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# The Problem

*More attention to the History of Science is needed, as much by scientists as by historians, and especially by biologists, and this should mean a deliberate attempt to understand the thoughts of the great masters of the past, to see in what circumstances or intellectual milieu their ideas were formed, where they took the wrong turning or stopped short on the right track.*

—R. A. FISHER, 1959, *NATURAL SELECTION FROM THE GENETICAL STANDPOINT*

*Adaptation, natural selection, and fitness* are the trinity of terms that form the core of the explanatory framework of modern evolutionary biology. However, unlike fundamental terms in physics, such as *mass, energy, or velocity*, these terms currently have no generally agreed-on meaning, either empirical or theoretical (see Ridley 2004; Futuyma 2005; Freeman and Herron 2007). This is obviously a problem; it is by no means a new one.

In 1866, seven years after the publication of the *Origin of Species*, Alfred R. Wallace wrote to Charles Darwin, proposing that Darwin eliminate the term *natural selection* from his work, replacing it with Herbert Spencer's *survival of the fittest*. As the independent elucidator of the principle, Wallace certainly did not object to the theory itself. His grounds were rather that "this term is the plain expression of the *fact*; Natural Selection is a metaphorical expression of it, and to a certain degree *indirect* and *incorrect*, since, even personifying Nature, she does not so much select special variations as exterminate the most unfavourable ones. . . . Natural Selection is, when understood, so necessary and self-evident a principle that it is a pity that it should be in any way obscured" (Marchant 1916, 141–142).

As the result of Wallace's suggestion, Darwin did work the "survival of the fittest" into subsequent editions of the *Origin*; nevertheless, he retained "natural selection," arguing "As in time the term must grow intelligible, the objections to its use will grow weaker and weaker" (Marchant 1916, 144). The continuing debate, 150 years after *The Origin of Species*, makes one wonder whether the term has in fact "grown intelligible."

## TELEOLOGY AND NATURAL SELECTION

In this book, I try to show that the concept of natural selection is often invoked to explain evolutionary transformations for which we have no evidence that the *mechanism* of natural selection, as currently understood, was wholly or even partially responsible for the transformation. I argue that we have never been able to overcome the major weakness of the metaphor of natural selection, the one that led Wallace to object so strongly to its use. This weakness is the implication that there is, in nature, an agent with actions analogous to those of the breeder in artificial selection, a teleological (goal-directed) agent that intentionally, and with foresight, “selects” variations directed toward the improvement of the organism.

The teleology implicit in the metaphor of natural selection subtly permeates many of the most basic concepts of evolutionary biology, including, most prominently, the concepts of adaptation and fitness. I believe that this implicit teleology has led to many of the numerous objections to the theory over the years. Moreover, and most importantly, this teleology is entirely unnecessary, and does not contribute anything to our understanding of the evolutionary process; instead, it often makes us think we have explained a phenomenon when we have in fact merely restated the case in different terms.

This book is far from an argument against natural selection, since the process elucidated by Darwin and Wallace is clearly an essential part of evolution. Nevertheless, I believe that many of our conceptions of the role that the process of natural selection plays in evolution (which generally come directly from Darwin’s) are unjustifiable additions to the basic process. These conceptions are often derived not from the *mechanism* of natural selection but only from the *metaphor*. Consequently, they partake of the teleology of the metaphor.

The general mode of thinking that I object to goes as follows: “character *x* plays a useful (‘adaptive’) role in the life of organism *y*; therefore, character *x* must have evolved by natural selection for this role.” The definitional equation of adaptations and past natural selection is fairly standard in evolutionary biology today: “a feature is an adaptation for a particular function if it has evolved by natural selection for that function” (Futuyma 2005, 265). When combined with the assumption that useful features or characters are in fact adaptations by this definition, a teleological role for natural selection results. In this role, natural selection is inferred to have directed evolution from an unimproved (poorly adapted) past state toward an improved (well-adapted) present state, merely on the basis that the present state exists and is well adapted.

For example, consider the following passage from Ernst Mayr, one of the founders of the modern synthesis: “Pelagic marine invertebrates have a great diversity of mechanisms by which to stay afloat in the water: gas bubbles, oil droplets, or an enlargement of the body surface. In each case natural selection, which is always opportunistic, made use of that part of the available variation that led most easily to the needed adaptation” (Mayr 1982, 590). We are presented

with an image of poor invertebrate larvae sinking to the bottom, desperately in need of some way to stay afloat, only to be saved by the improving force of natural selection. As pointed out by Croizat (1962), among others, this mode of thinking is not only teleological but also Lamarckian: a need gives rise to an organ to fulfill that need.

While the best solution might be to do what Wallace suggested so long ago—to completely extirpate the term *natural selection* from the lexicon of evolutionary biology—the term is by now too well established to replace. Instead, I would only propose that its use be restricted to those situations that are known to meet the criteria for the mechanism to act. These situations almost always involve current populations under study, general situations, or (possibly) molecular evolution, in contrast to particular historical transformations of phenotypes.

However, none of this discussion is particularly new or original. Many authors have argued against the historical definition of adaptation and function, and the simple equation of present adaptedness and past natural selection. Moreover, current textbooks (e.g., Ridley 2004; Futuyma 2005; Freeman and Herron 2007) are certainly sensitive to the issues involved. I believe that the continued teleological use of the concept of natural selection, in spite of the obvious problems involved, is due primarily to the absence of another evolutionary principle that can be used to interpret patterns of macroevolutionary transformation. Fundamental to my restriction of the term *natural selection* will be the reintroduction of another principle, related to and often confused with that of natural selection. This principle is founded on the concept of the necessary conditions for an organism's (or other evolutionary entity's) continued existence; it states that (by definition) the existence of any organism is contingent on its satisfaction of these conditions. The usefulness of the principle of the *conditions for existence* was first insisted on more than two hundred years ago by the great comparative anatomist, vertebrate paleontologist, and arch antievolutionist, Georges Cuvier.

