
WHAT DOES GENETIC
SELECTION MISS?
CONSIDERING THE CAUSAL ROLE
OF BEHAVIOR IN EVOLUTION

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ABSTRACT. While the Darwinian original concept of natural selection primarily includes the central role that the behavior of individual organisms may play as an active agent in the process of biological evolution, the architects of the Modern Synthesis tended to focus primarily on genetic heritage in order to explain evolutionary changes of populations. I shall argue that in doing so there is something important that evolutionary biology fails to grasp: the behavior of the organisms that need to act in their ecological environment if copies of their genes are to be transmitted. The concept of behavior helps to understand the way evolution works in the wild. Finally, examples are provided as to how ethology offers some enlightening insights that help reinterpret, in a way that does not imply a metaphysical hypostatization of the idea of nature, much of the current debate in relation to the very concept of natural selection as real force acting in the outside world.

KEY WORDS. Synthetic theory, evolution, natural selection, artificial selection, behavior, ethology, philosophy of biology, Baldwin effect, genetics.

INTRODUCTION

The topic in which I will concentrate on is the relationship between evolutionary biology and psychology, as well as the causal and conceptual connections bringing the notions of behavior and evolution together. In this paper, I shall address the ways in which the individual behavior of animal organisms may actually be given a crucial causal role within the process of evolution by natural selection, as it is understood in contemporary biology. As I will show, this role has been customarily neglected or even explicitly denied by the builders of the synthetic theory and the proponents of sociobiology alike because—they seem to have thought—for individual behaviors to function as active agents in the evolutionary process Lamarckism needs to be recognized as a viable mechanism gui-

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ding evolution. This, I will demonstrate, misses the point if there are necessary relations among what organisms do and the way their traits evolve. It is my contention that ignoring those relations obscures what evolution is really about. Consequently, I will argue in this paper that we need to place in a proper understanding of natural selection those referred causal links.

It is important to take into account what I *will not do* in this essay. I will not contend that evolution as regularly understood in present day biology actually occurs, nor will I provide evidence for evolution in this technical sense of the term. I equally will devote no space to the epistemic or empirical evaluation of alternatives to Darwinian evolution. In what follows, the synthetic theory is very much taken for granted in that it, I shall assume, has been extraordinarily well supported by large amounts of evidential facts while other so-called alternatives (namely the intelligent design among a few others) cannot even be considered as substantive scientific theories in biology for reasons I will not address here. Those reasons ought to be assumed tacitly (for more on this see Ayala 2000).

Biologists study living things and evolutionary biologists reconstruct how those living entities have statistically changed in relevant respects (this is to say, how their traits have evolved) over periods of time that are typically enormously long. Psychologists, on the other hand, as well as ethologists aim to describe and explain how those living creatures behave. This paper, though, is neither a work on biology nor an essay on psychology in that respect. This is not to deny that my general argument might very well entail important implications for such arenas (as in fact I expect), anyhow, those intersections notwithstanding, the focus of my analysis will be kept rather gnoseological in that it tries to illuminate what the relationships among those sciences have to be if the concept of natural selection is to be constructed accurately and fruitfully. Furthermore, I will show that this behavioral reconstruction of the notion of natural selection very much coincides with what Darwin pointed out when writing the *Origin*.

DARWIN'S DOUBLE HERITANCE

I will start out by making a historical point. Darwin's main contribution in his monumental work was not the introduction of the thesis according to which the living things we see today are the result of a process of organic transformation. This idea, however controversial, was very much in the air when Darwin wrote *On the Origin of Species*. The hypothesis of transformism was defended by several naturalists both before and after Darwin's book was first published (Ruse 1979; Bowler 1983; Bowler 1988; Alvargonzález 1996).

What is new about Darwinism is therefore not exactly the notion of evolution (to which Darwin extremely rarely refers in 1859) but rather the precise characterization of the mechanism by which evolution takes place. This mechanism consists of the differential selection of traits according to the adaptive value they have in the various environments in which organisms live and reproduce.

