Adaptationism

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1. Introduction

The "adaptationism" debate is about the role of natural selection in relation to other evolutionary factors. The term "adaptationist" is used for views that assert or assume the primacy, or central importance, of natural selection in the project of explaining evolutionary change. This "central importance," however, can take a variety of forms. The debate can also involve questions about *how* natural selection operates, and what sorts of outcomes it tends to produce. But most discussion of adaptationism is about the relative significance of selection, in comparison with the various other factors that affect evolution.

The term "adaptationism" is only a few decades old, but the debate itself is an extension of long-running debates that reach back to the early days of evolutionary theory in the late 19th century. Darwin himself constantly fine-tuned his claims about the relations between natural selection and other evolutionary factors, especially in successive editions of the *Origin of Species*. Many of the topics covered in recent debates can also be recognized in debates about gradualism, the role of mutation, and the significance of

Mendelism to evolutionary theory in the early 20th century (Provine 1971). During the early years of the "evolutionary synthesis," the debate between R. A. Fisher and Sewall Wright was in large part a debate about the role of subtle non-selective factors such as population structure and random drift (Fisher 1930, Wright 1932).

So the debate about the relative importance of selection is old, but it was transformed by a famous 1979 paper by Stephen Jay Gould and Richard Lewontin. They used the term "adaptationism" for one set of views about the primacy of selection. They then attacked that view, and defended a "pluralist" position in which many evolutionary factors are explicitly taken into account. Selection is then seen as constrained by a range of developmental and architectural factors, and evolutionary outcomes reflect accidents of history as much as ecological demands. Gould and Lewontin also attacked poor methodological practices that they saw as common within the "adaptationist" camp.

Although the debate initially appeared to be primarily biological and empirical, it came to occupy the attention of philosophers as well as biologists. In part this can be attributed to philosophers' keen interest in theoretical debates in evolutionary theory. But as the debate developed it became entangled in abstract issues in the philosophy of science. These include questions about idealization, teleological thinking, and the overall role of evolutionary theory in the scientific world view (Dupre 1987, Dennett 1995). The debate is now transforming and, to some extent, subsiding.

Our discussion here will have three parts. First, we discuss the development of the debate in more detail, focusing especially on recent transformations. Then we discuss distinctions between several different kinds of adaptationist position. Within "the" problem of assessing adaptationism, at least three distinct problems are often mixed together. This distinction enables us to sort the more empirical from the more non-empirical aspects of the problem.

Once this has been done, in the final section we present a novel treatment of some of the more empirical aspects of the debate. This analysis will be partly deflationary; we suggest

that some (though not all) conflicts in this area are not as real as they seem. They arise from paying insufficient attention to some crucial differences in the "grain" of evolutionary analysis.

2. The Development of the Debate

We will not trace deep history of debates about the role of selection and adaptation, but will start from the specific discussion initiated by Gould and Lewontin's "spandrels" paper.

Gould and Lewontin argued for several claims. First, they argued that evolutionary thinking had become far too focused on natural selection as a determinant of evolutionary change. A more subtle line of critique concerned how natural selection itself should be understood. Gould and Lewontin argued that organisms had come to be seen as patchworks of traits that had each been selected as a "solution" to some "problem" posed by the organism's environment. Gould and Lewontin saw two errors in this picture of organisms and environments. One error was a reductionist picture of organisms as collections or amalgams of distinct traits. We can call this, more specifically, an "atomistic" view of the organism. The other is what Lewontin has elsewhere (1983) called an "alienated" conception of the organism in relation to its environment. This second error can more simply be called an "externalist" conception of evolution. In this view, the environment is taken as a preexisting condition to which the organism must respond.

In their critique, Gould and Lewontin put a lot of weight on the etymology and metaphorical loading of the terms "adaptation" and "adaptive." They saw mainstream evolutionary theory as beholden to a picture of organisms that is in some ways pre-Darwinian and pre-scientific. Organisms were seen as fitting their environments' demands as a key fits a lock. Although evolutionists invoke natural mechanisms to explain this "fit" between organism and circumstances, the conception of this relationship

itself is, for Gould and Lewontin, too close to the tradition of natural theology, in which God has designed every organism to be ideally fitted for its circumstances and role.

