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Concepts and Methods in Evolutionary Biology

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Introduction

THE ESSAYS in this volume cover a wide range of topics including: the conceptual foundations of evolutionary theory and systematics; human sociobiology and the evolution of language; the role of experimentation and its relation to theory; a particular instance of the latter being how to model and empirically investigate the coevolution of organism and environment; and a defense of what I consider the proper philosophy of biology – mechanism – against its main rivals – holism and reductionism. The essays also span my career thus far in philosophy of biology; the first essay having been published in 1978, the last having just been completed. They do not cover all of my work, nor, of course, do they cover the whole range of topics in contemporary philosophy of biology. However, they touch on all of the major topics in the philosophy of evolutionary biology and can serve, I hope, as a good introduction to that field.

I have arranged these essays into three sections. The first contains four articles written relatively early in my career (1978–82); the second has four articles published between 1985 and 1988; and in the third are three of my most recent works. Although the sections are chronologically defined there is, not surprisingly, some thematic unity to each of the three sections.

Section I

The four articles in Part I all address questions that have become central to the philosophy of biology. Furthermore, the questions addressed are all tightly interrelated. In Essay 1, "Adaptation and Evolutionary Theory", I examine the role of the Principle of Natural Selection in evolutionary theory. I argue that it plays an explanatory role but that its cognitive status is quite different from what most philosophers had thought about explanatory laws. To play this role, adaptedness (or expected fitness) must be appropriately defined. And so in Essay 1, I introduce what has come to be known as the propensity interpretation of fitness (or, as I prefer, adaptedness). Mills and Beatty (1979) independently argue for the propensity interpretation in a way that largely, but not entirely, agrees with my analysis. If there are "results" in philosophy, this is one. Most, but not all, philosophers of biology today accept the basic correctness of this analysis of adaptedness (or fitness).

In Essay 2, "Biological Teleology: Questions and Explanations", I explore the question of whether evolutionary explanations of adaptations are teleological. I argue that the phenomena to be explained are, in a sense, teleological, but that the explanations are thoroughly mechanistic. Although this sort of selection-based etiological account of biological teleology has gained wide acceptance in philosophy of biology and in the general philosophical community, the topic continues to generate considerable controversy. These topics will also be broached in Essay 11.

Essay 3, " A Structural Description of Evolutionary Theory", considers the implications of my account of the propensity interpretation of adaptedness and the Principle of Natural Selection for the structure of the theory of evolution by natural selection. Although my description of the structure of evolutionary theory fits nicely the semantic conception of theories, it is independent of that philosophical view. (Essay 3 was written before John Beatty introduced the idea that the semantic conception of theories better fits evolutionary biology than did the syntactic conception coming out of logical positivism. In fact it was presented at the same Philosophy of Science Association session as Beatty's 1981 paper "What's Wrong with the Received View of Evolutionary Theory".) Because Essay 3 is not stated in the jargon of the semantic conception of theories one need not accept all that goes along with that general philosophic theory of theories to accept and understand my account of the structure of the theory of natural selection. I should add that although a number of philosophers of biology have defended the semantic conception of theories, and my account fits in nicely with that conception, my account of the Principle of Natural Selection is entirely unique.

Essay 4, "The Levels of Selection", opened up a new line of research for me which has occupied me ever since. Charles Darwin, and most evolutionary biologists following him, conceived of natural selection acting on differences among organisms within a population. This way of thinking raises the question of whether selection acts only at that level or whether it can occur at other levels of biological organization as well. This question became acute among evolutionary biologists during the 1960s and 1970s. (Primarily in response to the theoretical question of how altruism could evolve.) In Essay 4, I offer an analysis of what it means for selection to occur at a given level and suggest a hierarchy of levels of selection. (This analysis is sharpened and extended in Essay 8.) I also suggest that the so-called units of selection debate has been seriously misguided by a conflation of two quite separate questions. Unknown to me at the time, Richard Dawkins and David Hull were coming to the same conclusion. Using Hull's terminology, the point we were all trying to make is this: The question of what level of biological organization is interacting with its environment to create differential reproduction is quite different from the question of what are the entities that replicate their structure with accuracy and directness during the process of evolution by natural selection. In my view, this point is the single most important philosophical contribution to the debate over the units/levels of selection.