Having said this much, it is worth noticing that Darwin's account of natural selection and evolution included the suggestion that what organisms actively do in their environment may play a causal role in the process of their evolutionary change. Darwin wrote a great deal (see for example Darwin 1872) trying to clarify how this could happen and insisted that it was by the conversion of habits into instincts that evolution had shaped the creation of new behavior patterns (Darwin 1859). In this respect, individual conduct and (one is tempted to say) individual minds are given certain causal priority in Darwin's original framework for evolution.

This model remained essentially Lamarckian in that it assumes that habits, acquired during the organism's life span, could be directly inherited by the next generation. This has subsequently proven wrong, and partly due to the research carried out by Weissmann and others the sort of causal connection which Darwin attempted to introduce among active behavior and evolutionary change was simply overridden in later biology.

Today, biologists who are in line with the synthetic orthodoxy tend to regard evolution as consisting in a set of statistical changes in the genetic pools of populations (Dobzhasky, et al. 1977). Within this framework, molecular biology and genetics sometimes appear to be the real name of the game in understanding evolution and natural selection. This type of gene-centrism (Jablonka 2000; Barash 2001; Gould 2002) constitutes a picture from which any active role of behavior seems to have entirely disappeared. There are of course good reasons for this to be so, since Lamarckism as an evolutionary mechanism has been discredited as something both conceptually and empirically flawed to an extent that goes beyond repair.

However, one could challenge, if Lamarckism is really beyond repair. This raises an empirical problem, so I do not see principled arguments to deny that there might well be ways to articulate a viable Lamarckian alternative to neo-Darwinism. Yet such an alternative does not exist so far, and as long as biology researchers do not factually construct it, I see no reasons whatsoever to deny that the inheritance of acquired traits just do not occur in the real world. Nonetheless, what is truly crucial for my point is to underline that, whatever the reasons may have been, the concept of selection, far from remaining Darwinian in the original sense of the world, has been genetically and even biochemically interpreted in current bio-

logy in ways that Darwin himself could never have predicted. What I want to suggest concerning this change of focus is that the logic of neo-Darwinian biology has somehow gone astray in the process by ignoring fundamental aspects of how evolution functions.

This is not to say that the synthetic theory and the neo-Darwinian tradition have neglected the topic of behavior. It has very hardly done so. It might well be the case that individual behaviors are not any longer regarded as causes of evolution (for that would tantamount to a Lamarckian contention), but they are still readily interpreted as effects of the genetic changes that populations of biological individuals constantly experience. This is particularly the case with the biological thinking that work on sociobiology, ecology of behavior or evolutionary psychology to name just a few arenas. They typically grant that behaviors, as any other phenotypical trait, are selected due to their survival or reproductive fitness. According to this view, it just happens that genotypes cause phenotypes to behave in ways that are adaptive for the individuals genes or else are not transmitted to the next generation. Behavior has by no means been suppressed from biology; it is rather seen as epiphenomena or, to put it more accurately, is explained by what goes on in the genetic level. It doesn't matter. The differences between being reduced to and being explained by are much too subtle to escape the risk of becoming a *question nominis* and, in any event, my broader point remains that whereas the road from genes to behavior stays causally open for anyone to traverse (and in effect, to cross it again and again is all sociobiology is really about) (Barash 1977) the other way around is respectively sealed once and for all: «No trespassing... unless you are a Lamarckian.»

Those who agree with this unidirectional view of the relationships between behavior and evolution will be hardly satisfied with Robert Richard's contention that Darwin himself was not a neo-Darwinian in this strict sense of the term (Richards 1987). This may be so, they will be inclined to argue, but in any case such historical point does not demonstrate that there is anything wrong in the current biology nor it shows that the neo-Darwinian account of behavior is flawed in ways that call for rectification. And after all, they still can claim to be the heirs of the substantial core of Darwin's theory once it has been conveniently refined and rectified itself. Michael Ruse for example, among a number of others, has argued this point very emphatically.

There is, nonetheless, another tradition that also can justly claim the title of heir to Darwin. The individuals of that family tend to work on fields such as ethology, comparative psychology or animal traditions and have carried out a large wealth of empirical research on how behavior may be seen to interfere actively with organic evolution at least in some specific contexts. Very much acting in the original spirit of Darwinism, people like

Lloyd Morgan, Baldwin, Waddington, Tinbergen, Plotkin, Patrick Bateson or Eva Jablonka have emphasized how what animals do in their natural and ecological environment can at times causally control the way their genes change as well as how this can actually happen in manners that do not defy the Weismann barrier between genotypes and phenotypes. To them, as to Darwin himself in some of his works, the behavior of the individuals acting within their ecological contexts is all the name of the game.

