

Three Kinds of Adaptationism

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1. Introduction

Debate about adaptationism in biology continues, in part because within “the” problem of assessing adaptationism, three distinct problems are mixed together. The three problems concern the assessment of three distinct adaptationist positions, each of which asserts the central importance of adaptation and natural selection to the study of evolution, but conceives this importance in a different way. As there are three kinds of adaptationism, there are three distinct "anti-adaptationist" positions as well. Or putting it more formally, there are three different dimensions here, and strongly adaptationist views, strongly anti-adaptationist views, and moderate views are possible for each dimension.

Understanding the distinctions between the three adaptationist positions will not remove all controversy, but some progress can be made through clarifying the distinctions. In particular, progress can be made by recognizing that evidence against one kind of adaptationism need not also be evidence against other kinds. So the main aims of this paper are classification and clarification. I will describe the three kinds of adaptationism, and then discuss the evidence relevant to each. In particular, I will try to say which problems might be solved directly through empirical research, and which are more philosophical in character.

2. A Statement of the Distinctions

Here are the three kinds of adaptationism I recognize:

Empirical Adaptationism: Natural selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance.

This, I suppose, is the most familiar of the three views. As I understand it, this view is primarily a contingent, empirical claim about the biological world. Clearly this view can be held in both strong and weak forms; I have expressed it here in a strong form but it could be qualified in various ways. As empirical adaptationism is a claim about the actual biological world, in order to decide whether it is true we must engage in scientific investigation of that world -- we must apply the usual combinations of observation, experiment, hypothesis, model-building and so on. We must determine whether selection does, or does not, have the unique causal capacities claimed for it.

Explanatory Adaptationism: The apparent design of organisms, and the relations of adaptedness between organisms and their environments, are the big questions, the amazing facts in biology. Explaining these phenomena is the core intellectual mission of evolutionary theory. Natural selection is the key to solving these problems -- selection is the big answer. Because it answers the biggest questions, selection has unique explanatory importance among evolutionary factors.

This is the most misunderstood of the three adaptationist theses, and the one responsible for the most vexing conceptual problems in the adaptationism debates. The reason for this is the fact that explanatory adaptationism combines a straightforward scientific idea -- the idea that selection explains adaptedness -- with an idea that is a controversial mixture of science and philosophy. This more controversial idea is the claim that apparent design has special status as a biological phenomenon. A crucial point here is that selection can have this kind of central importance even if it is rare. Even if selection is not at all ubiquitous, even if it is massively constrained, even if it is positively feeble most of the time, so long as selection is able to solve the problem of apparent design it is the most important evolutionary factor.

In my formulation of explanatory adaptationism I distinguished two components of the problem that evolutionary theory is seen as solving. These components are (i) the apparent design of organisms, and (ii) their relations of adaptedness to their environments. I distinguish these two in order to avoid controversy. Some might think that these are the same issue, or that one of the two is primary, while others might hold that there are two distinct questions. An observer might first be struck by apparent design considered as a strictly intrinsic feature of organisms -- by the simultaneous complexity and reliability of many biological mechanisms, for example. Beyond that there is the apparent suitability of these mechanisms for dealing with specific environments. That is, it might be possible to be struck first by the complexity of the eye itself, and second by its facility for enabling useful vision. In my formulation I mention both issues, to be sure to capture both, although some biologists might recognize or emphasize only one. In later sections of this paper I will refer just to "the problem of design," although strictly speaking I mean "the problem(s) of apparent design and/or adaptedness."

Explanatory adaptationism combines a claim about biology's key problem with a claim about its solution. It would be possible, in principle, to accept that apparent design or adaptedness is the central problem, while preferring a non-selectionist solution. I will not discuss this (fairly radical) position here. Note that a position of that kind is probably harder to defend about adaptedness than about design. And in general, it makes more sense for non-selectionist views to reject the idea that design and adaptedness are the central questions in biology.

Also, an explanatory adaptationism which holds that selection is the only possible naturalistic and non-theological solution to the problem of design is stronger than a view holding that selection is just the actual solution (although other solutions are possible in principle). I will assume the stronger view here, although much of what I say will apply to both positions.

The third kind of adaptationism is a simpler idea:

Methodological Adaptationism: The best way for scientists to approach biological systems is to look for features of adaptation and good design. Adaptation is a good "organizing concept" for evolutionary research.

This kind of adaptationism is not a claim about the actual role of selection in the world; it is a policy recommendation for biologists, a suggestion about how they should think about organisms and how best to organize investigation. Unlike explanatory

adaptationism, this third view need not make any claim about which biological problems are the most important ones. Methodological adaptationism recommends a heuristic, and no more.

Distinctions of roughly the type I employ here are often applied to behaviorism, which is found in both psychological and philosophical versions. Amundson (1988) made a connection between these classifications of behaviorist views, and the adaptationism debates. The distinctions I make here are different from Amundson's, but his discussion influenced the present paper.

