

Selection, Adaptation, and Fitness

Short Course @ YSU
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Three Questions about Selection

- 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?



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, offspring 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)



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

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



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.



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

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



[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



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



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)



- 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



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)



What is actually being selected?



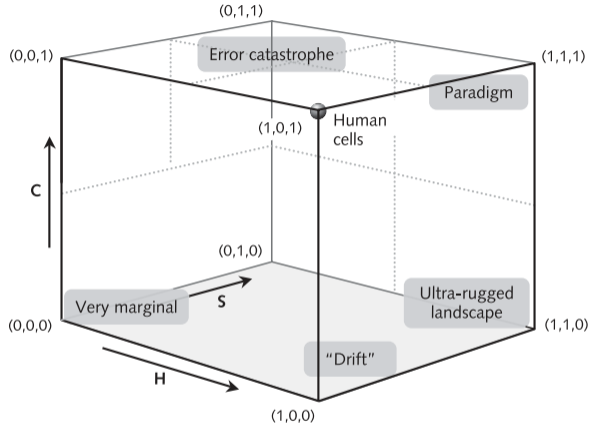
Replicators and Interactors

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)

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)



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)



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*.



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Inclusive fitness theory and eusociality

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“Units” or “Levels” of Selection

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

Pluralism?



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)



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)



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)