The atomism and externalism of mainstream English-speaking evolutionary biology should be replaced, Gould and Lewontin argued, by a view that recognizes the integrated nature of organisms, and also recognizes the reciprocal or two-way interaction of organisms and environments. The argument was not that *no* traits are solutions to environmental problems in the standard sense, but that a great many traits are not.

Further, according to Gould and Lewontin, the focus on adaptive explanation had led to careless and biased methodological habits in much of evolutionary biology. The aim, allegedly, had become that of finding *some* adaptive rationale for every trait that could be described. Explanation was incomplete until an adaptive story had been found, and the biologist's work was done once an adaptive explanation had been found that had reasonable fit to available data. Some parts of evolutionary thinking were turning into an exercise in concocting "just so stories." There was, according to Gould and Lewontin, little willingness to seriously consider different kinds of explanation, or to raise the standard of proof for an adaptive explanation to a level appropriate for science.

In sketching such alternative explanations, Gould and Lewontin coopted an architectural term, "spandrel." Spandrels are features of a structure that were not directly shaped by natural selection or deliberate design, but are *byproducts* of selection (or design) operating on other features. Though this term achieved wide currency via Gould and Lewontin's paper, it does not capture with much accuracy the shape of the alternative explanatory program that Gould and Lewontin were trying to describe. The core of this alternative program is the idea that evolutionary processes are subject to a long list of influences, many of them quite well understood in isolation, but interacting in very complex ways. For example, evolutionary biology had focused largely on the features of adult organisms, neglecting the fact that adults are the outcomes of developmental sequences that start with a single cell. A possible adult phenotype with very high fitness is evolutionarily irrelevant if it cannot feasibly be produced by the developmental

trajectory characteristic of that kind of organism. In indicating the structure of alternative explanations Gould and Lewontin also cited constraints on evolution deriving from the genetic systems of organisms, constraints imposed by an organism's "bauplan" or basic layout, and various roles for accident and happenstance (Kitcher 1987 gives a good survey of all these factors. See Pigliucci and Preston 2004 for a collection of work that focuses on the integrated nature of phenotypes.)

The argument in Gould and Lewontin's paper was expressed generally, but a crucial target both here and in subsequent discussion was the evolutionary study of behavior, especially human behavior. Sociobology had arisen as a specific research program a few years earlier (Wilson 1975), and Gould and Lewontin saw the problem of rampant adaptive speculation as especially acute and harmful in this area. Special criticism was also focused on the then-novel strategy of "optimality analysis," a set of formal tools that embody the assumption that selection will generally produce the best-possible solution to an adaptive problem (Maynard Smith 1978, Parker and Maynard Smith 1990).

Gould and Lewontin's critique generated a heated discussion. Some biologists – perhaps most – thought that Gould and Lewontin had caricatured the selection-oriented style of biological work. So some responses took the form of arguing that a reasonable sensitivity to non-selectionist factors was already present in mainstream biology and no corrective was needed. For instance, Maynard Smith (1982) points out that one part of setting up any optimality analysis is definition of the set of alternative phenotypes that are to be compared, and that this is equivalent to a description of developmental constraints. While it may be true that insufficient attention has been paid to exactly how those constraints should be formulated, Maynard Smith argues, it is not fair to claim that these constraints are absent from this type of analysis. Others argued that a strong focus on selection was both real and warranted, either by theoretical considerations or the successful track record of this approach (Mayr 1983. See also the next section below).

The intensity of this debate has subsided in recent years, but it would be wrong to say that the debate was "won" by either the adaptationists or anti-adaptationists. For most

evolutionary biologists, natural selection continues to play a privileged explanatory role, but no longer a solitary one. To varying degrees, the criticisms leveled by Gould and Lewontin have been internalized by the field, and are reflected in contemporary methodologies. (For reviews of these developments, see Kaplan and Pigliucci 2000 and various essays in Walsh forthcoming).

Evolutionary Psychology (EP), which is commonly viewed as the modern reincarnation of Sociobiology, is perhaps the field that has been most resistant to the anti-adaptationist critique. However, while this field is still primarily concerned with the identification of adaptive explanations for particular human behaviors, the approach is generally less naïve than many of the analogous efforts of the pre-"spandrels" era. For instance, one of the standard components of contemporary adaptive explanations of human behavior is the "Environment of Evolutionary Adaptation" (EEA). This concept acknowledges that the perceived adaptive value of a trait in a contemporary cultural context is irrelevant to an explanation of the evolutionary origin of that trait (Barkow, Cosmides, and Tooby 1992). An adaptive explanation must refer to selective value in an environment like the one in which most of human evolution is thought to have occurred (e.g., small groups, hunter-gatherer lifestyle). While many would still describe EP as a field with an adaptationist bent (in the perjorative sense), the EEA incorporates at least some sense of a historical constraint.