3. On the Relations Between the Three Views.

In understanding the links between these three positions the first and most important point is that all three are, in the strict sense, logically independent of the others. No one of these forms of adaptationism implies another. That is not to say that none of them supports another, but as far as literal implication goes, any combination of “yes’s” and “no’s” is possible.

The relation between the first two views -- empirical and explanatory adaptationism - - is the most complicated. First, it should be clear that one can accept empirical adaptationism without accepting explanatory adaptationism. The key part of explanatory adaptationism here is its claim that apparent design and adaptedness are the most important biological problems. One might hold that there is no such thing as “the most important” biological problem; maybe all biological problems have comparable importance or perhaps it is up to the individual to decide what they find most interesting. A view of this kind is inconsistent with explanatory adaptationism. But such a view is compatible with the idea that selection is, as a matter of fact, causally pre-eminent.

Even among those willing to make claims about the "most important problems" for biology, explanatory adaptationism might be rejected. It is also possible to argue that some other phenonema, besides apparent design and adaptedness, are the biologically central ones. Diversity is one rival candidate. Some evolutionists have written as if adaptedness and diversity are the two key problems. Another possible contender is order in biological systems. Or, moving away from these rather theoretically loaded concepts, it might be claimed that the central task for the evolutionary parts of biology, at least, is historical; the goal is to accurately represent the complete tree of phylogenetic relationships between species.

It is also possible to accept explanatory adaptationism without accepting empirical adaptationism. This is an important option, as some problems with the published literature

arise from a neglect of this possibility. It is entirely coherent to hold that when one surveys the biological world as a whole, selection is a minor player, while also holding that when one tries to explain the most vexing biological phenomena, selection is uniquely important. One can view the bulk of what goes on in evolving systems as mere “noise,” as unimportant happenstance. On this combination of views, selection is rare but it occurs often enough to answer the big questions, and these are questions that nothing else can answer.

I conjecture that Richard Dawkins holds the combination I have just described -- explanatory adaptationism but not empirical adaptationism. There is little doubt that he accepts explanatory adaptationism. The first chapter of The Blind Watchmaker (1986) is an extended defence of the claim that apparent design in nature poses a uniquely important problem for the scientific world view, and biology’s special task is to solve this problem. First the problem is raised and then, in subsequent chapters of the book, natural selection is enthroned as the solution. The same work supplies my main evidence for the idea that Dawkins rejects empirical adaptationism. This is seen in particular in his discussion of Kimura’s neutral theory of molecular evolution.

Neutralism (Kimura 1983) claims that most genetic variation observed at the molecular level is not to be explained in terms of selection; it is a consequence of mutation and random genetic drift. Neutralism is a denial of the omnipresence of selection -- a denial of empirical adaptationism -- and through recent decades there has been a lively debate between neutralists and their “selectionist” opponents. Dawkins, however, sees himself as having nothing invested in this debate. If the neutralists win he gains a useful tool (a reliable molecular clock) but their denial of selectionism does not even touch on his core claims. This is because the dynamics described by neutralism are agreed on all sides to have no direct role in the explanation of well-adapted, apparently-designed phenotypes. The neutralists are not even trying to answer the big questions about apparent design in nature; they are trying to describe genetic variation considered impartially as a whole. Selection might only explain 1% of all molecular genetic change, but (Dawkins and others will say) this is the 1% that counts.

So from the point of view of explanatory adaptationism, the debate over neutralism runs like water off a well-adapted duck’s back. The same is true of much of the debate over developmental constraints, the role of population structure and the genetic system in relation to selection, and also punctuated equilibrium. The explanatory adaptationist can grant a great many points made by critics, and need only stand and fight when the anti-adaptationist claims to be revising the overall structure of Darwinian explanation, and revising the role of selection in the explanation of apparent design. This is the pattern of a good deal of Dawkins’ response to his biological critics. For example: “[L]arge quantities of

evolutionary change may be non-adaptive, in which case these alternative theories may well be important in parts of evolution, but only in the boring parts of evolution..." (1986 p. 303) Daniel Dennett, in *Darwin's Dangerous Idea* (1995), also defends explanatory adaptationism, and he adopts a similar strategy to Dawkins much of the time. Other explanatory adaptationists who I take to be more cautious about empirical adaptationism include Robert Brandon (1990) and Kim Sterelny (Sterelny and Griffiths, forthcoming, and personal correspondence).

Although Dawkins and Dennett often exemplify explanatory adaptationism without empirical adaptationism, this is not how they always write. Sometimes they move to a more ambitious position, one which does make a claim about the amount of the biological world that has been shaped by selection. Dawkins talks of the special status of the problem of design, but also of the "sheer hugeness" of the phenomenon (1986 p. 15). A move to a stronger view is sometimes made in the form of an admonishment to those who would seek non-selectionist explanations too readily.

