape of “problems to be solved” was already out there in the world, waiting on organisms to arrive… So we need a kind of “co-construction” causal story, which is difficult to elucidate.

Adaptationism

The classic response here is to say that adaptation is an **initial hypothesis** – we start out assuming that adaptation happens and use that as our initial point of departure. Put a bit more polemically:

1. Break an organism into parts
2. Give an adaptive story for each trait
3. If a part doesn't look adaptive, invoke "trade-offs" with some other part
4. Move all non-selective processes to the background

Gould and Lewontin: this is the **adaptationist** or **Panglossian** paradigm

Adaptationism

> [It is a] necessary deduction from the theory of Natural Selection, namely – that none of the definite facts of organic nature, no special organ, no characteristic form or marking, no peculiarities of instinct or habit, no relations between species or between groups of species – can exist, but which must now be or once have been *useful* to the individuals or the races which possess them. (A. R. Wallace, 1867)

Spandrels

Problems with Adaptationism

- How can we *reject* an adaptive explanation, or declare that it really doesn't work?
- Adaptationism leaves out, or puts in the background, a shocking number of other processes
- Adaptation doesn't look like the right explanation for a class of very important phenomena – the architectural plans that create the broad structures of organisms

Exaptation

Defined by Gould and Vrba: Using parts that were created either by architectural constraints or for *other* selective purposes for a novel purpose

Example: the evolution of wings

Convergent Evolution

> First, evolutionary convergence is far more widespread than is generally appreciated, with the implication that the number of functional solutions is limited. This applies as much to molecular biology and cell chemistry as it does to phenotypes, behavior, and intelligence. Second, despite the immensity of the Tree of Life, the divergences that delineate its shape are unlikely to be random. (Conway Morris 2009, 1331)

What Now?

1. No adaptation, no selection: importance of neutral evolution and drift
2. No adaptation, selection for something else: correlation of growth
3. Selection without adaptation: have twice as many offspring – selected but not adaptive
4. Adaptation without selection: “accommodation,” another sense of adaptation
5. Adaptation and selection without optimality: many solutions to the same problem
6. Exaptation: using parts already present for new purposes

What Now?

> To abandon the notion of adaptation entirely, to simply observe historical change and describe its mechanisms wholly in terms of the different reproductive success of different types, with no functional explanation, would be to throw out the baby with the bathwater. Adaptation is a real phenomenon. (Lewontin 230)

Part 2: Units of Selection

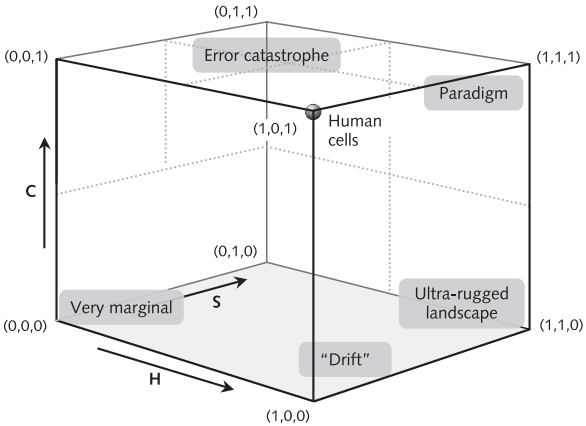
What is actually being selected?

Replicators and Interactors

David Hull (1980): selection is the differential replication of replicators, as a results of the interactions of interactors

The most common case: replicators = genes, interactors = organisms. But it's easy to think of other cases, too!

Peter Godfrey-Smith (2009)



H: Fidelity of heredity
S: Dependence of realized fitness differences on intrinsic properties
C: Continuity (smoothness of fitness landscape)

Group Selection

> When two tribes of primeval man, living in the same country, came into competition, if the one tribe included (other circumstances being equal) a greater number of courageous, sympathetic, and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would without doubt succeed best and conquer the other. (Darwin 1871, 1:162)

Group Selection

> This is the paradox that makes altruism such a fascinating subject for evolutionary biologists. As humans we would like to think that altruism can evolve, as biologists we see animal behaviors that appear altruistic in nature, yet almost by definition it appears that natural selection will act against them. This is the sense in which evolution appears to be an inherently selfish theory. (Wilson, 65)

Kin Selection

An act is selected for if its cost is less than its benefit, multiplied by the coefficient of “relatedness.”