Another sign of the integration of the anti-adaptationist critique into mainstream evolutionary biology is the explicit and widespread use of phylogenetics. At one point, there was significant debate within systematics over whether the most appropriate mode of taxonomic categorization was based on shared features or shared ancestry. That debate has largely been settled in favor of shared ancestry. It is now common to pursue the construction of taxonomic relationships among species in parallel with the study of the evolution of particular traits. Trait changes are explicitly mapped onto phylogenetic trees. In this view, selection always occurs in a historical context.

Another area where it is possible to see this integration is in the study of the evolution of development ("evo-devo"). Here the entity that is evolving is not a "trait" in the traditional sense, but rather a developmental trajectory (Raff 1996). Selection may still be the prime mover in changes in these developmental trajectories, but it is impossible to formulate a question about selection in this framework without explicitly considering developmental, "bauplan" constraints, the integrated form of the organism as a whole, and the possibility that changes in one trait may result in changes in other traits. It is natural, if not unavoidable, in this framework to assume that some traits have been the subject of direct selection and others have not.

The idea that organisms reshape their environments, rather than just adapting to them, is not new. However, there has been a recent renewal of interest in explicitly considering these processes (Odling-Smee, Laland, and Feldman 2003). The term "niche construction" is often now used for this process, specifically in an effort to undermine the concept of the "niche" as a preexisting thing that an organism must fit itself into.

As a final example, it is interesting to consider the development of molecular evolution and population genetics over the past three decades. One of the major research agendas in this area has been the development and application of statistical methods for identifying signs of selection from molecular data (e.g. DNA sequence data). This work is interesting in that its entire premise implies a selectionist perspective tempered by the type of caution urged by Gould and Lewontin. The idea that it is possible to identify particular genes that have recently been subject to a particular type of selection – and the idea that this is a worthwhile thing to do – implies that selection is of particular interest, and that if we can develop the right tools, we can find it. The idea that we have to develop powerful laboratory and statistical methods to find it implies that in many cases, selection may not be the most useful description of what is going on. The focus on statistical methods also takes on board the idea that it is appropriate to require a rigorous standard of evidence when making assertions about the role of selection.

3. Varieties of Adaptationism

One role for philosophical work in this area is distinguishing several different *kinds* of commitment that have been tangled together in adaptationism debates. That will be the focus of this section.

First, it is worth noting the gap between a commitment to a strong form of *adaptationism* and what might better be called *selectionism*. In the Gould and Lewontin critique, and in Lewontin's other work (eg., 1983), the focus is not just the primacy of natural selection, but a particular conception of how selection works and what it produces. For Lewontin, as noted above, mainstream evolutionary thinking has operated with a strongly asymmetric picture of organism/environment relations. The organism is seen as responding to structure in the environment that exists independently of what organisms are like and how they change. Not all of the biological work focused on natural selection has this character, though. In game-theoretic models of evolution, the "environment" encountered by any organism is constituted primarily by the behaviors of other organisms in the same population. These models tend to place great emphasis on selection, but they do not see populations as adapting to independently existing environmental features. So in a sense, game-theoretic work is selectionist without being adaptationist. In most discussion of adaptationism, however, this sort of distinction has not been made. Below we will follow the more familiar practice of using "adaptationist" for work that asserts the primacy of selection, whether or not the explanatory pattern is strongly externalist with respect to organism/environment relationships.

A more pervasive problem in the debate over adaptationism has been the mixing together of different senses in which selection might be said to be the "primary" or "most important" evolutionary factor. One sense is empirical: selection might be seen as the strongest force in evolution, or most efficacious causal factor. Another sense is not straightforwardly empirical at all, and has more to do with the role of evolutionary theory within science as a whole.

This second kind of position is illustrated especially by Richard Dawkins (1986). Dawkins is often associated with an extreme form of adaptationism. But this commitment is of a special kind. For Dawkins, the central importance of natural selection does not involve a claim about how *much* of what we see in the biological world has been shaped by selection. A huge amount of what we see might be due to other factors. Selection can in a sense still be "the most important" evolutionary factor, because only selection can answer the most important *questions* faced by biology.