HOW IS THE DARWINIAN CONCEPT
OF NATURAL SELECTION TO BE INTERPRETED?

Gustavo Bueno (2000) holds that the theory of evolution needs to approach the mechanism that connects the behavior of animals and their organic evolution without surpassing the Weismann barrier, which keeps phenotypes and genotypes mutually separate. In this sense, evolutionary principles like the Baldwin effect or the organic selection has alerted us to the possibility that those purely Darwinian causal chains occur and guide the evolutionary process. Baldwin's stance is worth considering; it suggested that Lamarckism was not needed to justify such causal connections. In this paper I want to suggest that Baldwin's effect is not necessary either. In fact, the very concept of natural selection, as Darwin developed it in his original theory, suffices to illuminate those causal imbrications between behavior and evolution. In what follows, I will try to vindicate the Darwinian original concept of natural selection as functioning at the individual and phenotypical level and will contend that the behavioral operations carried out by individual animals must be taken into account if such notion is to make any sense at all. To put things differently, insofar as behavior is ignored or interpreted as an epiphenomena caused by selfish genes, natural selection starts to appear as an irrelevant factor in accounting for evolution. I do not suggest here that the synthetic theory is flawed in any meaningful way (I start out by assuming that it is not) but I do suggest that it goes astray as long as it forgets that there is way more to evolutionary biology than biochemical frequencies: psychology is also needed to make sense of the Darwinian picture of what evolution involves. This is the bone I would like to pick here.

Let me start by saying the obvious. One of the more salient features of evolutionary theory is that even though Darwin constructed the concept of natural selection by considering artificial selection as a mechanism that needs to be extrapolated (Sober 2009), it can only work when it is not interpreted as something shaping the transformation of organic traits consciously. In this respect, it follows that selection in the Darwinian sense of the term is not an intentional agent who acts like a demiurge guiding

the process of adaptation that leads to the evolutionary change of the different traits present among populations. Indeed, how could this be so? There seems to be no way to interpret the mechanism of natural selection in such demiurgic fashion unless one is ready to regard nature as an intentional agent that acts like a super-agent would be expected to do. It is important to notice that Darwin was not prepared to sustain such an interpretation (however see Richards 1993, who argues that he may have been). And neither should we, for this would imply a very crude reification of the notion of nature and thus a metaphysical principle, which is superfluous for evolution. Selection does not need a super-agent of this type to do its work.

Darwin, one should grant, was very aware of this problem. He attempted to solve it by thinking of selection as a metaphor that casts a light on the actual biological processes taking place in the real world. Darwin's contention was that even though that metaphorical usage of the notion of selection might potentially prove misleading in some contexts, yet it was useful insofar as it showed that organisms evolve the way they would be expected to if a selective agent were in charge. Of course the assumption remains that there cannot be any agent of this sort.

Being so, it apparently follows that evolution by natural selection as Darwin conceived it represents a mindless process to which, strictly speaking, there is not selection proper or indeed anything at all that selects. This may sound paradoxical to some but, after all, we might well challenge: how could things be regarded differently without running the risk to inflate the sphere of evolutionary causes unnecessarily? In fact, there is trouble here since the question that now arises is what the point of using the term selection could be if what we need is to describe a situation in which nothing whatsoever may be adequately compared to a selector. Let us grant that this is precisely what a metaphorical usage of a term involves. This may be so, but then again this term seems to add nothing (nothing really explanatory) to the account of biological evolution and therefore the problem remains as to whether this metaphor could (or rather must) be parsimoniously eliminated. Furthermore, it is not only about the words: this standpoint entails that the very process of selection (whatever it may be called) is redundant and needs be explained away as an independent evolutionary factor with a causal impact of its own.

