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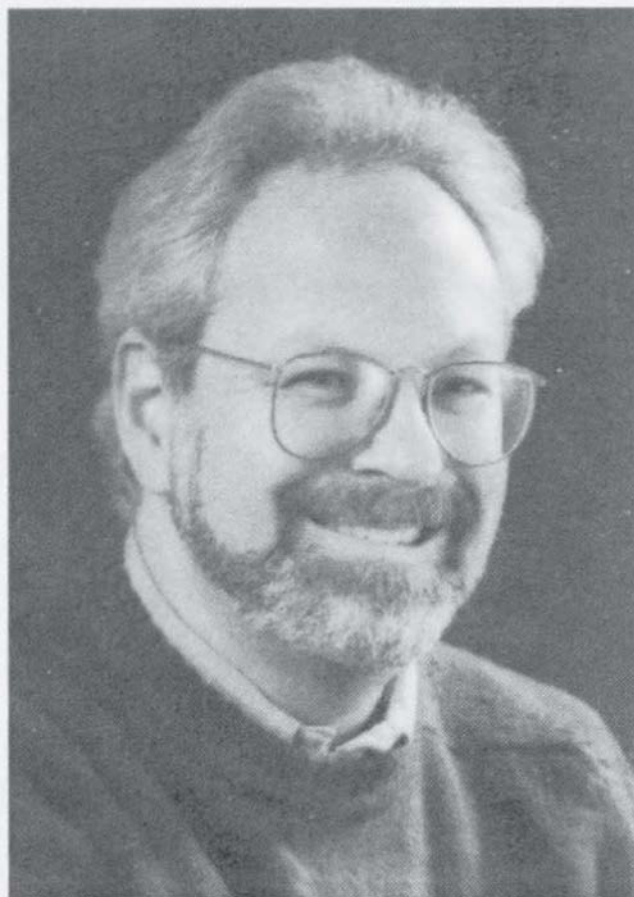
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Evolution and Optimality: Feathers, Bowling Balls, and the Thesis of Adaptationism

Elliott Sober

1. Does selection optimize?

Many sciences use the idea of minimization and maximization.

Ask a physicist about the path taken by a ray of light as it passes from air into water, and you may be told about Fermat's Law of Least Time (Figure 1). If a ray of light goes from point A to point B, it will follow the path that minimizes its travel time. Going from A to B by way of point O takes less time than going from A to B by any other route.

FIGURE 1

Minimization is maximization by another name; just as light minimizes its travel time t , it maximizes the inverse of its travel time $1/t$. The light's trajectory can be discovered by finding how some quantity is minimized or maximized. One understands nature by thinking of nature as going to extremes. This is extremal thinking, but is it optimization? Evidently not, because the physicist does not add to this description a concept of better or worse. It is neither good nor bad that light acts in this way; nor does light behave as it does because this behavior benefits the light, the air, the water, or anything else.

Natural selection resembles light propagation in one respect, but not in another. The laws¹ that govern the *process* of natural selection are the way they are, impervious to the costs and benefits they may impose. However, the *products* of natural selection – the traits that evolve because of natural selection – evolve because they are good for the individuals that display those traits.

Consider an example – an ancestral population of zebras in which all zebras run slow. Suppose a mutant or migrant zebra is introduced into this population who runs fast. This zebra will do better at evading predators than the others, and so it will have more offspring than the average slow zebra. To keep the example simple, let's imagine that zebras reproduce uniparentally, and that fast zebras have fast offspring and slow zebras have slow offspring. The result is that the trait of running fast will increase in frequency; there will be a higher percentage of fast zebras in generation two than there was in generation one. If this process is repeated for numerous generations, and fast zebras continue to do better than slow zebras in avoiding predators, the trait of running fast will gradually increase in frequency and eventually will reach 100% representation in the population.

Fast replaces Slow in this simple example, but how is the concept of optimization to be applied? We consider two phenotypic traits – Fast and Slow – and evaluate each for the fitness consequences it has. Running fast is a better trait for a zebra to have than the trait of running slow. This *description* of the fitness consequences of the traits is then converted into a *prediction*: if Fast is fitter than Slow, then the population will evolve to a configuration in which everyone is Fast.