Accordingly, Godfrey-Smith (2001) distinguishes three kinds of adaptationism.

> **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.

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

> **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.

Strictly speaking, all three of these views are logically independent. Any combination of "yesses" and "nos" is possible in principle. There are relations of *support* between them, but not relations of implication. And further, the relations of support between them are quite complicated. Evidence that supports one of the three may not support others. (See

also Lewens (forthcoming) for a more fine-grained categorization of possible views here, and Sterelny and Griffiths 1999 for further discussion of the key distinctions.)

Let us look more closely at the relations between empirical and explanatory adaptationism. Empirical adaptationism, as outlined above, is intended to be a contingent claim about the causal role of selection in the actual biological world. Explanatory adaptationism, in contrast, is a claim about the role of selection in the total edifice of scientific knowledge. It is a claim about the role of selection in solving what would otherwise be an insoluble scientific problem. Selection can play this role *even if it is rare*, even if most of what we see is the product of other evolutionary factors.

A useful illustration is provided by some responses to the rise of the "neutral theory" of molecular evolution (Kimura 1983). The neutral theory holds 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 clearly a denial of the omnipresence of selection. It is a denial of some forms of empirical adaptationism. Recent decades have seen a lively debate between neutralists and their "selectionist" opponents. But some others who see themselves as "selectionist" or "adaptationist" in their orientation to evolution see neutralism as no threat to their position at all. Dawkins (1986) is an example. This is because the processes described by neutralism are agreed on all sides to have no direct role in the explanation of well adapted phenotypes that exhibit "apparent design." The neutralists are not trying to answer questions about apparent design in nature; they are trying to describe genetic variation considered as a whole. So Dawkins sees himself as having nothing directly invested in the neutralism debate. To the extent that the neutralists win, he gains a useful tool (a reliable molecular clock), but the neutralist denial of "selectionism" does not even touch on his core claims. For a pure explanatory adaptationist, selection might only explain 1% of all molecular genetic change, but if this is the 1% that is responsible for highly adapted phenotypes that give the appearance of design, then this is the 1% that counts.

Assessing the explanatory adaptationist position involves two stages. One is the assessment of whether it is really true that apparent design is the "big question" for biology. Is focusing on this question no more than a personal preference, or even a misguided concession to a pre-Darwinianian, creationist point of view? The other stage is the assessment of whether selection is really the *answer* to the question, in the strong sense seen in the explanatory adaptationist tradition.

Some biologists have directly criticized the view that selection has a primary role in the explanation of apparent design (Kauffman 1987, Goodwin 1994), and have tried to develop more "internalist" explanations for roughly the same class of phenomena that adaptionists focus on. A more subtle and promising view of this matter might be extracted from more mainstream evolutionary thinking, however. According to this view, which can be associated with Wright's position in his debate with Fisher, we should see the evolutionary mechanism that can result in highly adapted phenotypes as comprising a *much more complex machine* than adaptationism envisages. For mutation and selection to produce highly adapted phenotypes, they must operate in a context in which many other evolutionary parameters take suitable values. Wright, for example, argued that partial subdivision of the population is needed for selection to avoid getting stuck on (what is now called) a mere "local optimum," a state of moderately high fitness that is inferior to the state that the population could in principle achieve via a more thorough exploration of the space of possibilities. (For assessments of the shifting balance theory, see Coyne et al. (1997) and follow-up discussions.)

Here we use Wright's appeal to population subdivision as an illustration of a role that could be played by a number of different evolutionary factors, any or all of which might be needed to enable evolution to produce highly adapted states of organisms. Mere mutation and selection alone, on this view, is too blunt an instrument. So some evolutionists would hold that even if explanatory adaptationism's view on the "big questions" in biology is accepted, it is an error to see selection as having primary importance in biology's answer. So this second part of the assessment of explanatory

adaptationism depends very much on empirical questions, while the first part, concerning the alleged "big question" for biology, is much less empirical.