Section II

The essays in this section, with the exception of Essay 8, address topics quite different from those of Section I. Essays 5 and 6 form a pair that developed out of work begun in 1980. In Essay 5, "Phenotypic Plasticity, Cultural Transmission, and Human Sociobiology", I offer a relatively novel analysis of the ecological conditions that favor the evolution of phenotypic plasticity (the ability of a genotype to produce a range of phenotypes). Then I argue that these conditions also favor a nongenetic, or what might be called cultural, transmission system. This argument is used to criticize the basic tenets of human sociobiology. Although arrived at largely independently, this argument shares some points with the truly excellent, but technical and difficult, book by R. Boyd and P. J. Richerson, *Culture and the Evolutionary Process*. In particular both Essay 5 and their book try to give an evolutionary account of how there could be selection for a nongenetic transmission system, a system that ultimately allows the evolution of genetically maladaptive traits. I have found that when students read both, thus seeing two different approaches converging on the same point, they understand that point better.

In Essay 6, "From Icons to Symbols: Some Speculations on the Origins of Language", Norbert Hornstein (a linguist) and I draw on the arguments of Essay 5 in arguing that human natural languages are best thought of as cultural transmission systems and that their evolution from iconic animal communication systems can be understood in this light. This article is unique in critically evaluating the claim that language is adaptive and in giving the account we give of the restrictive conditions under which language is adaptive. (See the target article by Pinker and Bloom and the commentaries in *Behavioral and Brain Sciences* 1990 for discussions of some of these points.) But it leaves much undone. That is, the speculative scenario, although theoretically plausible, is not backed up with any empirical evidence. Indeed I should point out that G. Wagner (1988) questions one of the key theoretical arguments that is central to both Essays 5 and 6. That argument, which undoubtedly is theoretically correct, is that everything else being equal, higher levels of phenotypic plasticity lead to lower levels of heritability and therefore lower response to selection. The empirical evidence Wagner cites does not support this prediction. The key empirical question for my argument is whether the relevant norms of reaction for competing human genotypes largely overlapped or not. Perhaps the article will serve to inspire someone better qualified than I to do the relevant empirical investigations.

Essay 7, "Individuality, Pluralism, and the Phylogenetic Species Concept", was written with the first author Brent Mishler (a biologist) and it expands on the earlier work of his (Mishler and Donoghue 1982) on species concepts. In it we argue that the Hull-Ghiselin thesis of species-as-individuals was a positive step forward but that it now needs to be replaced by what we call the phylogenetic species concept. We also argue for a sort of pluralism with respect to species (quite different from that advocated by Kitcher 1984a). We argue that different biological processes may form species in different cases – so that, *contra* the biological species concept, there is no single process differentiating all species. But, we argue, for any given case there is only one correct account of the species in that situation. This is an extremely controversial area in the philosophy of biology, but our work has gained some followers, especially among younger philosophers of biology working in this area.

Essay 8, "The Levels of Selection: A Hierarchy of Interactors", returns to the topic of Essay 4. In Essay 8 I significantly expand and refine the analysis begun in Essay 4, making full use of Hull's distinction between interactor and replicator. In this essay I go through a number of plausible levels of interactors, from the suborganismic to the superorganismic. For each interactor I show how one can determine what is the relevant replicator and show that there is not a neat correspondence between interactor level and replicator level. Although S. Salthe and N. Eldredge had earlier presented dual hierarchies of a more general sort, my analysis is the first to explicitly argue for a dual hierarchical approach to selection. It seems to me that this sort of approach is now becoming the received view in the field.