This simple idea is often misrepresented. One hears it said that natural selection maximizes the fitnesses of organisms. There is no such guarantee, as we can see by comparing Figures 2a and 2b. In both these figures, the fitnesses of the two traits are represented as a function of the proportion of fast organisms in the population. The two figures both express the idea that fast zebras do better on average than slow ones, regardless of whether running fast is common or rare. However, the two figures differ

in another respect. In Figure 2a, the two lines do not slope; this means that an individual's chance of surviving and reproducing depends just on its own running speed and not on the composition of the population in which it lives. In Figure 2b, the two lines slope downhill; this means that fast and slow zebras do worse and worse as running speed increases. In Figure 2a the fitnesses are frequency independent; in 2b, they are frequency dependent.

FIGURE 2

Which of Figures 2a and 2b more accurately represents the fitness consequences of running fast and running slow? That depends on the biology. It is possible to imagine scenarios that would favor each of them. For example, suppose that lions hunt by wandering around until they see a herd of zebra and then choose a zebra at random to chase. A zebra's chance of getting singled out for pursuit is unaffected by the population's composition, and its chance of getting caught is settled by how fast it runs. This would justify Figure 2a. On the other hand, suppose that fast zebras kick up more dust than slow ones, and that lions find herds of zebras by scanning the horizon for dust clouds. Once the lions find a herd, they are lazy; they prefer to chase slow zebras over fast ones, even though they could catch either type. This scenario favors the representation given in Figure 2b; fast zebras always do better than slow ones in the herd, but all the individuals in the herd do worse and worse as the average running speed in the herd increases.

My point in discussing these figures is not to give a realistic picture of how lions hunt zebras, but to make a conceptual point about fitness and selection. The broken lines in Figures 2a and 2b represent the average fitness of the organisms in the population. This average fitness is called \bar{w} ("w-bar"). Notice that \bar{w} goes up as the population evolves in Figure 2a, but goes down as the population evolves in Figure 2b. Selection improves fitness in Figure 2a, but selection reduces fitness in Figure 2b.

Optimality methods in evolutionary biology do not assume that natural selection always conforms to Figure 2a. An optimality model can accommodate the destructive effects of selection depicted in Figure 2b just as easily as it can accept the improving effects depicted in Figure 2a. The optimality idea is not that selection improves fitness, but that the fittest of the available phenotypes will evolve; there is no expectation on the part of optimality modelers that zebras will evolve machine guns with which to repel lion attacks (Krebs and Davies 1981) or that organisms will evolve the ability to live forever and reproduce at an infinite rate (Maynard Smith 1978).

2. Evolutionary forces

Objects released above the surface of the earth accelerate downward at a rate of 32 feet/second². Or rather, they do so unless some force other than the earth's gravitational attraction acts on them. A similar principle can be stated for the process of natural selection. The process will produce a certain type of change unless other forces intervene.²

To formulate this idea, we need to begin with a definition: Natural selection occurs within a population if and only if there is variation in fitness in the population. Selection cannot act on running speed unless zebras run at different speeds. And it isn't enough that they run at different speeds; this variation in phenotype must make a difference for their chances of surviving and reproducing. If all running speeds are equally fit, then there is no natural selection with respect to those traits.

That is our definition, and here is the proposed principle: *in a population subject to*

natural selection, fitter traits become more common and less fit traits become more rare, unless some force prevents this from happening.³ My use of the terms "force" and "principle" should be taken with a grain of salt. All I mean is that when there is variation in fitness, one expects fitter traits to replace less fit traits unless something prevents this from happening.⁴ If fast zebras are fitter than slow ones, the population will enlarge its proportion of fast individuals unless a countervailing force gets in the way.

What might these preventing forces be? There are several (Maynard Smith 1978). First, random events can prevent fitter traits from increasing in frequency. If Fast is fitter than Slow, this simply means that fast individuals have a higher probability of surviving to reproductive age. However, this difference in probabilities does not guarantee that a higher proportion of fast individuals will survive. Consider an analogy. Suppose two coins are both biased towards heads, but that one has a more extreme bias than the other. Maybe the first coin's probability is 0.9 and the second coin's is 0.7. If each coin is tossed ten times, there is no guarantee that the first coin will land heads more often than the second. However, if the coins are each tossed a thousand times, it becomes more certain that the first coin will yield a higher frequency of heads. Just as sample size is relevant to saying what will happen when coins are tossed, so population size is relevant to saying how certain it is that fitter traits will outperform less fit traits. Small populations open the door for chance effects.