We will make only a few comments here about the third adaptationist position, methodological adaptationism. There are several distinct ways by which such a view might be motivated. First, an argument might be given on the basis of a prior commitment to empirical adaptationism. Another style of argument, often made informally but expressed explicitly by Mayr (1983), is an argument from simple induction. Some biologists hold that regardless of what we might make of the other two forms of adaptationism, the track record of strongly selectionist thinking in biology has been so impressive that this approach should be continued. If this argument is made, an interesting counter to it can be given on the basis of Lewontin's other work (1983), which expresses a historicist view of the matter. For Lewontin, it was productive during an earlier stage in the development of biology to apply an adaptationist mindset, but we have now passed that stage. What was once a useful organizing framework has now become an impediment to further progress.

We will look in more detail at the problem of assessing empirical adaptationism. First, it is worth noting a way in which the standard vocabulary is misleading here. Questions about empirical adaptationism are often described as questions about the "power of selection" to determine the course of evolution and to produce highly adapted states of organisms. But as Sober (1987) has noted, these questions are as much about the "power of mutation" as the power of selection. Often, the crucial question to ask in these cases is a question about the supply of *variation* in an evolutionary process, rather than a question about the size of fitness differences. This is one reason why our formulation of empirical adaptationism above includes a statement about the abundance and unconstrained nature of the supply of variation.

In the section following this one, we will present a new way of thinking about the problem of empirical adaptationism. According to this view, some of the apparent oppositions in this area can be dissolved via a more careful treatment of the "grain" of

evolutionary analysis. In this section, though, we will first discuss an earlier attempt to describe a direct "test" of empirical adaptationism.

This test was offered by Steven Orzack and Elliot Sober (1994). Orzack and Sober did not employ distinctions of the kind used in this section, but what they call "adaptationism" is basically a version of empirical adaptationism. Their "adaptationism" is the view that natural selection is the most powerful evolutionary force, and able to create near-optimal phenotypes.

They propose that we test this view by asking the following question: are predictions about evolution that are based only upon information about forces of natural selection just as good, or nearly as good, as predictions based on consideration of the entire range of evolutionary factors? The way to answer that question, in turn, is to investigate a large range of specific biological phenomena, and work out how adequate a purely selection-based model is for explaining each. In each case we ask whether an account of the phenomenon that considers *only* the role of selection fits the data as well as a richer model that considers a wide range of factors. If this approach is vindicated in the great majority of cases, then adaptationism is vindicated as a general claim about the biological world.

We think that the Orzack and Sober proposal was quite useful as a first attempt to make questions around empirical adaptationism more concrete and tractable. In particular, it is useful as an attempt to make empirical sense of the idea of selection as "the most powerful force" – an idea that is often intuitively attractive but is, at least in part, metaphorical. However, their proposal has some internal problems, and can also be seen to omit a factor that is crucial for making overall sense of the situation. Internal problems are discussed in this section; the missing factor is discussed in the next.

First, we note that the test that Orzack and Sober propose involves a comparison of simpler with more complex models of the same phenomenon. Given that the richer model includes all the factors that the simpler one has, the richer one cannot do worse than the simpler one. It can only do as well or better. So how *much* better does the complex model

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have to do before it is to be preferred? Such questions are hard to assess because they require that we make quantitative comparisons between two very dissimilar things: the complexity of a particular model and the goodness of fit to observed data. In practice, formal tools such as the Akaike Information Criterion or Bayes Information Criterion are often employed in making this comparison. These criteria impose a penalty for each model parameter. The favored explanation is the one that provides the best fit to the data, but only after this penalty has been applied. These methods often contain arbitrary features, however. One interesting recent approach that avoids some problems has been proposed by Rissanen (2005), and uses the concept of "normalized maximum likelihood." In this approach the goal is to find the model that permits the shortest possible description of the system, where the "system" includes both the model and the data being modeled. In principle, one would determine the number of bits required to specify the model, and the number of additional bits required to describe the data within this model. Each bit of information is equivalent, whether that bit is applied to the model or the data. However, even this refinement still does not adequately account for other, more human, aspects of the problem. Prior to any analysis one must determine which aspects of the data need to be explained. While this approach could be used to adjudicate among explanations for particular phenomena, it will not address disagreements among biologists about what features are most deserving of explanation. Likewise, a given model must be specified within the context of many unspecified or implicit assumptions. It may often be the case that the disagreements over the role of selection reflect different – perhaps implicit – views on what should be assumed prior to studying a particular problem.