Time and again, biologists baffled by some apparently futile or maladroit bit of bad design in nature have eventually come to see that they have underestimated the ingenuity, the sheer brilliance, the depth of insight to be discovered in Mother Nature's creations. (Dennett 1995 p. 74).

The more ambitious view that Dawkins and Dennett sometimes suggest is one that combines all three forms of adaptationism. This is a view in which design is seen as ubiquitous even when it is not obvious, and the main methodological risk for biologists derives from a willingness to put forward non-selectionist explanations when an adaptive function is not immediately visible.

When an explanatory adaptationist makes claims of this more ambitious sort, the standard range of anti-selectionist criticisms becomes relevant. Then the adaptationist must confront the issues of developmental constraint, drift and the rest. Lewontin has expressed exasperation at Dawkins' apparent blindness to these issues; Dawkins focuses his account of Darwinism entirely on selection "while the entire body of technical advance in experimental and theoretical evolutionary genetics of the last fifty years has moved in the direction of emphasizing non-selective forces in evolution" (1997 p. 30). Lewontin's interpretation of the recent history of evolutionary genetics will be controversial to many, but my point is that the explanatory adaptationist can simply downplay many of the issues that Lewontin has in mind. For the pure explanatory adaptationist, the centrality of selection to evolution is untouched by the ongoing refinement of population genetic work on the relation

of selection to drift and the dynamics of multi-locus systems. So long as such work does not call into question the idea that selection is the sole systematic source of apparent design, it can be viewed by the explanatory adaptationist as mere detail. The empirical adaptationist does not have this luxury. The empirical adaptationist who says that selection is everywhere must confront neutralism; the adaptationist who says that selection alone can predict where an evolving system will go must deal with the population genetics of linkage. As I said earlier, I do not see Dawkins (or Dennett) as consistently restricting their adaptationism to explanatory adaptationism, so I view some of Lewontin's exasperation as justified.

Empirical and explanatory adaptationism are logically independent of each other, and methodological adaptationism is logically independent of both. Someone could hold that although selection is in fact the dominant evolutionary factor, the prudent researcher will approach each case with a cautious attitude in which non-selective explanations should be ruled out before selection is invoked. Such an attitude rejects methodological adaptationism, as I understand it. Perhaps G. C. Williams' Adaptation and Natural Selection (1966) exemplifies this combination of views. Williams is certainly an advocate of selectionist explanation, but he also stresses that adaptation is a "special and onerous" concept that must not be invoked unless it is shown to be really necessary. He discusses adaptive explanation in detail in his 1966 book, but largely with the goal of preventing the overuse of adaptationist concepts (especially, of course, group-selectionist uses).

Alternatively, a scientist might find that, as a matter of fact, the most helpful way to proceed is to look for a selective explanation in every case, even if many phenomena are eventually shown to have non-selective origins. Adaptive thinking might be held to be useful for organizing research even in a world in which non-selective forces have a great deal of causal power. One version of this view, stressed in comments by both a referee of this paper and by Kim Sterelny, argues that methodological adaptationism might be particularly useful if non-selective factors like developmental and genetic constraints are elusive and hard to discover. Then when the hypothesis of optimality is investigated first, deviation from the optimum provides evidence that other factors are at work, and perhaps the nature of the deviation will give clues about where to look next. Analogous possibilities show the logical independence of methodological from explanatory adaptationism.

In this section I have asserted the logical independence of each view from the others. However, there is no doubt that some kinds of adaptationism, when combined with other premises, do support other kinds. I will spend less time on this topic because the points I will make are fairly obvious.

If one is an empirical adaptationist, then if one also believes in starting out an investigation by looking at the "best guess" or most likely possibility, this gives some

support to methodological adaptationism. Gould and Lewontin's famous 1979 "Spandrels" paper challenges both methodological and empirical adaptationism, and one of their key aims is to remove the support that methodological adaptationism derives from an acceptance of empirical adaptationism.

Conversely, a person who found that using the adaptationist methodology seemed usually to lead to good results might then have good reason to embrace empirical adaptationism. On the other hand, it is harder to imagine an argument starting from a pure methodological adaptationism and leading to explanatory adaptationism, though an argument in the other direction might make sense. It is also hard to see an argument from empirical adaptationism to explanatory adaptationism; explanatory adaptationism has its roots elsewhere.

4. Problems of Evidence: Empirical Adaptationism

The next three sections will look at how we might decide for or against each of the three adaptationist positions.

Issues of evidence and testing are simplest in the case of empirical adaptationism. That is not to say that empirical adaptationism is an easy claim to test, but at least the starting point is clear. Empirical adaptationism is a claim about the actual biological world, so it should be tested scientifically. What is needed is a way of comparing the relative causal importance of natural selection and other evolutionary factors.