Another "force" that can prevent fitter phenotypes from evolving is the underlying genetics – the pattern by which phenotypes are coded by genotypes. In my simple example about the zebras, I assumed that zebras reproduce uniparentally and that offspring always perfectly resemble their parents. With sexual reproduction, complications can arise. Consider the phenomenon of heterozygote superiority. Suppose there are three running speeds – Slow, Medium, and Fast – where the fittest of these three is coded by a heterozygote. If fast individuals have the *Aa* genotype, medium individuals have *AA*, and slow individuals have *aa*, then selection will not lead the population to evolve to the configuration of 100% Fast. What will evolve is a balanced polymorphism in which all three running speeds continue to be represented in the population. There are other genetic arrangements, more complicated than that of heterozygote superiority, that lead to the same result. It is possible for genetics to "get in the way" – to prevent the fittest phenotype from evolving.

A third factor that can prevent the optimal phenotype from evolving is time. If a population begins with a range of phenotypes, it will take time for natural selection to transform this population into one in which the optimal phenotype has gone to fixation. If biologists start studying this population before sufficient time has elapsed, they will discover that the population is polymorphic. Here again, it is a contingent matter whether the best phenotype among the range of variants has attained 100% representation.

The list of possible preventers could be continued (cf. e.g., Reeve and Sherman 1993), but I think the pattern is already clear. When selection is the only force guiding a population's evolution, the fittest phenotype evolves. However, when other forces intrude, other outcomes are possible. Selection can produce optimality, but it also can fail to achieve this result.

"Pure" natural selection has predictable results, but the world is never pure. Populations are never infinitely large, which means that random drift always plays some role, however small. Still, the question remains of how closely nature approximates the pure case. It is an empirical matter whether natural selection was the only important influence on the evolution of a particular trait in a particular population, or if nonselective forces

also played an important role. The Newtonian analogy continues to apply. The earth's gravitational force induces a component acceleration on objects released at its surface. However, since the earth is not surrounded by a vacuum, falling objects always encounter air resistance. It is therefore an empirical matter whether the trajectory of a falling body is guided preeminently by gravity or if other forces play an important role. We know that objects are not the same in this respect; the trajectory of a feather differs markedly from the trajectory of a bowling ball. In physics, we are quite accustomed to this pluralistic view of the relative importance of different forces; as we now will see, this is a useful analogy for thinking about optimality issues in evolutionary biology.

3. From ontology to epistemology

So far, I have described the process of natural selection and said what its effects are likely to be. When it acts alone, one result will obtain; when selection acts simultaneously with nonselective forces, other results are possible. These assertions describe the *forward-directed* properties of the laws of evolution – given an array of forces, what will be the result?

Let us now ask a *backwards-directed* question. If we observe a trait in a population, what array of evolutionary forces should we postulate to explain it? If we see that zebras run fast, should we infer that natural selection was the *only* important cause of the trait's evolution, that it was *one* of the important causes, that it played a *minor* role, or that it played *no* role at all? We now have shifted from ontology to epistemology. The ontology of the theory of natural selection describes the results that different constellations of forces will have. Our present epistemological question concerns how we are to know what the forces were, given that we observe the population's present configuration. How are we to infer past from present – the causes from their observed effects?

We now have located the conceptual arena within which evolutionary biologists continue to debate the thesis of "adaptationism." Not surprisingly, this *ism* word means different things to different people. Some regard the so-called debate about adaptationism as a pseudo-problem; they feel that the serious issues are beyond scientific dispute. I want to describe a quite different view of this controversy that Steven Orzack and I have developed collaboratively (Orzack and Sober 1994; Sober 1993), and which Reeve and Sherman (1993) also defend. We feel that there is a serious scientific question here whose answer is not yet in hand. We think that less is actually known about the truth of adaptationism than critics and defenders often suggest. Agnostics often get attacked from both sides; both theists and atheists dislike being told that no one knows what they claim to know.

In order to isolate the substantive scientific issue that still remains unsettled, I'll now describe several remarks one commonly hears – from biologists, philosophers, cognitive scientists, and others – on both sides of this controversy.

4. Six Sayings about Adaptationism

Saying Number 1: "Natural Selection is the only natural process that can produce adaptive complexity."