These considerations suggest that a test of adaptationism should ideally focus on a contest between 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? This 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 claim would be vindicated, on this 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. That is, 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 this proposal derives from an application of Richard Levins' views about models (Levins 1966. See also Wimsatt 1987, Weisberg forthcoming). 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. A precise fit to particular phenomena can be traded off against generality. The contest between models described above 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?

We think that something like this trade-off is often on the table in contemporary modeling of behavioral evolution. Game theory has become an important tool in this area (Maynard Smith 1982). Game-theoretic approaches to behavior choose to "invest" heavily in a detailed specification of the fitnesses of different strategies, and how they change with frequencies and circumstances. As a consequence, however, game-theoretic models must make radical simplifications about other evolutionary factors, especially the role of the genetic system. Often they even abstract away from different ways in which a stable distribution of behaviors might be realized in a population of individuals (Bergstrom and Godfrey-Smith 1998). The game-theoretic strategy embodies the idea that it is more informative to give a detailed specification of selective forces, and a minimal treatment of everything else, rather than "investing" some of the complexity of the model in a careful treatment of other factors.

When we envisage a contest between models of comparable complexity, we also avoid a problem that Brandon and Rausher (1996) found 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 simplified selectionist model succeeds predictively then it is said to be vindicated – even if some *other* simplified model would do just as well in a similar test. As Brandon and Rausher say, if there is to be an unbiased test between simpler and richer models, then a range of different kinds of simpler model should be included. This point is right, and the problem is avoided under the revised proposal in which the comparison to be made is always between comparably simple models.

We see this "contest between models" scenario as itself a simplified way of thinking about a more complex set of empirical questions. Not all aspects of the problem of empirical adaptationism can be assessed by a direct comparison of models in their dealing with data (Godfrey-Smith 2001, Sterelny and Griffiths 1999) In this paper, though, we will continue to operate within a somewhat formal and idealized approach to the problem. But in the next section, we will introduce a richer framework than the ones used so far.

There is a simple way of motivating the shift from the framework used in this section to the one assumed below. In both the original proposal of Orzack and Sober, and the modified one outlined just above, there was no distinction made between different "grains" at which evolutionary processes can be described. In the "contests between models" discussed above, any biological phenomenon could be chosen and made subject to an instance of the test. The *same* approach was employed at *all* levels of grain. But perhaps the key to the problem, or a large part of it, lies in distinguishing between several different grains at which evolutionary processes can be described. This is a straightforward idea, but in the next section we will make it more precise with the aid of a formal framework that is popular, although controversial, within evolutionary biology itself.

4. The Role of Zoom and Grain

One of the most prominent metaphors in evolutionary biology is that of the adaptive landscape (Wright 1932, Gavrilets 2004). In its simplest form, the landscape represents a mapping from an organism's genotype or phenotype to its fitness; natural selection is the tendency for populations of organisms to move "uphill" in this landscape – that is, towards regions associated with higher fitness. Populations move locally on the landscape because mutations are assumed to have small effects.

There are many concerns about the validity of the adaptive landscape metaphor, and some biologists favor discarding it altogether (Moran 1964). Most biologists are still comfortable with the idea of a fitness being associated with a particular phenotype. However, it is now commonly accepted that this fitness is context dependent. That is, the shape of the landscape – the locations of fitness peaks and valleys – may be extremely sensitive to the distribution of organisms on the landscape, in both the past and the present. Furthermore, the relationship between an organism's genotype and its phenotype is increasingly seen to be a complex one, mediated through developmental pathways and environmental interactions.

Some who reject the whole idea of the adaptive landscape claim that the image of individual organisms or populations climbing fitness peaks suggests the sort of intentionality that often haunts sloppy evolutionary reasoning. The assumption of continuity of movement on a phenotypic landscape also seems to disregard the disjoint nature of phenomena like Mendelian inheritance and recombination. So for some critics, the adaptive landscape metaphor implicitly reinforces some of the same kinds of problematic simplifying assumptions that Gould and Lewontin's critique targeted.

With these caveats in mind, we suggest that this metaphor may be nonetheless be useful for understanding how seemingly contradictory scientific approaches to evolutionary questions can, in fact, be complementary. We also suggest that one's perception of the

extent to which evolution is characterized by adaptation shapes – and is shaped by – the level of resolution at which one considers evolutionary processes.