In this discussion I will not attempt to analyze "relative causal importance" in detail, although there are conceptual problems surrounding this concept, and the topic of causation is one in which basic issues are still unresolved in philosophy. But one brief note about the idea of the "power of selection" should be made. Evolutionists talk of the "power of selection" to seek out optima when what is meant is the power of the variation-plus-selection combination. For example, suppose the issue is whether "antagonistic" pleiotropic effects can be overcome, via modifier genes that prevent the expression of bad traits pleiotropically linked to good ones. Then (as Sober said in an earlier paper) the question at hand is really "the power of mutation" to come up with an appropriate modifier (Sober 1987 p. 116). No amount of selective advantage for this hypothetical gene makes it more likely to arise. So the "power of selection" in the causation of biological characteristics should generally be understood as the power of the basic variation-plus-selection combination that is central to Darwinism. When I talk of the "power of selection" here, I mean the power of this combination.

Orzack and Sober (1994) have outlined a specific program for testing "adaptationism." The adaptationist position they have in mind corresponds approximately to my empirical adaptationism; their aim is to test the idea that natural selection is the most powerful evolutionary force, and able to create near-optimal phenotypes. This claim (their "O") is not exactly the same as empirical adaptationism as I understand it, because (as a referee pointed out in comments on this paper) my empirical adaptationism does not require that individual organisms exhibit optimal phenotypes. If the population reaches an evolutionarily stable polymorphic state as a consequence of frequency-dependent selection, for example, Orzack and Sober regard this as telling against the adaptationist view they are assessing, but I do not regard this as telling against empirical adaptationism. This difference between myself and Orzack and Sober will not matter to most of my discussion.

They propose that we test adaptationism by asking the following question: Are predictions based only upon selection as good, or nearly as good, as predictions based on consideration of the entire range of evolutionary forces? We should investigate a large range of particular biological phenomena, and work out how adequate a purely selection-based model is for explaining each. Orzack and Sober call these simpler models "censored," as the models have had all or most non-selective factors removed. If, in a particular case, a censored selectionist model fits the data so well that little or nothing would be gained from adding more evolutionary factors to the analysis, adaptationism is vindicated in that case. If adaptationism is vindicated in the great majority of cases, it is vindicated as a general claim about the biological world.

I doubt that a test between models can be used to adjudicate all the issues surrounding empirical adaptationism, but it is a good start. However, there might be a better way to structure the contest. Or rather, a second type of contest between models could be conducted alongside (and overlapping with) the contest described by Orzack and Sober. Rather than envisaging a competition between an optimality model and a more detailed alternative, I envisage a contest between a range of models of comparable complexity. If we are constrained to include in our model some specific number of parameters, and a specific level of tractability, then should we "invest" only in a very detailed specification of the selective forces relevant to the situation, or should we use a less complete specification of the selective forces along with some information about other factors as well?

The comparison might be one between adaptationism and pluralism, but it also could be one between an adaptationist model and a model in which some single non-selective factor is described in great detail and made to carry all the predictive weight. The non-selective factor in question might be drift, or perhaps the "laws of biological form" described by a modern-day rational morphology. Empirical adaptationism as a general view

is vindicated, on my proposal, if in the majority of cases a better fit to the data is achieved by a selection-based model than is achieved by any other model of comparable complexity. Empirical adaptationism is vindicated if a description of the relevant forces of selection is more informative than any other description at a similar level of detail.

In some respects my view derives from an application of Richard Levins' views about models (Levins 1966. See also Wimsatt 1987). Models can have a range of virtues and goals. Different levels of tractability and understandability are sought in different types of investigation, and great generality may or may not be desired. Although I am not committed to the specific taxonomy of goals that Levins thinks must be traded off -- precision, generality and realism -- I agree with Levins that there are trade-offs between different goals when constructing models. Sometimes simple models which can be understood very fully are sought; sometimes more detail is incorporated, with a consequent loss in ease of comprehension. A precise fit to particular phenomena can be traded off against generality. My proposed test of empirical adaptationism is designed to take these facts about model-building into account. Relative to the scientific goals at hand, and the general style of model which is suitable for the occasion, which type of information is more useful: information about selection, or information about something else?

As the proposal I am outlining involves a comparison between models of comparable complexity, it avoids a problem that Brandon and Rausher (1996) have alleged in Orzack and Sober's approach. Brandon and Rausher claim that Orzack and Sober's proposal is biased in favor of adaptationism. This is because in Orzack and Sober's proposal, if a censored selectionist model succeeds predictively then it is said to be vindicated -- even if some other censored model would do just as well in a similar test. At one point Orzack and Sober do discuss the situation where more than one censored model fits the data, and they say that additional evidence is needed in such a case (p. 364). The problem that Brandon and Rausher correctly point out is that Orzack and Sober's main statement of how the test of adaptationism works does not have this structure; it does not treat the possibility of equally good censored models (p. 363). Certainly this possibility does have to be fitted into any test of adaptationism. One way is to aim at working out whether selectionist models of a given type are better or worse than non-selectionist models which are similarly complex and aimed at meeting similar scientific goals.

