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Timothy Shanahan
Loyola Marymount University, timothy.shanahan@lmu.edu

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Author(s): Timothy Shanahan

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DISCUSSION: BEATTY ON CHANCE AND NATURAL SELECTION*

TIMOTHY SHANAHAN

Department of Philosophy
Loyola Marymount University

In his (1984) John Beatty correctly identifies the issue of the role of chance in evolution as one of the liveliest disputes in evolutionary biology. He argues, on the basis of a carefully articulated example, that "Even on a proper construal of 'natural selection', it is difficult to distinguish between the 'improbable results of natural selection' and evolution by random drift". His other remarks indicate that he is thinking of conceptual as well as practical indistinguishability. In this discussion I take issue with one of the consequences Beatty draws from his example. I argue that the example at most shows that the effects of drift and selection are sometimes difficult to separate in practice, but that the stronger conceptual claim is not warranted. The deeper problems raised by the example are seen to demand causal, rather then conceptual, analysis.

In his (1984) John Beatty explicates the relationship between chance and natural selection in evolutionary theory. He rejects the widespread view that the fitness of an organism is simply that organism's *actual* reproductive success, because this renders the distinction between random genetic drift and natural selection opaque. Instead he expresses his preference for a propensity interpretation according to which: "[T]he fitness of an organism is the number of offspring it is physically disposed to contribute *in a particularly specified environment*" (p. 192; compare Mills and Beatty 1979). On this interpretation natural selection could be understood as sampling on the basis of such fitness differences, and random drift as sampling irrespective of such fitness differences. An apparent virtue of this approach is that the somewhat nebulous question of the roles of chance and natural selection in evolution could then be stated more perspicuously as "the question of the relative evolutionary importance of *sampling without regard to fitness differences vs. sampling with regard to fitness differences*" (pp. 190–191).

Beatty favors the propensity interpretation over the common, but erroneous, view of fitness because the latter view manifestly fails, in *every* case, to distinguish drift and selection. Following the above considerations, however, he adds: "But I am afraid that, as much as I would like

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the distinction between natural selection and random drift to be a clear-cut one, it is not as clear-cut as the preceding discussion suggests" (p. 192). Even on the propensity interpretation, it seems, there will be *some* cases in which drift and selection are indistinguishable, namely, where the results of natural selection, if such they be, are not what we would expect. He gives the following example to support his claim that: "Even on a proper construal of 'natural selection', it is difficult to distinguish between the 'improbable results of natural selection' and evolution by random drift" (p. 183). We are to imagine two kinds of moths, light and dark, which live in a forest in which 40% of the trees have light-colored bark, and 60% of the trees have dark-colored bark. In addition there are in the forest color-sensitive predators which prey on the moths. We would expect, ceteris paribus, that in such an environment the dark-colored moths would be fitter, since the forest as a whole affords them more protection from predators than it does for their light-colored neighbors.

So far so good. But suppose, Beatty goes on, that in one particular generation we discover that a greater proportion of dark moths than was characteristic of the population as a whole, and similarly a smaller proportion of light-colored moths, were killed by predation. Suppose also that we have evidence that the dark moths were perched on light trees when attacked, and the light moths were perched on dark trees. Although the percentage of dark trees is greater than the percentage of light trees, the dark moths landed on the light trees more often.

This is the example. Beatty then raises the following question: "Is the change in frequency of genes and genotypes in question a matter of natural selection, or a matter of random drift?" Given the definitions of natural selection and drift introduced earlier, this question can be reformulated: "[I]s the change in question the result of sampling discriminately or indiscriminately with regard to fitness differences?" (p. 195). He sees a problem in answering this question unambiguously. On the one hand, it is difficult to maintain that the predation of dark moths on light trees is indiscriminate sampling. After all, such moths presumably are dead because they were too conspicuous to predators. "On the other hand," he says, "it is also difficult to maintain that selection alone is the basis of the change. At least, it is difficult to maintain that the fittest were selected" (pp. 195–196). He concludes from this example that

> it seems that we must say of some evolutionary changes that they are to some extent, or in some sense, a matter of natural selection *and* to some extent, or in some sense, a matter of random drift. And the reason (one of the reasons) we must say this is that it is conceptually difficult to distinguish natural selection from random drift, especially where *improbable results of natural selection* are concerned. (p. 196)

Beatty's argument, if sound, would be interesting because of its implications for the structure of evolutionary theory in which selection and drift are understood to be conceptually distinct, but interacting, forces. On the other hand, if the moth example shows only that the two processes are practically difficult to distinguish in some cases, then it merely illustrates a fact that biologists are only too aware of already. This example, therefore, deserves closer examination.

Beatty locates the difficulty in the moth example as that of distinguishing between natural selection and drift, since each possibility seems problematic. He doesn't say why it is difficult to maintain that selection alone was the basis of the change, but presumably he has in mind the fact that the dark moths are fitter than the light moths with respect to their predominantly dark forest home, so they couldn't have been discriminated against on the basis of fitness differences, which were clearly in their favor.

But is this analysis correct? It depends, of course, on what we take to be the relevant environment of the dark moths that were killed. Is it the forest that contains a certain percentage of dark and light trees, or is it the light tree each ill-fated dark moth was perched upon when it was killed? A dark moth may be fitter than a light moth with respect to a forest containing more dark trees than light trees, but if we take a smaller unit for our reference environment, for example, the particular tree each moth is perched upon, then those same dark moths may be less fit with respect to *that* environment than the light moths are. In other words, the identification of the relevant environment becomes crucial for the assignment of fitness values, and consequently for the determination, in any given sampling event, of the roles of drift and selection.