There are three possible responses to this. On the one hand, one could be inclined to recognize that selection just does not exist as an independent force functioning in the real world and must be consequently ignored in biological explanations on how the different traits evolved over time. The principle of Occam razor applies here showing why it is epistemologically reasonable, for the sake of simplicity, to conflate those evolutionary factors that evolution actually does not need (Brunnader 2007; Walsh 2007).

Anyhow, it is also possible to attempt to make the case for the role of the concept of selection in biology. To do so would require a biological framework in which natural selection is seen as a super-evolutionary force of its own, rather than a variety of different mechanisms producing or stimulating change over evolutionary time as Barros (2008) has suggested. I don't see reasons to deny in principle that it is possible to find out ways to do this that do not entail a strongly metaphysical reification of nature, but those ways, if they exist, would in any case need to be evaluated empirically as well as conceptually. As long as I know, no explanation of the type has been carried out, and insofar as the job remains to be done, it would not be entirely unfair to assume that it might well be undoable.

These two alternatives, obvious as they may seem, do not exhaust the range of possibilities at hand. It is my contention that there is room for natural selection to play an unavoidable role in biological explanations of evolution. To sustain this contention, we have first to look at the type of biological processes that ethologists and psychologists have been dealing since those scientific disciplines were born. Looked from an ethological viewpoint, animals are not just the by-product of a set of selfish macromolecules working of their own but rather intelligent agents that carry out different patterns of behavior within their ecological contexts. Part of what they do (to be sure, a biologically essential part) has to do with feeding themselves (or with avoiding to be eaten anyway) and with reproduction (namely, with mating) and it is key to understand that those objectives can only be properly achieved if the animals involved select other organisms on grounds of the perceptive traits they carry.

This, I take, is the real content of the concept of natural selection as a causal force shaping evolution: the purely phenotypic process by which some animals select others by virtue of the sensorial inputs they organoleptically receive. Those traits are then selected by others agents who in behaving like selectors literally interrupt the process of gene-transmission (with regards to hunting behavior) or promote it (in terms of sexual selection). It is therefore not the case that there is one super-agent guiding evolution as the metaphorical interpretation of the concept of natural selection could intimate. Nature "per se," let us grant that much, does not select anything but this does not mean that there is no behavioral agents in place. It just happens that there are many.

By way of example, let us consider the case of the phenomena that is called batesian mimicry. This kind of mimicry refers to an evolutionary situation in which harmless species imitate the warning signals of a harmful specie directed at a common predator. The relevant question to be asked here is what has caused the harmless species to evolve the misleading traits they carry. There is not denial as to the obvious fact that one possible answer is that the cause has been the genes controlling the

relevant phenotypic features. This is not a mistake (in fact, there is a way in which that much is obviously correct) but misses the point in that it gives rise to a further question that cries out for explanation. After all, if the butterfly presents misleading warning signals because of the relevant genes it carries, what did cause those genes to be transmitted? A molecular explanation does not account for this problem.

There is another way in which it is obviously the individual predator (for instance, the bird) posing a common threat for both species of butterflies that has caused the signal warnings to recur. He has done so by selecting the individual butterflies who carry them (or more accurately, by not selecting them) based on their visual-perceptive characteristics. It is behavior, not genes, which are key here and insofar as causation is concerned, it would be true to say that behavior has the relative priority in this context. It would not be correct to maintain that the behavior of birds selecting butterflies lacks any causation whatsoever (as a matter of fact it does have many causes at different explanatory levels), but what certainly would be equally wrong is to deny that their behavior as selectors causes the genes of the butterflies to be transmitted or not.

Examples like this could easily be multiplied in a virtually indefinite manner (for more on this topic, see Tinbergen 1958; Endler 1986; Ongay 2008; Ongay 2009; Ongay 2010). What interests me in this context nevertheless is not so much to accumulate particular instances of relevant biological situations to illustrate my general thesis, yet to put it directly and (perhaps) unavoidably abruptly. Let me consequently finish by stating such thesis in brief. When we look at the processes illuminated by decades of ethological research it begins to be obvious that molecular biology fails to capture the way evolution works on the ground. Perhaps (or rather undoubtedly) the variations occurring at the genetic level modify the way organisms act, but what ethology teaches us is that it does not take to be a Lamarckian to notice that there are situations in which the causal direction is actually reverted.

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