On this theory, apparent altruism is actually egoism, in favor of “my genes” as they are expressed in *other organisms*.

Group vs. Kin Selection

Published: 23 March 2011

Inclusive fitness theory and eusociality

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Nature **471**, E1–E4(2011) | Cite this article

“Units” or “Levels” of Selection

- genes (Dawkins)
- traits
- organisms
- groups of organisms (Wilson, Wade)
- species?
- ecosystems?

Pluralism?

Multi-Level Selection

Okasha (2006):

- MLS1: “the particles are the ‘focal’ units, that is, the units whose demography gets tracked; the collectives in effect constitute part of the particles’ environment… the fitness of a collective is defined as the average fitness of the particles within it”
- MLS2: “both particles and collectives are focal units… collective fitness is defined independently, though it may on occasion be proportional to average particle fitness”

Wilson's "Cheap Individualism"

> ...averaging the fitness of individual types across groups is a useful, intuitively reasonable procedure... it merely cannot be used to define individual selection because it leaves nothing outside of it. (Wilson, 68)

An Empirical Question

> The basic issue then is whether organisms, by and large, are using strategies for genic survival alone, or for both genic and group survival. If both, then which seems to be the predominant consideration? If there are many adaptations of obvious group benefit which cannot be explained on the basis of genic selection, it must be conceded that group selection has been operative and important. (Williams, 58)

Part 3: Fitness

In what sense is natural selection selecting “fitter” organisms?

Reproductive Success

> The individuals who have more offspring are fitter in the Darwinian sense. (Lerner 1958)

The “Tautology Problem”

If “fitness” = “realized reproductive success,” then “the survival of the fittest” = “the survival of those that survived”

> Clearly, we cannot say that the difference in fitness of *A* and *B* *explains* the difference in actual average offspring contribution of *A* and *B*, when fitness is defined in terms of actual reproductive success. Yet, evolutionary biologists seem to think that type frequency changes can be *explained* by invoking the relative fitnesses of the types concerned. (Mills and Beatty, 265)

The Propensity Interpretation of Fitness

> Thus, we suggest that fitness be regarded as a complex *dispositional* property of organisms. Roughly speaking, the fitness of an organism is its *propensity* to survive and reproduce in a particularly specified environment and population. (Mills and Beatty, 270)

Problems: Time-Scale

> Long-term probabilities imply foresight no more than short-term probabilities do. And the fact that selection occurs one generation at a time does not mean that it is wrong to define a quantity that describes a trait's long-term expected fate. [...] Long-term fitness is a coherent concept that may be useful in the context of certain problems; however, its coherence and desirability do not undermine the concept of short-term fitness. (Sober 313)

Problems: Fitness of what?

The same question that we posed above in talking about levels of selection returns, just for fitness...

Problems: Property vs. Measure

> It is hard to know how to reconcile fitness as a propensity, based on the heritable physical characteristics of an organism (i.e., the interpretation of fitness that addressed the explanatory circularity problem and the mismatch problem) with [mathematical measures like expected numbers of offspring]. [...] Brandon (1990) seems to differentiate what fitness is (how it is defined, what it is ontologically, which is the non-mathematical formulation) from how it is measured, which suggests that it is mistaken to think of the mathematical formulation of fitness as a definition of fitness at all (or as the propensity interpretation in particular). (Millstein 2016, 608)

How does natural selection lead to the creation of new species?

What's a Species?