When one begins to consider an evolutionary problem, one must first choose a scale, or grain, of analysis. We can think of this as choosing how large a region of the adaptive landscape we want to include in the analysis. Choosing a larger region means considering a wider variety of alternatives (alleles, genotypes, phenotypes, strategies, etc.), but does not permit the same depth of analysis that could be performed on a smaller region. Also, if most evolutionary processes (e.g., mutation and selection) result in local movement on the landscape, then inclusion of a larger region implicitly considers these processes over a longer timescale.

To see the importance of grain in relation to attitudes towards adaptation, we will consider three different scales of analysis. To make the application of this framework simple and clear, we will suppose that these are three scales at which the same very large landscape is being viewed. The landscape itself is phenotypic; it represents fitness (height) as a function of phenotypic variables describing individuals. In some ways, what we are imagining here is something that is not fully coherent, because we are supposing that the same measure of fitness can be applied to organisms of very different organisms (elephants and jellyfish, for example). But we think that the landscape idea has genuine heuristic power here nonetheless.

At the highest, most "zoomed out" level, evolutionary analyses consider broad patterns of occupancy across large regions of the landscape. At this level of analysis, populations are represented by single points. (This creates problems in the case of extremely sexually dimorphic species, like some barnacles, but we will idealize away from that problem.) At this level of grain, the natural questions to ask include the following: what portion of conceivable peaks are occupied by populations in the real world? To what extent are the occupied peaks the highest peaks? How thoroughly and how predictably does natural selection explore the adaptive landscape?

To most biologists working at this highest level of analysis, what is most striking is the emptiness of the landscape. In the history of life on earth, organisms have explored a vanishingly small fraction of the conceivable ways of making a living, and the idea that the modes of life that we see today somehow represent the "best" of these possible forms has been broadly rejected. Rather, populations have been restricted to a small subset of local peaks by chance, as well as by historical and developmental constraints. From this vantage point, the power of natural selection to produce adaptation appears quite limited.

The situation changes if we zoom in on a particular region of the landscape, perhaps containing only one or a few peaks. At this intermediate level of grain, whole populations still tend to occupy single points, but they are vague or smudged ones. These analyses also typically focus on variation in a small number of dimensions, assuming (often implicitly) that the traits represented by the other dimensions are invariant over the timescale of the analysis, and evolve independently of the trait or traits under consideration.

A question asked in this second context might take the form, "Given that there is a population that is in this region of the landscape, where, within the region, should we expect to find that population?" The answer that many biologists would give is that we expect to find the population at or near one of the local peaks. Given enough time and a local topography that is conducive to a thorough evolutionary exploration of the region, we might even expect to find the population at or near the highest of those local peaks.

Perhaps more commonly, however, research at this scale starts with the empirical observation that a population occupies a particular location within the region. The task is then to uncover whether and why there should be a peak in that location. At this intermediate scale, many will hold that the salient feature of evolution is local adaptation. Populations tend to be found near peaks, as opposed to in the adjacent valleys. Some biologists may disagree with that claim, but the crucial point is that selectionist conclusions drawn at this level of analysis do not contradict non-selectionist conclusions drawn at the higher level. The fact that the population is in this region of the landscape,

as opposed to some very distant one, is simply one of the background assumptions made when working at this second level of analysis.

Now let us consider a third level of "zoom" with which we might view the landscaspe. We now focus in great detail on a very small region. When we do this, certain features of evolution that are typically ignored at the higher levels become critically important. Rather than thinking of a population as occupying a single location, or a small, diffuse area, in the landscape, we explicitly consider the distribution of individuals that make up the population, and the very complex processes of change that this distribution is subject to. Analysis of the evolutionary dynamics of the system must account for drift and mutation, as well as selection, and, in the case of diploid organisms, Mendelian inheritance and recombination. The way the population moves on the landscape from generation to generation is not continuous, at this level of grain. Points appear suddenly, some distance from their parents.

As we focus more on the details of evolution at this lowest level, the adaptationist features that were prominent at the intermediate level of analysis recede in importance. Other evolutionary processes involving random fluctuations, interactions among alleles or loci, and constraints inherent in the mechanism of inheritance become more important aspects of our understanding. Here again, there will be some disagreement among biologists about which factors are in fact most significant. But many will hold that at this lowest level, as we also saw at the highest level, what is often most salient are those features of evolution that frustrate adaptation. And once again, the crucial point here is that de-emphasizing selection at this lowest level is not at all inconsistent with applying a strongly selectionist approach at the second, middle level.