In his essay "Universal Darwinism," Richard Dawkins (1986) updates the classic philosophical design argument for the existence of God. If one examines the vertebrate eye, for example, and wants to explain its complexity, its organization, and why its parts conspire so artfully to allow the organism to see, the only naturalistic explanation one can think of is natural selection. Rather than conclude that adaptive complexity points to the existence of an intelligent designer, Dawkins argues that it points to the existence

of a “blind watchmaker” – i.e., to the process of natural selection, which is not only blind, but mindless.

Richard Lewontin (1990) has pointed out that there are complex and orderly phenomena in nature that do not demand explanation in terms of natural selection. The turbulent flow of a waterfall is mathematically complex, but it is not the result of a selection process. The lattice structure of a crystal is highly ordered, but this is not the result of natural selection.

Dawkins might reply that waterfalls and crystals have not evolved; they are not the result of descent with modification. In addition, the complexity of waterfalls and the orderliness of crystals confer no advantage on the waterfalls or the crystals themselves. Dawkins’ design argument could be formulated as the thesis that when evolution leads a trait to be found in all the organisms in a population, and that trait is complex, orderly, and benefits the organisms possessing it, the only plausible explanation of the trait’s ubiquity is natural selection.

This argument leaves open a serious issue that Lewontin’s response suggests. Is it possible to be more precise about the concepts of “complexity” and “order” in such a way that the special features of traits that require selective explanation are made clear? I do not have an answer to this question, but in the present context I think we may set it to one side. In my opinion, we should grant that natural selection provides a plausible explanation of the vertebrate eye, and that no alternative explanation is now available. Adaptationism does not have to claim that none will ever be conceivable. Even though waterfalls and crystals attained their complexity and their orderliness by nonselective means, it is entirely unclear how nonselective processes could explain the structure of the vertebrate eye.

Dawkins takes this point to establish the correctness of adaptationism. However, the arch “anti-adaptationists” Gould and Lewontin (1978), in their influential paper “The Spandrels of San Marco and the Panglossian Paradigm – A Critique of the Adaptationist Programme,” assert that “Darwin regarded selection as the most important of evolutionary mechanisms (as do we).” What, then, is all the shooting about, if both sides agree that natural selection is important, indeed indispensable, as an explanatory principle?

Dawkins’ argument provides a good reason to think that natural selection is an important part of the explanation of why the vertebrate eye evolved. However, this does not tell us whether the traits exhibited by the eye are optimal. Perhaps when we anatomize the organ into traits, we will discover that some of its features are optimal whereas others are not. As noted before, selection can be part of the explanation of a trait’s evolution without that trait’s being the best of the phenotypes available. The issue of adaptationism concerns not just the pervasiveness of natural selection, but its power.

Saying Number 2: “Adaptationism is incompatible with the existence of traits that initially evolve for one adaptive reason but then evolve to take over a new adaptive function.”

One of the main points of the spandrels paper is that it is important not to confuse the current utility of a trait with the reasons that the trait evolved in the first place. Natural history is filled with examples of *opportunistic switching*; traits that evolve because they perform one function are often appropriated to perform another. Sea turtles use their forelimbs to dig nests in the sand, but these forelimbs evolved long before turtles came out of the sea to build nests (Lewontin 1978). Insect wings evidently began to evolve because they facilitated thermal regulation and only later helped organisms to fly (Kingsolver and Koehn 1985); for further discussion, see Reeve and Sherman (1993).

If adaptationism embodied a commitment to the view that there is little or no opportunistic switching in nature, the pervasiveness of this pattern would undermine adaptationism. However, most self-proclaimed adaptationists have no trouble with this idea. To be sure, some adaptationists have made the mistake of assuming that the current utility of a trait is the reason that the trait initially evolved. But this appears to be a mistake on the part of adaptationists, not a thesis that is intrinsic to the idea of adaptationism. It is useful to separate the proposition of adaptationism from the people who happen to espouse it (Sober 1993).

The idea of opportunistic switching places natural selection in the driver's seat. Selection governs the initial evolution of the trait and selection governs its subsequent modification. The point is that the functional requirements that determine which variants are fittest change in the course of the trait's evolution. If adaptationism is a thesis about the power of natural selection, the existence of opportunistic switching is not central to the dispute.