The problem of identifying the relevant environment, while often difficult, is not obviously a conceptual problem but rather involves the difficulty of correctly isolating and weighting the causal factors connecting various environmental properties to an organism's survival and reproduction. The precise details of how this is to be done are at present fuzzy, but the general outline of a solution can be sketched. (An anonymous referee for this journal informs me that Robert Brandon has interesting work in progress on this problem. I'm afraid that here I can only muddle along with the admittedly rather rough-hewn analysis that follows. Readers are, of course, invited to improve upon it.)

For purposes of precise evolutionary explanation we should include in our analysis the most fine-grained environment in which the properties of interest actually play a causal role in the survival and reproduction of that organism. Because of the immediacy of some environments to an organism's survival and reproductive interests, such environments will generally play a relatively more important role in our analysis of that organism's fitness than will wider, more inclusive environments. This principle does not exclude consideration of patchy environments—on the contrary, the greater an organism's ability to discriminate and take advantage of uneven environments, the more weight must be assigned to that environment in contributing to an organism's fitness. Indeed, we can think of each organism as belonging to an indefinite variety of environments which overlap to various degrees; the environmental component of its "absolute fitness" is a function of all of these, weighted in an inverse proportion to each environment's importance at the moment. Thus the fitness of an organism changes, as its relationships to various environments change, through time. As if this weren't daunting enough, the fact that other highly mobile organisms constitute part of the environment of most organisms makes the prospects of determining "the" fitness of any organism at a specified time staggering to contemplate. (It should be noted that speaking of the fitness of genotypes, rather than of organisms, doesn't help, since the fitness of a genotype is just the average of the fitnesses of the organisms possessing that genotype.)

Fortunately, however, the determination of *the* (absolute) fitness of an organism is rarely if ever necessary, since such "overall fitness", as such, plays no causal role in an organism's survival and reproduction (Sober 1984). What matters is, rather, the causally salient features of its environment, which do in fact affect its survival or reproductive success. This can be seen by returning to the moth example. There is certainly no conceptual difficulty in thinking that the dark moths that were killed while perched on light trees were discriminated against on the basis of their lower fitness in virtue of their relationship to that particular environment. Given the scenario as it is presented, the particular light-colored trees the dark moths were perched upon, as well as the color-sensitive predators, constitute the primary causal factors in that sampling event. These factors, in effect, "screen off" less relevant causal factors (such as the patchiness of the forest as a whole) from the moths' survival and reproductive success. (Compare Salmon (1984) on the notion of screening-off. Brandon (1982) shows how this notion can be fruitfully applied to biological analysis.) Their overall fitness, determined in part by the patchy forest home they inhabit, is in this case causally irrelevant. (Why these particular moths lit on light-barked trees when dark-barked trees are more common is an interesting, but strictly different, question. See below.) This is not to deny the causal relevance of more inclusive environments in the entire life history of an organism, but is meant to distinguish components of fitness which are, or are not, relevant to the analysis of a given change in gene frequencies. Beatty is right to index the fitness of an organism to a *specific* environment, since this is the causally significant consideration. But because he fails to adequately consider the causal role of the micro-environment (the individual trees) of the organisms in question, his analysis quite literally risks missing the trees for the forest.

Another part of the apparent conceptual difficulty in Beatty's example may result simply from a foreshortened perspective. The identification of evolutionary forces must usually be inferred indirectly from trends over several generations back to their environmental and genetic causes. The example concerns a change in gene frequency within a single generation. In this case we have no way of telling whether the moths just happened to land on the trees they did, or whether they landed on those trees because of some genetically influenced disposition. A study of this population of moths over several generations might disclose whether this behavior was a recurrent one, and thus indicative of a genetic basis for the behavior. Of course, merely observing either a uni-directional or a completely random change in gene frequencies in the moths over several generations would not suffice to *prove* that the changes were due to selection rather than to drift, or vice versa, any more than obtaining all heads upon flipping a coin a large (or even infinite) number of times proves that the coin is biased (van Fraassen 1977). The point here is just that in the absence of detailed knowledge of the relevant causal factors responsible for an evolutionary pattern, even one spanning many generations, we cannot infallibly identify the evolutionary forces responsible for changes in gene frequencies. This problem is of course magnified if we are dealing, as in Beatty's example, with just a single generation. I suspect that the appearance of a conceptual difficulty stems in part from the very real practical difficulty of correctly analyzing the moth example in the absence of the necessary causal information, not from any essential conceptual indistinguishability between drift and natural selection.

The primary thesis of this discussion should already be tolerably clear from the foregoing remarks, but it can now be made explicit. Beatty considers the problem posed by the moth example to be, at least in part, a *conceptual* one. But this risks confusing our inability in some cases to identify the relative values of the evolutionary processes at work with the difficulty of clearly stating the differences between these processes. The question raised by the moth example is not whether drift and selection are conceptually difficult to distinguish—they are not. Rather, the moth example raises the question of how we are to individuate environments for, and make valid inferences from evolutionary patterns to, the determination of causally relevant properties responsible for fitness differences and changes in gene frequencies. Hence, the problem is one of detailed causal, rather than conceptual, analysis. The moral to be drawn from Beatty's paper and the present discussion, therefore, is the necessity of supplementing the study of evolutionary phenomena with the detailed analysis of the causal factors responsible for those phenomena.

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