A contest between models has attractive features as a test of adaptationism. As Orzack and Sober stress, there is some hope of reaching a solution in a reasonable amount of time. Some ideas often discussed in the adaptationism debates will be hard to address in this framework, however. The contest between models is well-suited to asking questions about the power of selection in very specific circumstances, where many background

conditions have been explicitly or implicitly filled in. When we ask, as Orzack does, about how selection works on the sex ratio in wasps, we are already assuming that we are dealing with insects, which are animals, that their reproduction is sexual, and so on. Some of these background assumptions can themselves be addressed in the same way: "Why is there sex?" is a famous question for selectionists. But other questions: "Why are there insects?" are much harder to get a grip on by means of modeling. Perhaps Orzack and Sober will say "good riddance" to issues that cannot be expressed precisely enough to be tested via a contest between models.

Some of the less precise questions may be worth keeping though. And even within standard methodological traditions in evolutionary biology, there are alternatives to model-building. One is the tradition that uses comparative methods. Maynard Smith (1978) used Clutton-Brock and Harvey's (1977) work on sexual dimorphism in body size in primates as a paradigm example of an empirical test of an adaptationist claim. Here the issue was whether male-male competition or differentiation in resource use generates the dimorphism. The former was supported over the latter.

Comparisons of this type can be used to test not only specific adaptationist claims, as in Clutton-Brock and Harvey, but can also be applied to broader questions about the relative power of selective forces. A range of adaptationist positions can be expressed as views about how readily selection can override the constraints of history. That is, one kind of adaptationist commitment can be expressed by saying that, with certain kinds of traits, when species A is more closely related to B but more similar in ecological relations to C, A will resemble C more than B. No one would claim that this is true for all traits and all degrees of relatedness, but there is a family of adaptationist attitudes that can be expressed by qualifying this principle in different ways. When assumptions of this kind are used to guide investigation, the successes and failures associated with such principles give us information about the power of selection. When adaptationists stress convergent evolution (as Dawkins 1986 and Mayr 1983 do, for example), we are seeing an appeal to this type of reasoning. In cases of convergent evolution, ecological factors are spectacularly better at predicting similarities, in certain biological characteristics, than history is.

Sterelny (1997) also formulates yet more moderate versions of adaptationism that are to be tested comparatively but do not claim that selection overrides history. Comparative methods are also defended over optimality modeling by Horan (1989). Orzack and Sober do not discuss comparative methods in their 1994 paper. As they are focused on a version of adaptationism which claims that selection produces optimal phenotypes, comparative methods are less relevant. But comparative methods are an important way of assessing

claims about the power of selection, and hence relevant to empirical adaptationism as I understand it.

So I accept one approach to testing empirical adaptationism which is roughly similar to Orzack and Sober's proposal. But I add the possibility of comparative testing, and no doubt there are other feasible possibilities as well. These details are not so important to my aims in this discussion. My main point is that empirical adaptationism is a family of claims about the actual biological world; it is a family of claims about the causal power of the basic Darwinian package of variation and selection, in comparison with other evolutionary factors. So the way to assess empirical adaptationism is via various kinds of empirical research.

5. Problems of Evidence: Explanatory Adaptationism

The problem of assessment is most acute in the case of explanatory adaptationism. I will set aside the issue of whether variation and selection really do adequately explain apparent design; I assume that they do, in accordance with standard Darwinian ideas. The harder question is the status of the first component of explanatory adaptationism, the idea that the problem of apparent design is in some sense the most important biological question.

The chief problem is that although many of us might agree that we find apparent design interesting, this is apparently just a fact about us. We onlookers are puzzled by some things and untroubled by others, but why should we take this to reflect differences between objectively puzzling and objectively unpuzzling states of affairs in nature itself? We might find other phenomena less striking than the intricacy of the human eye -- suppose we find toenails less striking. But toenails are just as real as eyes, and they have an evolutionary history as well. Dawkins might rhapsodize about one but not the other, and such rhapsodies might have their place in books intended for a popular audience, but should the dispassionate biologist pay any attention to this? Even if the biologist happens to find some questions more interesting than others, why does that support the idea that there is an objectively "most important" biological question? Important to whom?

