
Post-Spandrel Adaptationism

MICHAEL R. ROSE
GEORGE V. LAUDER

A new adaptationism is creeping back into mainstream evolutionary biology. While the true believers of sociobiology and pan-selectionist molecular biology never lost faith in the adaptive significance of the characters they study, other varieties of evolutionary biologist have only recently resumed discussion of adaptation. This book is for them, as well as for their students who need to be introduced to contemporary adaptationism.

I. The Death of the Old Adaptationism

The old adaptationism started dying toward the end of the 1960s. A seminal event in this decline was the publication of "Adaptation and Natural Selection," the 1966 book by George C. Williams, which discredited the vague invocation of group selection and other infirmities of adaptationist reasoning. Williams (1966) emphasized that the concept of adaptation is "special and onerous" and should not be applied lightly. Many did not take his advice, leading to the final proclamation of death by Stephen Jay Gould speaking at a 1978 meeting of the Royal Society of London. This talk would later become widely known in the form of an article, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" (Gould and Lewontin, 1979). In this article, Gould and Lewontin supplied a number of criticisms of the glib style of reasoning about adaptation that had become popular among many evolutionary biologists since World War II. In particular, they sought to discredit "adaptationism" as a style of research in evolutionary biology in which all features of organisms are viewed *a priori* as optimal features produced by natural selection specifically for current function. Instead, Gould and Lewontin advocated a more pluralistic view of evolutionary investigation, recognizing that traits may arise by other means than natural selection. They demanded that evolutionary biologists explicitly consider alternatives to a strictly selectionist

ADAPTATION

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view of organismal design.

This paper had such a substantial impact on the fashions of evolutionary biology that the very term "adaptationism," and sometimes even "adaptation" itself, became pejorative. To a significant extent, the term adaptation was banished from the lexicon of evolutionary biology, for fear of being associated with the dread adaptationism. One of us attended a seminar in the early 1980s at which the speaker announced that he would not use the word adaptation in his talk. Rather, to avoid controversy and association with the negative implications of adaptationism, he would use the word "banana" whenever he meant adaptation. This approach was not without merit then, as merely using the word adaptation frequently brought forth strong feelings and arguments only marginally related to the seminar at hand. Other papers of the time reinforced concerns about adaptationism (Lewontin, 1977; Gould, 1982) and deepened the reluctance of evolutionary biologists to confront problems of adaptation head on.

Another factor in the decline of adaptationism in the late 1960s was Richard Lewontin's work on population genetics and electrophoresis (e.g., Lewontin and Hubby, 1966). Up until that time, it had been possible for figures like Theodosius Dobzhansky and Arthur Cain to plausibly, or at least conceivably, explain the differentiation of populations and genetic variation within populations almost entirely in terms of selection. Since then, successive developments in molecular biology have laid bare greater and greater amounts of both evolutionary differentiation between species and genetic variation within populations (e.g., Li and Graur, 1991). This astronomical amount of molecular genetic variation and differentiation made it implausible that each variant had been shaped by natural selection to have that particular configuration.

Recent molecular biology has gone further still. The old, Mendelian view of the genome as a string of genetic beads, each containing the information for making a discrete character, or enzyme, has been demolished. In most organisms, there are abundant quantities of noncoding DNA, DNA that also does not appear to have any regulatory function. Not only is this DNA present in the form of noncoding deserts between genes, it even interrupts genes as "introns" (Li and Graur, 1991). Furthermore, some of this DNA appears to replicate itself and insert copies randomly about the genome, and thus has been proposed to operate as "selfish DNA" (Doolittle and Sapienza, 1980; Orgel and Crick, 1980). The present conception of the genome has little to do with the old orderly library of adaptively constructed genetic information, the image of the genome conveyed to many of us as undergraduates.

But there have been other nails in the coffin of adaptationism, such as the growing understanding that natural selection is not a process that necessarily enhances adaptation. There are several facets to this point. The first is that even the classical overdominant, viability selection, random-mating, one-locus, deterministic model only leads to maximization of *mean* fitness, not the fitness of every genotype. A genetic load due to segregation remains, such that the fitness of any particular individual need not be near that of the maximum in the population. With nonlinear interactions in the determination of fitness, even

simple fertility models do not necessarily maximize mean fitness; indeed, mean fitness can decrease in the course of selection (e.g., Pollak, 1978). The development of robust two-locus theory, especially by Karlin and Feldman (e.g., 1970), revealed that epistasis and linkage disequilibrium could undermine the "hill-climbing" effect of natural selection on mean fitness, assumed by both Wright and Fisher. Further developments in the realms of multilocus models and modifier theory have only produced further paradoxes of this kind. Even in the world of theory, the evolutionary attainment of adaptation may be problematic.