Section III

The final section of this volume consists of work either just published (Chap. 9) or just completed and previously unpublished. This work breaks new ground for me and, I would like to think, for philosophy of biology as a whole. Essay 9, "Theory and Experiment in Evolutionary Biology", represents the beginnings of my next major project. Increasingly it is being recognized that 20th century philosophy of science has been theory-centered. The logical positivists focused on the products of science; indeed not even the real products but their "rational reconstructions", and ignored experimental practice. This was bad, then things got worse. The post-positivists, Kuhn, Feyeraband, Lakatos and others, totally perverted experimental science by pretending that experimental (and observational) science was "theory-laden" and so, ultimately, all science is theoretical science. This has led to all sorts of irrationalisms both in philosophy of science and beyond. A small, but growing, number of philosophers of science have begun redressing this major deficiency in 20th century philosophy of science. (Ian Hacking's *Representing and Intervening* is perhaps the best work in this emerging area.) However, most of this work focuses on physics. In Essay 9 I argue the evolutionary biology, or more generally population biology, is importantly different from physics with respect to experimental practice. The difference has to do with what biologists call the "realism" of their experimental conditions. Indeed, insofar as one accepts Dobzhansky's (1968) dictum that "nothing makes sense in biology except in the light of evolution", this difference represents what to me is the most striking difference between biology and physics. For instance, I think this difference illuminates the so-called "evolutionary contingency thesis", or the thesis that biology has no laws, which has been supported by Hull, Beatty, Mayr, Gould, and others.

Essay 10, "The Coevolution of Organism and Environment", is coauthored with Janis Antonovics. (This is an expanded version of our paper by the same title to be published in *The Proceedings of the Second Pittsburgh-Konstanz Colloquium in Philosophy of Science*.) He and I have collaborated over a number of years on both conceptual and empirical work relating to the concept of environment. This collaboration led to what is perhaps the most original part of my 1990 book, *Adaptation and Environment*, in which I draw distinctions among three concepts of environment operative in population biology – the external, the ecological and the selective environments. Essay 10 starts with a much debated question in the philosophy of ecology: Can empty niches exist? Richard Lewontin (1983) has argued that they cannot and that this fact should lead to a major revision in how we think about the process of adaptation, or the process of evolution by natural selection. Antonovics and I use the distinctions among external, ecological and selective environments to clarify Lewontin's position. We show that it is a conceptual truth that selective environments have no existence apart from the organisms that occupy (and construct) them. Further, we support the claim, which we take to be Lewontin's position, that external environments have no existence independent of their organisms. But this claim, if true, is a contingent truth about how evolution often works, and is true only from a diachronic, or evolutionary, perspective. That is, we argue that external environments are conceptually independent of their organisms and that they can be measured independently of the organisms, but they exist in a reciprocal cause and effect relationship with the evolving organisms. In other words, external environments coevolve with organisms. We illustrate these points by developing a simple, yet in some important respects realistic, computer model of organism environment coevolution. Finally, and most importantly from the point of view of the practice of evolutionary biology, we describe a method of empirically investigating this coevolutionary dynamic. Thus I hope that this essay will appeal not only to the philosopher or biologist interested in the conceptual foundations of the theory of adaptation, but also to empirically oriented evolutionists.

The final essay, "Reductionism versus Holism versus Mechanism", has been written expressly for this volume. In it I argue that both reductionism and holism are failed philosophies of biology and largely for the same reasons. As ontological theses they are false; as methodological maxims they encourage bad science. Both are antiempirical in that they impose largely a priori metaphysics on the biological world. In their stead I argue for a philosophical position I call *mechanism.* My distinction between mechanism and reductionism helps show how contemporary biology can be thoroughly mechanistic while not reductionistic. Thus, for example, I argue that evolutionary explanations of adaptations – the locus of biological teleology – are completely mechanistic. This mechanistic, nonreductionist philosophy of biology underlies all my work in this collection, and so I think this article serves well as a concluding essay.