I see this line of thought as a posing a difficult challenge to the explanatory adaptationist. If it is correct, explanatory adaptationism is revealed to be little more than the personal preference of some biologists and philosophers; they find selection important because it answers questions that they happen to care about. Earlier I argued that explanatory adaptationism is able to sidestep some hard issues about how selection interacts with other evolutionary factors. If the objection I discuss now is right, it will be apparent that explanatory adaptationism avoided those scientific responsibilities because it is not a scientific view at all, but just a set of preferences that some people happen to hold.

I stress that it is an optional matter whether a person finds the problem of design to be fundamental. No less eminent a biologist than Kimura, for example, has expressed what I take to be a different view.

Many people, directly and indirectly, have told me that the neutral theory is not biologically important, since neutral genes are by definition not concerned with adaptation. The term 'evolutionary noise' has often been used to describe the role of neutral alleles in evolution, with such a contention in mind. I believe this is a too narrow view. First, what is important in science is to find the truth, so the neutral theory should be of value if it is valid as a scientific hypothesis. (1983 p. 325)

It is not that Kimura finds adaptation to be uninteresting. I take it that his view is that the scientist should, qua scientist, seek a true explanation for all biological phenomena in an even-handed way, and not elevate the "interesting" ones over the others. I should also note that Kimura continues the quoted passage by also raising a possible indirect role for neutral mutations in explaining some adaptive evolution.

In a view that denies the primacy of the problem of design, some questions can still be seen as "bigger" than others, in the sense that they are about a larger portion of the world. Questions about all trees are bigger than corresponding questions that are just about redwoods. Some questions require more information to answer than other questions do. And some questions have more practical importance than others, of course. But the position I am describing holds that there is no sense in which one question can be objectively "bigger" or "more important" than another which will support explanatory adaptationism. Even if a problem is or was particularly troubling to the scientific community, the scientists' states of perplexity are not to be confused with aspects of the world they study.

Earlier I discussed Dawkins and Dennett as explanatory adaptationists. What might their replies to this argument be?

As I understand both writers, they aim to take the high ground in this debate; they hold that apparent design is, as a matter of objective fact, a special phenomenon whose explanation is central to the task of biology. For both writers, this view has two components. The first is an argument that apparent design is a real phenomenon, and the second is a claim that this phenomenon presents special problems for scientific, secular world views. I will not discuss the first component of this view here, but I will respond to the second.

Both Dawkins and Dennett defend explanatory adaptationism by making a strong claim about the role of explanations of design within intellectual life and culture as a whole. Dawkins sees apparent design as the one thing that, before Darwin, could rationally motivate

a traditionally religious outlook on the natural world. Darwin, by destroying the Argument from Design, thereby reshaped the entire intellectual landscape. The concept of natural selection is a pin holding much more than evolutionary biology in place; it is holding together the scientific/enlightenment world view.

Dennett's conception of the role of Darwinism in intellectual life is, if anything, even more ambitious. For Dennett, it is selectionism that prevents us engaging in an erroneous pattern of thinking that is so widespread that traditional religious thinking is only one instance of it. Darwinism enables us to do without "skyhooks," miraculous interventions that explain the occurrence of design, purpose and meaning.

So one way to defend explanatory adaptationism is to appeal not just to what natural selection does for biology, but what it does for science as a whole. Selection is seen as a critically important part of a larger intellectual enterprise, the enterprise of developing and defending a secular world-view.

One can agree with some elements of this position, as I do, without agreeing about its implications for biology. When we consider the place of biology within the larger scientific world-view, natural selection does play a special role. It provides the key to answering Arguments from Design for the existence of various Gods, and it provides the schema for a pattern of explanation that might be useful (although it also might not be useful) in other sciences as well. It should be noted at this point that, as writers like Gould and G. C. Williams have stressed, the most effective way to use evolutionary theory to reply to the theological arguments is to stress the mixture of good and bad design that we find in organisms; there are cases where God would surely have done things differently (Gould 1980, Williams 1997). But in any case, the efficacy of evolutionary replies to theological arguments is extrinsic to the scientific work done by biologists themselves. Or at least, there is no need for biologists to shape their work around these larger projects. The job of describing the significance of biological theories for questions about religion, purpose and so on belongs primarily to philosophy of science. So when a philosopher looks on at biology, natural selection might shine out like a beacon, in a way that no other evolutionary factor does. But that does not give natural selection any more causal power within evolving systems themselves. An accurate biological description of how selection interacts with (say) development should not be affected by these extrinsic considerations.

When I say that explanatory adaptationist arguments are in some ways more relevant to philosophy of science than to biology, I do not mean that only philosophers can engage in these descriptions -- that Dennett but not Dawkins should be allowed to do it. I mean rather that there are two different intellectual tasks here: describing how evolution

works in actual cases, and assessing the significance of evolution for the scientific enterprise as a whole.