An integral component of Gould and Lewontin's spandrels of San Marco framework is the idea of structural or developmental constraints (see Gould, 1977; Alberch, 1982; but also Maynard Smith et al., 1985; Amundson, this volume). Sometimes this concept has been so overextended, constraints being discovered so promiscuously, that its conceptual content seems minimal. If everything is constrained in some way then the explanatory power of the idea of constraints is greatly diluted. However, there is an indubitable core to this criticism: the structure of the genotype-to-phenotype mapping (see Lewontin, 1974). A naive adaptationism might suppose that there are different genes for each aspect of the organism which can be separately molded by natural selection to the ends of optimal adaptation. The demonstrable existence of pleiotropy and epistasis, which connect up the expression of genetic variation among loci in nonlinear ways, makes this view untenable. Research in laboratory evolution, among other areas (cf. Loeschcke, 1987), strongly supports the notion that suites of characters evolve jointly, often in unpredictable ways (Rose et al., this volume). In addition, recent research in developmental genetics (e.g., Atchley and Hall, 1991) has amply demonstrated the complex ontogenetic linkages among characters and suites of characters. Adaptations are embedded in murky complexes of physiological constraints, constraints that may render the action of natural selection remarkably obscure.

Yet another factor in the demise of the old adaptationism was the rise of phylogenetic research. The immediate post-spandrels period of the 1980s was marked coincidentally by a decline in infighting over phylogenetic principles and techniques, battles that had been fought within the systematic community for nearly 20 years. Increased methodological harmony fostered a flowering of interest in applying phylogenetic methods to problems of form and function in organisms. The analysis of organismal design matured during this time from a simplistic search for how individual traits might be adaptive, to broader issues of phylogenetic trajectories, design constraints, and the analysis of intrinsic design elements and their historical consequences (Lauder, 1981; Emerson, 1988; Wake, 1982). Explicit mapping of characters on trees emphasized the history of traits or of character complexes and showed how previous hypotheses of adaptive significance could be refuted by demonstrating historically discordant patterns between structure and environmental change.

A final factor in the demise of the old adaptationism has been a developing understanding of the many levels of natural selection as a process. From the evolution of selfish DNA sequences (see Hurst, this volume) to interdemic selection (see Wade, this volume) to selection at the level of clades (Vermeij and Novacek, this volume), natural selection can operate in contexts that were only intermittently conceived before the 1970s, excluding perhaps the

work of Sewall Wright (e.g., 1977, 1978). This is in some ways a spectacular testimony to the original intuitions of Darwin, but it poses some grave problems for the study of adaptation. It certainly does not need to be the case that selection at all levels operates with the same direction, much less magnitude. Formally, this must lead to "adaptive consequences" that cannot be predicted from the study of one level of selection on its own.

II. After the Funeral: The New Adaptationism

This litany of lamentation for adaptationism could go on, but funerals are to be endured for only so long. From a Celtic standpoint, what really matters is the wake, the party after the funeral. During the wake, the past is reviewed, and the loved one is praised and often criticized. In a sense, after the burial, the mourners find a way to go on with their lives. This book is a wake for adaptationism, in its old form. Here we celebrate some of its triumphs, but resignedly. We offer our own criticisms, but out of affection rather than hostility. But most importantly, we have to go on with our lives. We continue to study the problem of adaptation, a manifestly real biological phenomenon, after the Spandrels of San Marco.

So, it could be asked, what does post-spandrel adaptationism look like? What kind of future is there for evolutionary biologists who wish to study selection and its consequences? Is there anything left to the concept of adaptation that can still inform evolutionary research?

To a large extent, the chapters of this book are our answer, in themselves. However, it would be remiss of us not to attempt some sort of integrative reply to this question, beyond merely pointing to multiple lines of research in this area. Therefore, we venture a few opinions about the new adaptationism that is being born around us.

First, there are a variety of technical improvements on the old adaptationism that have not so much changed its direction as strengthened its force. For example, the more formal use of phylogenies in the comparative method has greatly improved the intellectual rigor of interspecific comparison (Brooks and McLennan, 1991; Felsenstein, 1985; Harvey and Pagel, 1991). No longer is it acceptable for species to be treated as independent data points and gross correlations with environment used as evidence of adaptation (see Losos and Larson, this volume). This does not remedy a number of profound problems for the comparative method, such as the legitimacy of inferences of selection mechanisms (Leroi et al., 1994), but it at least saves comparative biology from the kind of egregious errors that arise when one ignores history.

Likewise, Hudson, Kreitman, and colleagues are pushing at the limits of our ability to infer the action of selection from DNA sequences (e.g., Hudson et al., 1994; Kreitman and Hudson, 1991; Hudson, this volume). From comparisons of differentiation within and among species, they are developing some ability to demonstrate the action of balancing selection as opposed to neutral gene evolution. This work does not, however, readily lead to the inference of the particular nature of the selection mechanisms involved, as the continuing mystery concerning the action of selection at the *Adh* locus in *Drosophila melanogaster* illustrates (e.g., Laurie and Stam, 1994).

