

NATURAL SELECTION, BEHAVIORAL CONDITIONING, AND THE PROBLEM OF THE FIRST INSTANCE: COMMENTS ON TERRY SMITH'S PAPER

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Terry Smith's (2019) article is an insightful discussion of the relationship of operant conditioning and natural selection, and of Skinner's understanding of that relationship. However, there is one part of the article that I think is mistaken. The detail in question concerns whether natural selection can solve what Skinner (1953) calls "the problem of the first instance." This is the problem of explaining why a trait changes from being uninstantiated in a population to being instantiated.¹ Given the weight that Skinner and others placed on the analogy between natural selection and operant conditioning, the problem of the first instance matters to psychology, and not just to evolutionary biology, as Smith explains.

When Smith considers qualitative traits, he argues that selection cannot cause a new trait to appear in a population; selection does not result in new traits appearing in the population; it acts merely to remove traits from the population, thereby causing some or all of the remaining traits to increase in frequency. However, when Smith considers quantitative traits, his negativity turns positive; he concludes that selection can cause new traits to appear. He makes his case for this second conclusion by describing an example about bird migration that Skinner (1975) discusses in which selection causes the mean value of a quantitative trait in a population to increase, while the variance around that mean value remains roughly the same; the result is that some individuals have trait values at the end of the process that were not present at the beginning. Smith thus agrees with

¹ This question is different from the question of whether selection can explain why a given individual has one trait rather than another. I argued in Sober (1984) that the answer to this second question is *no*; selection explains changes in trait frequencies in a population, while the rules of heredity, not natural selection, explain why individuals have the traits they do rather than alternative traits. There has been a large literature debating that question; for a recent review of that literature, see Witteveen (2019). Just to be clear, the present paper concerns the following question:

(Q1) Can selection explain why *there now exists one organism in a population that has trait T, whereas earlier the number was zero?*

The question I addressed in 1984 was this:

(Q2) Can selection explain why *Jane has trait T rather than alternative trait A?*

These two questions differ in two ways:

- (1) There is an existential quantifier in Q1 and a name of an individual in Q2.
- (2) Alternative traits are mentioned in Q2, but not in Q1.

Unfortunately, some discussants of the Jane problem have thought that the issue there is whether natural selection is "creative." In fact, the creativity issue pertains to Q1, not Q2.

Skinner on both counts; selection on qualitative traits cannot cause new traits to appear, whereas selection on quantitative traits can.

When I first read Smith's paper, I found this split view of what selection can and cannot accomplish odd, but personal incredulity is not an argument. In casting about for a reason, I came up with this. Let's consider a case in which quantitative traits *entail* qualitative traits. Suppose the individuals in a population have different heights and there are three height categories (short, medium, tall) to which these individuals may belong.² Height is a quantitative character, whereas short, medium, and tall are qualitative. Suppose an individual has height h_1 only if it is short, h_2 only if it is medium, and h_3 only if it is tall. At the start of the selection process, no individual has height h_3 and no individual is tall. If selection can cause h_3 to appear in the population, it should also be capable of causing tall to appear. Not only *can* this happen; it *must* happen if an individual has h_3 only if it is tall.

If quantitative and qualitative traits are in the same boat with respect to the problem of the first instance, which boat are they both in? Here's a genetic example that I think provides an answer. Suppose a diploid sexual population starts with all individuals being AA homozygotes at a given locus and a B mutation then occurs at that locus; the result is that now there is one AB heterozygote among all those AA individuals. Let's consider two alternative selection regimes that might arise in this heterogeneous population. In the first, AB is lethal, and the one AB heterozygote in the population dies before reproducing. In the second, both AA and AB individuals are viable and fertile, and AB is fitter than AA; the result is that the AB individual reproduces by mating with an AA individual, and so the next generation includes several individuals that are AB, not just one. In subsequent generations, AB individuals continue to reproduce by mating with AA individuals until eventually two AB individuals happen to mate with each other, thereby introducing a new genotype into the population, BB. In this example, selection's following the second regime (rather than the first) has caused the population to contain its first BB individual (rather than no BBs at all). This genetic story can be overlaid with two different stories about phenotypes. In the first, the three genotypes cause three different point values of a quantitative trait (e.g., height); in the second, the three genotypes cause three different qualitative traits (e.g., the three height categories of short, medium, and tall). Selection can cause novel qualitative traits to appear in the population just as it is able to cause novel quantitative trait values to arise.

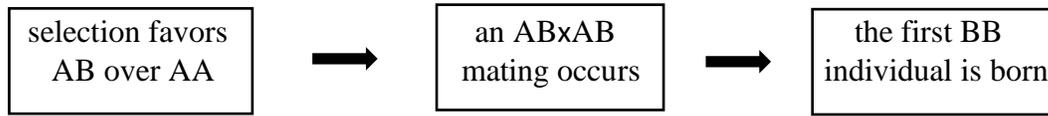
This example illustrates how sexual reproduction can produce novel traits. It doesn't add new singleton genes to a population; that's the job of mutation and migration. Rather, sex produces novel gene *combinations*. The novel combination in my example is the BB genotype; genotypes are *pairs* of genes. With sexual reproduction, novel gene combinations can and will arise, whether or not there is selection. What selection does is influence *which* novel gene combinations are constructed.³ It is notable that the idea that selection never creates anything new is usually made with viability selection in mind, not fertility; in the within-generation process of organisms surviving from egg to adult, selection eliminates variants rather than creating new ones. Matters change when adults reproduce.