Saying Number 3: "Adaptationism is incompatible with the existence and importance of constraints that limit the power of natural selection."

The word "constraint" has been used in many different ways; biologists talk about mechanical constraints, developmental constraints, phylogenetic constraints, genetic constraints, etc., etc. Underlying this diversity, however, there is the idea that constraints limit the ability of natural selection to produce certain outcomes. To the degree that adaptationism emphasizes the power of natural selection, it apparently must minimize the importance of constraints (Reeve and Sherman 1993). As we will now see, this is correct for some so-called constraints, but not for others.

I described the role of "genetic constraints" in Section 2. The manner in which genotypes code phenotypes can prevent the fittest phenotype from evolving. If this pattern of coding is fixed during the duration of the selection process and does not itself evolve, then it is properly called a constraint on natural selection. Adaptationism as a research program is committed to the relative unimportance of such constraints. The assumption is that a simplifying assumption about heredity – that like phenotype produces like phenotype – is usually close enough to the truth; the details of the underlying genetics would not materially alter one's predictions about which phenotypes will evolve.

I now want to consider two examples of a constraint of a different sort. Maynard Smith (1978) points out, in his discussion of running speed, that an animal's running speed increases as its leg bones get longer, but that lengthening the leg bone makes it more vulnerable to breaking. This means that running speed is not optimized on its own, but that selection is constrained by the effect that running speed has on vulnerability to injury. The optimality modeler responds to this consideration by thinking about which bone shape is best, given the competing requirements of speed and strength. The existence of constraints does not refute the optimality approach, but gives it shape.

The second example I want to consider is the work on "antagonistic pleiotropy" of Rose and Charlesworth (1981). They found that female *Drosophila* have high fecundity early in life and low fecundity late, or have low fecundity early and high fecundity late. Females do not have high fecundity both early and late. For the sake of an example, imagine that this finding is due to the fact that all females have the same number of eggs. They vary in how they apportion these eggs to different stages of the life cycle. The fixed number of eggs thus serves as a constraint on the distribution of reproductive effort.

Once again, the biologist need not take this result to show that an optimality model is

inappropriate. Rather, the question will be formulated to take account of the constraint: given that all females have the same number of eggs, what is the optimal distribution of eggs to different phases of the life cycle? If two distribution patterns are represented in the population, the optimality modeler will want to explore the possibility that this is a polymorphism created by natural selection.

The example described by Rose and Charlesworth might be termed a developmental constraint. The reason is that if a fruitfly lays lots of eggs early in life, this has consequences for what she will be able to do later. The example from Maynard Smith is less happily subsumed under this label, since leg length and leg strength are established simultaneously, not sequentially. Perhaps it should be called a "mechanical" constraint instead.

Notice that in both these examples, a naive analysis of the problem might suggest that there are four possible combinations of traits, whereas the reality of the situation is that there are just two. For example, we might naively suppose that zebras can have long leg bones or short ones, and that, as a quite separate matter, they can have strong leg bones or weak ones:

		Leg strength	
		strong	weak
Leg length	long	w	x
	short	y	z

The entries in this 2-by-2 table represent the fitnesses of the four combinations of traits; w is the highest value and z the lowest. If selection operated on all four of these variants, the optimal outcome would be the evolution of legs that are long-and-strong. However, given the correlation of leg length and leg strength, there are just two variants, whose fitnesses are x and y . What will evolve is either long-and-weak or short-and-strong, depending on which trade-off is better.

In this type of example, talk of constraints is really a way to describe the variation that natural selection has to act upon (Reeve and Sherman 1993). The question is not whether the fittest of the available phenotypes will evolve, but what the available phenotypes in fact are. If adaptationism is limited to a claim about the power of natural selection to ensure that the fittest of the available phenotypes will evolve, then the existence of constraints of this type is irrelevant.⁵

In the spandrels paper, Gould and Lewontin emphasize the importance of the concept of evolutionary spin-off; a trait can evolve because it is correlated with another trait that is selected, rather than being directly selected itself.⁶ The chin is apparently such a trait, and the architectural idea of a spandrel was used as an emblematic metaphor for this general category. Chins do not evolve independently of jaw structure; it is a misconception to think that chins evolved because they conferred some adaptive advantage. However, if jaw structure evolved under the guidance of natural selection, and chins evolved as spin-off from selection on jaw structure, then it may still be true that natural selection has caused the best available phenotype to evolve. The overarching category of *correlation of characters* subsumes mechanical constraints, developmental constraints, and evolutionary spin-off.