To construct a specific example, consider the case of sickle-cell disease, which afflicts individuals who inherit two copies of a mutant allele of the Hemoglobin alpha chain gene. Despite the devastating effects of this condition, this mutant allele is present at an appreciable frequency in certain populations, because heterozygous individuals, who carry one copy of the mutant allele and one copy of the normal allele, have an increased

resistance to malaria. It is instructive to consider how different scales of analysis of this system drive different relationships to adaptationism.

We can first analyze this system in the context of population genetics – considering how the selective effects of malaria and of sickle-cell anemia alter the relative frequencies of the mutant and normal alleles. This perspective highlights the way in which Mendelian inheritance undermines humans' capacity to adapt to the presence of malaria. A population composed entirely of "adapted" heterozygotes is inherently unstable: our mechanism of inheritance recreates both classes of maladapted homozygote every generation.

At a slightly higher level, we begin to see signs of adaptation. If we expand our view to encompass the mutation event that created the mutant allele, we see that human evolution has found the beginnings of a solution to the problem of malaria. From an adaptationist point of view, heterozygous resistance to the disease certainly represents an advance over a population where everyone is susceptible. If we expand, hypothetically, to an even longer timescale, we can imagine solutions to the problem that are not disrupted by the diploid genetic architecture. For example, the right mistake in recombination could create a chromosome that carried both the normal and mutant alleles. This new allele might confer malaria resistance to its carriers without producing sickle-cell anemia in homozygotes.

As it happens, natural populations in Africa do, in fact, contain an allele (C) that confers resistance in homozygous state without harmful sickling, but this allele has low fitness in heterozygous state with each of the prevalent alleles (A and S), so it has been unable to advance from very low frequency (Templeton 1982, Gilchrist and Kingsolver 2001). Here we see the role of a different kind of fine-grained constraint, the requirement that a new favorable allele be advantageous when appearing as a heterozygote with locally common alleles. Again, when operating within a coarser-grained perspective we can expect new alleles to eventually arise that overcome this constraint.

If we continue to zoom out, the appearance of adaptation begins to recede again. Why, for instance, do we not have a fundamentally different immune system that would make malaria a non-issue? Our susceptibility to malaria suggests a whole other class of features limiting our adaptation. We are subject to numerous historical and developmental constraints. Perhaps most importantly, however, is that our capacity to adapt to our environment is limited by the fact that many aspects of our environment – such as the malaria parasite – are simultaneously adapting to us.

Let us note explicitly some of the features of the three levels of grain that make adaptive features of evolution more, or less, prominent. At the finest level of grain, existing features of the genetic architecture are treated as fixed constraints against which selection must act. At the intermediate level, we suppose that some of these can be altered by such things as modifier alleles. At the intermediate level, time-scales are also longer than they are at the finer level. So at the intermediate level, we can suppose that there is a constant steady flow of new variants arising in the population. So the likely fate of any *particular* mutation is not important. (The distinction between shorter time-scales in which the set of available variants is fixed, and longer ones in which the set of variants is not fixed, has also been treated in formal modeling framework by by Eshel and Feldman (2001) and Nowak and Sigmund (2004), with conclusions that complement the present analysis.)

So our suggestion is that some of the apparent oppositions between adaptationist approaches and their alternatives might be resolved through careful attention to the grain at which evolutionary processes are being described. It is important that making a suggestion of this kind involves taking a stand on some substantive biological issues. In particular, some will contest our claim that at the finest of our three levels of grain, non-selective factors have great importance. Some would say that even at this fine-grained level selection tends to dominate, and that the role of other factors has been over-sold by theoreticians who are enamored of the subtleties of complex population genetics models. Our main aim here is not so much to rule out such a position, as to present a better framework with which these questions can be assessed. One way to represent different kinds of adaptationist commitment is in terms of size of the region, within the range of

possible levels of "zoom," in which evolutionary change tends to have an adaptive character. Some will say the region is large, others will insist that it is small. But we think that without this conceptualization of the situation, or something akin to it, it is very difficult to *frame* the debate in a way that makes it tractable. Some attention to these questions of grain is already present, often implicitly, in much biological practice. Our suggestion is that a more explicit and systematic treatment of this factor could be of considerable use in clarifying, and then resolving, fundamental questions about the role of selection in evolution.

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