First problem: we have a clear "pre-theoretic" idea of what species are, which leads to a clash between a "common-sense" concept and a "scientific" concept

“Taxonomic Disorder”

> The problem is manifested in the existence of scores of alternative definitions for the term “species,” no fewer than 24 of which have been designated as distinct species concepts. (de Queiroz 1263)

A Few (!) Examples

- BSC / interbreeding (either by reproductive isolation or by mechanisms for recognizing members of the same species)
- ecological (same ecological niche)
- phylogenetic (either cladist, or coalescence theory, or by qualitative characteristics)
- evolutionary (the evolution of separation between lineages)
- phenetic (only phenotypic characteristics)
- historical individuals (Hull)
- metapopulation lineages (de Queiroz; taken to be a minimal definition of what's shared by all the others)

> All of them either explicitly or implicitly equate species with separately evolving (segments) of metapopulation lineages, where a metapopulation is an inclusive population made up of a set of connected populations, and a lineage (at the population level) is a population extended through time or an ancestral-descendant series of time-limited (instantaneous) populations. (de Queiroz 1263)

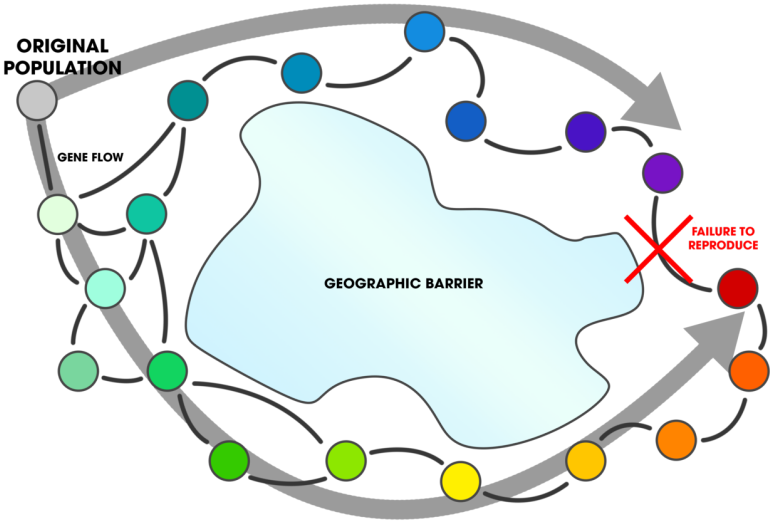
> [O]n the historical entity interpretation, similarity is a red herring; it is not the issue at all. What really matters is how many organisms are involved and how much the internal organization of the species involved is disrupted. If speciation takes place when a small, peripheral isolate succeeds in bringing about a genetic revolution, then the parent species can still be said to persist unchanged. (Hull 374)

Ambiguity of the Question

Second problem (de Queiroz): what even are we arguing about?

1. a metaphysical question: What are the necessary properties of a species?
2. an epistemic or methodological question: How do we distinguish species in nature?
3. the nature of speciation: What processes create and maintain species?

Ring Species



Different Answers?

Different Answers?

Phylogenetic analysis of the history of mitochondrial DNA, which is inherited matrilineally, reveals that the ancestors of polar bears and brown bears diverged into isolated lineages about 150,000 years ago. Phylogenetic analysis of nuclear DNA, on the other hand, which is inherited from both parents, reveals a much earlier divergence around 750,000 years ago. Did polar bears split from brown bears 150,000 years ago or 750,000 years ago? The answer is “yes.” (Haber and Molter 2019, 2)

Open Questions

- Does natural selection “optimize” for some particular quantity, or not? (cf. Grafen 2014)
- Is the formalism of group selection completely reducible to that of individual selection? (cf. Nowak et al. 2010)
- What is the empirical relationship between selection and drift? (cf. Wade & Goodnight 1998)
- Is natural selection “creative,” or not? That is, is selection part of the explanation for the *existence* of traits, or just the *distrbution* of traits? (cf. Beatty 2016, 2019)
- How do we understand, motivate, or defend “pluralism” about levels of selection, or concepts of species, or…?