Let us now consider the idea of "phylogenetic constraint." When selection causes a trait to evolve, the trait evolves against a background of other traits that are already present in the population. Gould's (1980) example of the panda's "thumb" illustrates this point: for ancestral pandas to evolve devices for strapping bamboo, these devices had

to be modifications of traits that were already present. The spur of bone in the panda's wrist was a variant that was able to arise against this ancestral background biology; the panda was not going to evolve from scratch an efficient implement for stripping bamboo. Similar remarks apply to the skeletal structure that allows human beings to have upright gait. Phylogeny "constrains" subsequent evolution in the sense that it provides the background of traits, whose modifications constitute the novelties that natural selection gets to act upon (Reeve and Sherman 1993).

I hope it is clear that the recognition of phylogenetic constraints is not at all inconsistent with the claim that the optimal available phenotype evolves. Naive adaptationists may forget about the importance of background biology; however, sophisticated adaptationists are still adaptationists.

In summary, if adaptationism asserts that natural selection ensures that the fittest available phenotype evolves, its relation to the concept of "constraint" is less than straightforward. The view is in conflict with genetic constraints being important and pervasive, but it does not conflict with the existence and importance of mechanical, developmental, or phylogenetic constraints.

Saying Number 4: "Adaptationism is untestable; it involves the uncritical formulation of just-so stories."

It is possible to formulate an adaptationist thesis about *all* phenotypic traits, about *most* of them, or about some particular phenotype found in a particular population. Let us start with the last of these.

The trait I want to consider is sex ratio – the mix of males and females found in a population. R.A. Fisher (1930) analyzed sex ratio by formulating a quantitative optimality problem: what mix of sons and daughters should a parent produce, if the goal is to maximize the number of grandchildren? Fisher showed that with certain assumptions about the population, the sex ratio strategy that will evolve is one in which parents *invest equally* in sons and daughters.⁷ Given that human males have a slightly higher mortality rate than females, Fisher's model predicts that slightly more males than females will be conceived, that slightly more males than females will be born, and that the sex ratio among children will become even at the age when their parents stop taking care of them.

This adaptationist model is an instructive example with which to evaluate the charge that adaptationism is untestable. Fisher's explanation of sex ratio in human beings is testable. The obvious thing to check is whether its quantitative predictions about sex ratio are correct. In addition, Fisher's model rests on certain assumptions (e.g., that there is random mating), which also can be tested.

A further property of sex ratio theory is worth noting. Hamilton (1967) discovered that Fisher's argument is a special case of a more general pattern. If there is random mating, equal investment is the strategy that will evolve. But if there is inbreeding, a female-biased sex ratio will evolve. We can apply this body of theory to numerous species that exhibit different sex ratios, in each case checking whether the patterns of parental investment, mating system, and sex ratio are as the theory predicts. From the point of view of testing an optimality model, the sex ratio found in a single species is, so to speak, a single data point. To properly test a theory, several data points are needed. It is for this reason that a comparative perspective on testing adaptationist hypotheses is extremely important.

One often hears it said that adaptationist explanations are too "easy" to invent. If one fails, it is easy to invent another. This is sometimes true, but it is not always so. What

other explanation can we construct for the slightly male-biased sex ratio in human beings at conception that slowly changes to an even sex ratio later on? And how easy is it to invent a new and unified explanation of the pattern of variation in sex ratio that is found across different species? I'm not saying that no alternative explanation could exist, just that it is not so easy to invent one. The truth of the matter is that *some* adaptationist explanations are *difficult* to test. It is a double exaggeration to say that *all* adaptationist explanations are *impossible* to test.

The charge of untestability is often formulated by saying that if one adaptationist hypothesis turns out to be wrong, another can be invented to take its place. This comment does not assert that specific adaptive explanations are untestable; in fact, the complaint suggests that specific models *can* turn out to be wrong, which is why the need for new models arises. Rather, the criticism is leveled, not at a specific adaptationist explanation, but at an adaptationist claim that is more abstract. The claim that *there exists* an adaptive explanation of a specific trait is hard to prove wrong; such *existence claims* are harder to refute than specific concrete proposals.