Once the issues are separated in this way, the more philosophical component of explanatory adaptationism can be assessed in its own terms. That topic is too big for more than a brief comment here. There is no doubting the role played by natural selection in answering the religious Argument from Design, and the role of evolutionary theory in establishing the foundations for a wholly naturalistic view of humankind. But it is also possible to place natural selection so much at the core of our view of our place in nature that there is massive distortion of that view. Such distortion is seen in Dawkins' conclusion, from a discussion of our relations to natural selection, that we are "gigantic lumbering robots" programmed by our genes (1976 p. 21). This claim by Dawkins is often read (and criticized) as an expression of genetic determinism. Put into context though, I think it is clear that Dawkins was not making a claim about the tightness of the causal link between genes and behavior; instead it was a claim about the significance of the genetic influences on behavior. Dawkins was saying: whatever else might be causally relevant to behavior, it is the genes that matter most to how we should interpret what we do. Construed in this way, Dawkins' notorious claim expresses a more philosophical error than genetic determinism.

In sum, then, I accept that the problem of apparent design has some special features, as explanatory adaptationists claim. But these features are more philosophical than biological. The roots of explanatory adaptationist thinking are found not so much in biological data, but in views about the place of biology within science and culture as a whole. As a consequence, explanatory adaptationism cannot be empirically tested in the relatively direct ways that apply to empirical adaptationism.

6. Problems of Evidence: Methodological Adaptationism

In understanding how evidence can bear on methodological adaptationism, the first step is to dispose of views that claim we have no option in the matter. Commentators from Immanuel Kant in the 18th century to Dennett in the 20th have held that adaptationist thinking is in some sense an inevitable part of our approach to the biological world. As Dennett puts it, "Adaptationist thinking is not optional; it is the heart and soul of evolutionary biology." If we were to displace adaptationism from its central position, says Dennett, not only biology but "modern biochemistry and all the life sciences and medicine" would collapse (1995 p. 238). But whatever we might think about the track records of adaptationist thinking and its rivals, there is no worse track record than the track record of views that claim that some particular scientific approach is inevitable and non-optional. Dennett is, ironically, taking the

same unwise risk that Kant took when the latter claimed that there could never be a Newton for the biological sciences, someone who could show how organisms could arise from natural laws: "[W]e may confidently assert that it is absurd... to hope that maybe another Newton may some day arise, to make intelligible to us even the genesis of a blade of grass from natural laws that no design has ordered." (Kant 1790 p. 54). Less than seventy years later Darwin proved Kant wrong. Who knows what alternative organizing principles are possible for biology?

Once arguments from inevitability are rejected, two reasonable lines of argument remain. The first is an argument from empirical to methodological adaptationism. The second is an inductive argument from the consequences of past applications of adaptationist methodologies.

I take it that the strategy of argument from empirical to methodological adaptationism is clear. If selection is the most powerful evolutionary force, and responsible for most of what we see, then given our limited scientific resources there is some reason to guide investigation of each specific phenomenon around the "best bet" for explaining that phenomenon. I say "some reason" because I do not think the argument is immune to challenge. Even if some particular option is our "best bet," there might be good reasons to proceed in a more impartial way, perhaps to regard the absence of adaptive explanation as an appropriate "null hypothesis." Also, if it can be shown that methodological adaptationism tends to be associated with certain bad scientific habits (as Gould and Lewontin claimed in their 1979 paper), we might resist methodological adaptationism while accepting empirical adaptationism.

So there is an argument, albeit a contentious one, from empirical to methodological adaptationism. Some prominent defences of adaptationist methods have this pattern; they proceed by accepting that methodological adaptationism rests upon a moderate version of empirical adaptationism, while resisting the idea that methodological adaptationism requires a very strong empirical claim, such as the claim that nature optimizes. Maynard Smith, for example, has always denied that the usefulness of optimality methods requires that nature actually optimizes, but accepts that "if it is not the case that the structure and behavior of organisms are nicely adapted to ensure their survival and reproduction, optimization methods cannot be useful" (1978 p. 96. See also Maynard Smith and Parker 1990).

Suppose, however, that a biologist thinks there are no good reasons to believe in empirical adaptationism. Could there be any other motivation for methodological adaptationism? Kitcher, for example, has expressed this as a challenge: if optimality theorists do not want to base their methods in empirical claims about selection, they need to come up with an alternative justification (Kitcher 1987 p. 85).

Another possibility does exist. Rather than seeking a theoretical grounding for methodological in empirical adaptationism, one can take a simple consequentialist approach. Perhaps it can be shown that, whatever one thinks about the other adaptationist ideas, applications of methodological adaptationism have tended to yield impressive scientific results in most cases. This is an inductive argument, from a historical record of success to the conclusion that we should encourage future biologists to organize their work in the same adaptationist way.

A forthright example of the consequentialist approach is found in Ernst Mayr's response to Gould and Lewontin's 1979 paper. The view that Mayr defends might be a mixed form of adaptationism, but he stresses methodological issues in particular.