Second, the study of natural selection in the wild has been greatly improved, partly through the development of higher critical standards (e.g., Endler, 1986) and partly through the development of methodologies based on quantitative genetics theory (e.g., Arnold, 1983, 1986; Lande, 1978). Recent studies of natural selection in the wild (see Reznick and Travis, and Sinervo and Basolo in this volume) represent a striking advance over previous work. Such studies often incorporate field experimentation lasting many years to demonstrate that environmental and selective manipulation can replicate extant differences among populations. The combination of long-term field observations on multiple replicate populations, field manipulations, and laboratory-based genetic data is a powerful one for the study of selection.

Third, many disciplines which in the past made frequent and gratuitous use of the concept of adaptation have greatly restricted their inferences of adaptation and have focused instead on doing what they do best. For example, the disciplines of comparative morphology and biomechanics were shaped for years by the notion, implicit if not explicit, that virtually every character is molded in isolation by selection for its current role. Such views are no longer widely held, and these areas are now turning to focus on both the design principles of biological systems (Niklas, 1992; Thomason, 1995; Vogel, 1988) and the historical transformation of structure and function during evolution (e.g., Wake and Roth, 1989). Functional morphology and biomechanics, as disciplines whose goal is the analysis of biological design, may still have a critical role to play in arguments about adaptation (see Lauder, this volume), but their new focus both broadens the intellectual base of these disciplines and brings a new comparative and historical rigor to adaptationism. Furthermore, the study of organismal development, not long ago a mainly descriptive discipline, is now the subject of comparative evolutionary investigation using molecular techniques (e.g., Hall, 1992; Hanken and Thorogood, 1993; Raff et al., 1990), as well as important new quantitative genetic analyses (e.g., Atchley et al., 1990; Atchley and Hall, 1991). These approaches bring the promise of increased clarity to our understanding of how traits arise and of the intercorrelations among traits; both issues are critical to the study of adaptation.

In the area of laboratory evolution, work with *Escherichia coli* and *Drosophila* (see Rose et al., this volume) has greatly improved our opportunity to observe natural selection as close to the tips of our noses as possible. A notable trend in this area has been a significant increase in the number of replicate populations used per experiment (e.g., Lenski et al., 1991). Another trend has been the use of multiple, distinct, selection treatments.

In addition to these specific components of the adaptationist structure, the last decade has also seen repaired foundations for the structure. The books by Dawkins (1987), Brandon (1990), Sober (1984, 1989), Williams (1992), and Dennett (1995) all focus on conceptual issues critical to future progress in the analysis of adaptation. While this will remain more an area of discussion than simple progress, unlike for example recent work on the statistical use of phylogenies, such mortar-work will be essential as the edifice of adaptationism vaults farther within evolutionary biology and even beyond.

III. New tunes for the New Adaptationism

But there are other aspects of the study of adaptation that are more than variations on old themes. One of these is the growing role of selective adaptation in nonevolutionary realms, in artificial intelligence, automated design, and the like (see Frank, this volume). Ironically, while evolutionary biologists distanced themselves from the concept of adaptation during the 1980s, a number of scientists from other fields, even engineers, have embraced it enthusiastically as the most powerful way to solve key problems. Adaptation is a much bigger concept than evolutionary biologists, proponents and critics alike, may have realized.

A second novelty that is beginning to surface is the perversity or, if you will, the creativity of adaptation. This is apparent in the spectacular oddities of the fossil record, from the Burgess Shale (Gould, 1989) to the dinosaurs of the Gobi desert (see Novacek, this volume). But it is also apparent in the oddities and paradoxes of laboratory evolution, which inspired one of us to compare evolution to Alice's Wonderland (Rose et al., this volume).

A third challenge for the new adaptationism is the remarkable conservatism that has been found in the genetic mechanisms that underlie the design of even widely divergent organisms. It seems that nearly every week a new gene or gene family is isolated that has a common effect on developmental patterning in mammals and *Drosophila*. The extent of fundamental conservatism among structurally divergent clades sharing only distant common ancestry has been far greater than could have been conceived even fifteen years ago. The new adaptationism must deal with the fact that major components of extant organismal design may represent more a reshuffling of ancient parts than a combination of novel features arisen *de novo* in response to specific selection forces.

A final theme of recent note is the extent to which random events in the history of life may have radically changed the environmental and biological context for adaptation. It now seems likely, for example, that large meteor impacts may occur with reasonable frequency on the geological time scale, and that such events may be associated with significant changes in patterns of biological diversity. Such large-scale disruptions provide new opportunities for selection and reshuffle relative species diversity among major clades. Clades that survive may do so for reasons unrelated to traits that were deemed to have been "adaptations" prior to the disruption, and we have only begun to explore the effects of such changes on historical trajectories of organismal design.

Still other new themes are no doubt emerging in the minds of those who study adaptation. Now, exactly 30 years after the 1966 publication of "Adaptation and Natural Selection," post-Spandrel adaptationism is just beginning to develop. The certainties of the old adaptationism are gone. The new adaptationism is but an unruly toddler, exploring its environment with reckless curiosity, impatient to discover the secrets hidden about the evolutionary wonderland.

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