#### A ROLE FOR HISTORY

Because of the nature of the subject matter, the approach I take in this book is at times critical, at times theoretical, but first and foremost, historical. In fact, as the book emerged, I was surprised to see how much time needed to be spent on the historical background to the story. Or rather, the historical background turned out to be a major part of the story. The issue of teleological explanation has been with us since the dawn of Western philosophy, to an extent presumably realized by all philosophers, but certainly not by most working biologists. To understand the depth of the problem of teleology, it is not enough to begin with Darwin or even with the battles of the Enlightenment. It is necessary to recognize that the problem of teleological explanation in Western science goes back to the debate between the ancient atomists, on the one hand, and Socrates, Plato, and Aristotle, on the other.

Only by understanding the long history of the debate can one hope to understand the circumstances that produced the intellectual *milieux* within which Cuvier and Darwin developed their ideas. Only through the lens of history can one see how other options might have been available, options overlooked due to the predominant beliefs of the times. Most importantly, only through history can one understand how a naturalistic, mechanistic theory of natural selection came to be associated with the design metaphor, when for two thousand years naturalistic philosophers had opposed any intimation of design in nature.

I follow the debate over design from the Greeks, through Darwin, to the modern synthesis. I show how Darwin's perspective, founded on a natural theological view in which adaptedness is something more than mere existence, influenced the formalization of his theory in the structure of mathematical population genetics, most notably at the hand of Sewall Wright. I show that the issues at stake in a number of key controversies of twentieth-century evolutionary biology—including that over Wright's "adaptive landscape" and Fisher's "fundamental theorem," the meaning and significance of genetic load, and the relative roles of natural selection and genetic drift in evolution—can be clarified by viewing these controversies in light of the principle of the conditions for existence. Furthermore, by examining this history, I show how Cuvier's principle can be used to help resolve some of the most troublesome conceptual issues in evolutionary biology today. These include the meaning of key terms such as *fitness*, *adaptation*, and *natural selection*, the distinction between natural selection and genetic drift, and the role of constraints in evolution.

My aim throughout is to examine, as Fisher advised, "the thoughts of the great masters of the past," to attempt to see "where they took the wrong turning or stopped short on the right track." The method I follow, which might thus be called "historico-critical," is bound to seem at times like history, at times like philosophy, and at times like biology. These days, history and philosophy of science are fields of their own, fields with their own training and specialist journals. Yet if history and philosophy of science are to do anything for science itself, one would hope that they might inform our understanding of the persistent issues of science, the issues that will not go away. The problem of biological "design," of teleology, is clearly one such issue. In its modern guise, this is the problem of the proper definition of function, adaptation, and natural selection. History can help us here. It can do so because the conceptual problems we face (unlike the empirical ones) are mostly of our own making, coming from uncritical acceptance of thought structures handed down to us from our predecessors.

#### OVERVIEW OF THE BOOK (AND HOW TO READ IT)

The book is divided into four parts. In the first part, I provide the necessary philosophical background by reviewing the forms that teleological explanations of the structure of the universe take, and examining which of these are acceptable to

science. In particular, I distinguish conditional teleological explanations, which are acceptable, from purposive and deterministic teleological explanations, which are not. I show that Cuvier's principle of the conditions for existence is a conditional teleological principle.

In the second part, I pursue the debate over design from its origins in ancient Greek philosophy through the Enlightenment to Cuvier and Darwin. I show that the "Epicurean hypothesis" was an ever-present threat, a threat the design argument was intended to counter. I argue that Cuvier, with his broad training in philosophy and his distrust of "systems," was able to find the common ground between the materialists and the teleologists in his recognition of the principle of the conditions for existence. By contrast, I argue that Darwin, coming from a background in British natural theology, bequeathed us an evolutionary theory preserving some of the contradictions in natural theology, an implicitly teleological evolutionary theory in which the adaptedness of organisms is only loosely connected to their existence.

In the third part of the book, I show how the teleological aspect of Darwin's theory was translated into the mathematical language of population genetics, particularly by Sewall Wright. This teleology is exemplified by Wright's metaphor of the adaptive landscape; it is absent from Fisher's fundamental theorem. I examine the debate over genetic load, showing that confusion over the meaning of fitness arising out of Wright's (and Haldane's) teleological view of selection led to confusion between two distinct issues: the total variance in relative rate of increase available for evolutionary change, and the mean absolute rate of increase (mean "fitness") of a population. Finally, I examine the fundamental distinction between natural selection and genetic drift, starting from a consideration of how they are measured, and suggest that it may not be as fundamental as Wright suggested.

In the fourth part of the book, I step back to take a larger view and survey evolutionary biology from the perspective I have been developing. I first consider the meaning of adaptedness. I examine in particular its relation both to natural selection and to the conditions for existence, bringing in some empirical examples to ground the discussion. Next, I ask how we can talk about macroevolution without lapsing into teleology, and show that the principle of the conditions for existence can play a key role here. I end by considering some of the ways in which the conditions for existence can serve as a unifying concept in evolutionary biology, tying together such disparate fields as quantitative genetics, the levels of selection, evo-devo, ecology, physiology, and conservation biology.

Many of the reviewers of the manuscript asked me, Who is this book for? This is a valid question, as my approach and subject shift from history to philosophy to biology and back throughout the book; moreover, some parts involve mathematics (if only simple algebra), which can put off many readers. I would answer that this book is written, first and foremost, for *biologists*. Biology is the scientific study