I remember well walking on a bridge across the Charles River with a good friend in 1979, our last year as graduate students. We were musing on what we might be doing five years from that time. (Now five years seems like a rather short time span, but to a graduate student, at least to us, it seemed like an eternity.) Neither of us was certain. I was extremely enthusiastic about philosophy of biology, but was not at all sure that there were enough problems there to keep me occupied much longer. I could not have been more wrong.

When I was a graduate student I knew of five philosophers of biology: Marjorie Grene, David Hull, Michael Ruse, Mary Williams, and William

Wimsatt. I have since been fortunate enough to get to know each of them, but at the time they were just names on papers I came across in my readings. I went into philosophy of biology on the basis of an extremely simple idea – I loved biology and philosophy of science, and so it seemed reasonable enough to try to combine the two. My mentors were by training and profession biologists, not philosophers. In my first year of graduate school I wrote a paper on evolutionary explanations and had the good sense to send a copy over to an evolutionary biologist of whom I had heard. You may have too, his name is Ernst Mayr. Mayr did the most wonderful thing; he told me that my paper was incredibly naive, but he did so in a way that could not have been more encouraging.

From Mayr I got the idea that philosophical problems in biology are an integral part of the practice of biology, especially evolutionary biology. In part because of this I have never seen biology, or any of the rest of science, as merely providing examples to test and/or illustrate philosophical theses. That it may well do, but the motivations for my work have been primarily biological. For instance, the levels of selection debate can certainly be used to illustrate points concerning holism and reductionism, but my primary reason for dealing with this fascinating topic comes out of the biology. Mayr at times pretended, not entirely convincingly, to be annoyed at having to deal with the philosophical problems that arose in his work. His annoyance with philosophers of science at the time was real enough, but the huge volume of his subsequent work in history and philosophy of biology supports my belief then that he enjoyed doing philosophy.

My other mentor was Richard Lewontin. Like Mayr, he was generous with his time and incredibly encouraging. Unlike Mayr, he gave me the impression that there was nothing he would rather do than discuss philosophical issues in biology. Although my Ph. D. was to be in philosophy and I was seeking a job in a philosophy department, I do not think I could have had better role models. (And professional affiliations be damned, I certainly think Mayr and Lewontin are two of our most original and stimulating philosophers of biology.)

By any measure – journal space, sessions at professional meetings, jobs – philosophy of biology has exploded as a subdiscipline of philosophy of science since the late 1970s. A second generation of philosophers of biology has become well established. I am thinking here of John Beatty, Richard Burian, Philip Kitcher, Bob Richardson, Alexander Rosenberg, and Elliott Sober, among others. And a younger generation promises to continue the healthy growth of the discipline.

One of the things that, in my view, makes philosophy of biology so exciting today relates to what I discussed above; namely, the level of interaction between professional biologists and philosophers. In my work, and in particular in the work represented here, I have tried to address problems of relevance to the practice of biology and to do so in a way that is accessible to professional biologists, while at the same time being accessible to philosophers. It is no accident that three of the articles in this volume are coauthored (one with a linguist, the other two with biologists). As I see the field, it is to be expected that problems will arise that no one person has the expertise with which to deal. Collaboration of this sort also helps one avoid needless professional jargon; jargon that in the current academic setting serves as a sort of unhealthy isolating mechanism.

Of all the subfields within philosophy of science dealing with the special sciences (philosophy of physics, philosophy of psychology, etc.) philosophy of biology has the highest level of cooperative interaction between philosophers and scientists. For this reason it is, I think, the most exciting, productive and progressive area within all of philosophy of science. This, of course, may change and will change if philosophers of biology lose touch with the reality of biology and of the practice of biological science. But I think the near-term future of the field looks bright. I for one am fairly certain of the sort of work I will be doing five years from now.

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Since the essays in this volume have been written over a period of years I have retained the original acknowledgments for each of the essays. However, here I would like to gratefully acknowledge support from the National Science Foundation (Grant No. SBR-9321485) which aided in the preparation of this volume, and in particular in the writing of Essay 11.

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