Considering the evident dangers of applying the adaptationist program incorrectly, why are the Darwinians nevertheless so intent on applying it? The principal reason for this is its great heuristic value. The adaptationist question, "What is the function of a given structure or organ?" has been for centuries the basis for every advance in physiology. (Mayr 1983 p. 153)

Many readers will object to Mayr's use of the word "every" here; some will also object to replacing it with "most." But as far as the form of the argument is concerned, it illustrates the consequentialist pattern. I suspect that quite a few biologists would fall back on a justification of this type: "You can say what you like about selectionist fallacies, but it worked for Darwin and Fisher!"

As before, although the consequentialist pattern of argument is a reasonable one, it can certainly be challenged. Again, Gould and Lewontin's 1979 "Spandrels" paper argues that there is a definite tendency towards unscientific behavior associated with adaptationist thinking. Although the use of *ad hoc* manoeuvres to salvage disconfirmed hypotheses is not peculiar to biology, let alone to adaptationism, Gould and Lewontin think that the adaptationist methodology does tend to encourage it.

Further, even if we were convinced that methodological adaptationism was a successful strategy through the history of biology, an inductive argument to future success might be resisted. A close study of the history might suggest that although adaptationism was fruitful in the past, its success was specific to historical conditions that no longer obtain. It might be argued that while adaptationism took us some distance in the struggle to develop evolutionary theory -- and was crucial to Darwin's original breakthrough -- biology has now outgrown the adaptationist approach. Lewontin has sometimes suggested this

historicist view (1983). So the consequentialist approach is a real alternative route to justifying methodological adaptationism, but one with its own problems.

Throughout this paper I have assumed that adaptationist methods are applied, or not applied, to the biological world as a whole. That is, I have not discussed the possibility of accepting methodological adaptationism in a form restricted to some specific areas of biology, and rejecting it in other areas. I have made this assumption for the sake of simplicity, but intermediate views are certainly possible. One might hold that methodological adaptationism is a good strategy when studying foraging behavior, but a bad strategy when studying biological form and pattern. To pick a more obvious case, many biologists with strongly selectionist views will make an exception for molecular traits.

Maynard Smith, for example, has sometimes claimed that his commitment to adaptationist methods is specific to the investigation of some types of phenomena and not others, and that a biologist can tell with reasonable accuracy where adaptationist methods belong and where they do not. For example: "In general, the structural and behavioral traits chosen for functional analysis are of a kind that rules out neutrality as a plausible explanation" (Maynard Smith 1978 pp. 96-7). Then the application of adaptationist methods to a specific field such as foraging theory might be based on a claim of empirical adaptationism that is also specific to that area, or on an inductive argument from past success in that area. The error that must be avoided in that case (an error that I do not attribute to Maynard Smith) would be to (i) choose certain traits and not others for adaptive explanation, based upon background knowledge, but then (ii) argue from the success of adaptationism in that specific area to its applicability to all biological phenomena.

The possibility of holding an adaptationist view that is restricted just to some specific class of biological phenomena applies to empirical and explanatory adaptationism, as well as methodological.

More generally, in this paper I have simplified the topic at hand by focusing mostly on "pure" claims for and against the different adaptationist positions. I cannot claim to have discussed every possible adaptationist view, because so many mixed, moderated and restricted adaptationist positions are possible. I do claim, however, that the three-way distinction I have made here is the most important distinction between adaptationist positions. Most of the other possible positions can be arrived at by modifying or combining ideas discussed in this paper. To make the discussion as clear as possible, I have also focused on authors who express strong attitudes about these issues and who are often diametrically opposed to each other -- authors such as Dawkins and Lewontin. In focusing on these polar opposites, I do not intend to downplay or obscure the possibility of middle-ground positions. Certainly many working biologists occupy various regions in the middle

ground. But my hope is that a better understanding of the poles will also cast light on the middle ground.

7. Conclusion

There are three different forms of adaptationism corresponding to three views about the roles of adaptation and selection in biology. The primary aim of this paper has been to distinguish these three forms of adaptationism and describe them as clearly as possible. I hope to have presented each of the views in a form that can be accepted by both friends and foes of these positions. Such, at any rate, is my reason for taking few sides in this paper, and resisting the temptation to use more colorful names for some of the positions.

Evidence for or against one type of adaptationism often is not evidence for or against the other forms; this is a source of misunderstanding which has significantly hindered discussion. I have tried to classify a few of the influential statements made on either side of these issues, but there are many writers I have not tried to classify and some (including Maynard Smith) about whom I am uncertain. Although none of these issues are easy, the hardest problems concern explanatory adaptationism, a view that combines biological and philosophical claims in a complex and contentious brew. Here, I think, lies the source of much of the heat in the adaptationism debates.

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