In the story just told, did selection cause the BB trait to appear, or was that event caused merely by the mating of two AB individuals? I think this question poses a false dichotomy. The

² There may be individuals that can't be classified in any of these three qualitative categories; they are "borderline cases." The existence of such individuals does not affect the point I want to make.

³ This is an old and familiar point, made repeatedly in the heyday of the Modern Synthesis and more recently. See Beatty (2016, 2019) for an able review of that history.

appearance of BB in the population has two causes, one more distal and the other more proximal, and they, together with the first appearance of BB, form a causal chain:



I think it is appropriate to treat causality as a transitive relation in this case, and so we can conclude that selection caused the first instance of the BB genotype to appear.⁴ I should mention that the causal diagram is incomplete. There are other distal causes – the introduction of a B mutation into a population of AA homozygotes, for example. And there is a link in the causal chain between the first item and the second – the increase in frequency of the AB genotype.

If I am right that natural selection can cause new traits to appear in a population, regardless of whether the traits are quantitative or qualitative, then the analogy between natural selection and operant condition fails to sustain Skinner’s conjecture (which Smith quotes) “that operant selection of human behavior ultimately applies only to properties that are continuous and quantitative in nature.”

In his footnote 8, Smith raises a further question when he writes:

Human behavior exhibits instances of qualitatively novel responses that are appropriate to the context. Selecting for novelty can increase the likelihood of novel responses, but it does not reliably produce responses that are appropriate to context. *This problem does not exist in the case of phylogeny, where qualitatively novel traits do not show a pattern of being appropriate (adaptive) on first occurrence.* They initially occur without reference to appropriateness and are then selected only if they enhance fitness (italics mine).

Smith’s use of the word “pattern” in the italicized sentence indicates that he doesn’t deny that natural selection *occasionally* causes novel qualitative traits to appear that are adaptive when they first occur. I take him to be saying that that turn of events doesn’t happen often enough to count as a pattern.

Let’s consider Smith’s claim in the context of the genetic example I gave earlier, where a B mutation occurs in a population of AA homozygotes, and eventually two AB individuals mate

⁴ In the story I told, I took care to describe events contrastively. I talked about selection taking one form *rather than another*, of an ABxAB mating taking place *rather than not*, and of one individual instantiating the BB genotype *rather than no individual doing so*. This contrastive formulation, I believe, permits the following transitivity argument to be deductively valid:

X₁ rather than X₂ causes Y₁ rather than Y₂.
Y₁ rather than Y₂ causes Z₁ rather than Z₂.

X₁ rather than X₂ causes Z₁ rather than Z₂.

However, if the contrasts don’t “line up” properly, the resulting argument will fail to be valid:

X₁ rather than X₂ causes Y₁ rather than Y₂.
Y₁ rather than Y₃ causes Z₁ rather than Z₂.

X₁ rather than X₂ causes Z₁ rather than Z₂.

See Helgeson (2012) for discussion of how confusion about transitivity has befuddled discussion of question Q2, which I mentioned, and then set aside, in footnote 1.

to produce a BB offspring. I earlier assumed that AB is fitter than AA and that AA individuals are short, AB individuals are medium, and BB individuals are tall. I'll now add a new detail – the assumption that BB is fitter than AB. We now have an example in which heterozygotes are intermediate in phenotype and in fitness. It's an empirical question how often this arrangement occurs; there are known cases in which it does not (heterozygote superiority and heterozygote inferiority), but my impression is that biologists think that intermediate heterozygotes are pretty common.⁵

If natural selection causes novel qualitative traits to appear that are adaptive at their first appearance, the question is why. One part of the answer just given is sexual reproduction, which causes novel gene combinations to arise. Notice that this part of the explanation appeals to something that is separate from the selection process itself. Selection can occur without sexual reproduction. If Smith is right that conditioning processes often cause novel qualitative traits to arise in ontogeny that are adaptive at their first appearance, the question is why. One answer, which behaviorists reject, is that novel behaviors sometimes do not arise at random but rather are the result of intelligent planning.⁶ Behaviorists will reject this answer, but that does not make the question go away. If the facts about natural selection are any guide, answering the question about ontogeny will require attention to facts that are extrinsic to the process of conditioning.

Acknowledgments

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⁵ In evolutionary theory, mutation, not selection, is the place to find situations in which a novel trait is probably not adaptive. Darwin, though he knew nothing of Mendelian genetics, anticipated what is still the standard picture:

Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental; yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice, – events and circumstances all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up through the power of selection, whether this be natural or artificial selection. (1868, p. 249)

Mutations have their causes, but mutations do not occur because they would be good for the organism. The net result is that most mutations are deleterious or neutral, and only a few are advantageous. This view is sometimes expressed by saying that mutations occur “at random.” What is being rejected here is that mutations are “guided.” The latter idea has historically been associated with the idea of theistic intervention, but the idea of guided mutation can be separated from the idea that mutations are caused by a benevolent intelligence (Sober 2014).

⁶ This is an idea that Popper (1972) embraced in his evolutionary epistemology – science is a selection process in which theories compete, but the competing theories are not constructed at random.

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