It is important to recognize that the difficulty posed by existence claims is not limited to adaptationism. For example, consider the on-going debate about whether the human language faculty is an adaptation to facilitate communication.⁸ An alternative proposal that has been discussed is that the abilities that permit language use evolved for a quite different reason and only subsequently were co-opted to facilitate communication. This is an existence claim; it says that a spin-off explanation exists, but does not provide the details of what the explanation is supposed to be. This type of conjecture is just as hard to test as existence claims that say that a trait was directly selected for some reason we-know-not-what.

Popper's (1959) falsifiability criterion entails that such existence claims are not just *difficult* to refute, but *impossible* to refute, and therefore are not scientific statements at all. Shall we therefore conclude that adaptationism and anti-adaptationism are both unscientific – a pox on both their houses? Not at all – existence claims are testable, though they are not falsifiable in Popper's overly restrictive sense. If an adaptationist model about a specific trait is confirmed by data, then the anti-adaptationist existence claim about that trait is disconfirmed. And symmetrically, if an anti-adaptationist model about a specific trait is confirmed, then the adaptationist existence claim about that trait is disconfirmed. This is the pathway by which the existence claims advanced both by adaptationism and by anti-adaptationism as well can be tested. They do not inhabit a no-man's land beyond scientific scrutiny (Reeve and Sherman 1993).

Adaptationist just-so stories are sometimes easy to make up.

The same is true of anti-adaptationist just-so stories. Adaptationism as a general thesis about all or most phenotypic traits is difficult to test. The same is true of pluralism, which views selection as one of several important causes of trait evolution. Specific adaptationist proposals are sometimes weakly supported by flimsy evidence, but the same can be said of some specific anti-adaptationist proposals. If adaptationism is a thesis about what has happened in nature, one cannot reject that thesis because biologists have not always tested the thesis with perfect rigor.

Saying Number 5: "Populations of organisms are always finite, always experience mutation, and frequently experience migration and assortative mating. Optimality models fail to represent these nonselective factors and therefore are false."

a role in influencing trait evolution. However, the debate about adaptationism does not concern the *existence* of such factors, but their *importance*. An optimality model predicts that a trait will evolve to a certain frequency. A perfectly realistic model, which accurately describes both selective and nonselective forces, also makes a prediction about what will happen. Adaptationism asserts that these predictions will be the same or nearly the same.

Because adaptationism is a relatively monistic position, an adaptationist model will always fit the data less well than a pluralistic model. This is because an optimality model can be regarded as nested within a pluralistic model. Roughly speaking, they are related in the way the following two equations are related:

$$H1: y = ax$$

$$H2: y = bx + cw + dz.$$

In these hypotheses, y is the dependent variable, x , w , and z are independent variables, and a , b , c , and d are adjustable parameters whose values must be estimated from the data. Because $H1$ is nested within $H2$, $H2$ will always fit the available data better than $H1$.⁹

Hypothesis choice in science is not guided exclusively by a concern for fitting the data. Scientists do not always prefer the more complex $H2$ over the simpler $H1$. Simplicity also plays a role in model selection, although the rationale for the weight given simplicity is not completely understood.¹⁰ Typically, scientists will see how well the simpler model $H1$ fits the data; only if goodness-of-fit significantly improves by moving to $H2$ will $H1$ be rejected. A pluralistic model will always fit the data better than a relatively monistic model that is nested within it, but how much of an improvement pluralism provides depends on the data.

Saying Number 6: "Adaptationist thinking is an indispensable research tool. The only way to find out whether an organism is imperfectly adapted is to describe what it would be like if it were perfectly adapted."

I think this last saying is exactly right. Optimality models are important even if they turn out to be false (Reeve and Sherman 1993; Sober 1993; Orzack and Sober 1994). To find out whether natural selection has controlled the evolution of a particular phenotypic trait, one must discover whether the fittest available trait has evolved. To do this, one must have some grasp of what the fittest trait actually was. What is the optimal trade-off of leg strength and leg length? What is the optimal sex ratio in a randomly mating population? These questions are important to adaptationists and to anti-adaptationists alike.¹¹

5. Concluding Comments

The most important point I can make about the ongoing controversy over adaptationism is that adaptationism as a method of doing biology is distinct from adaptationism as a claim about nature. Methodology and ontology need to be separated. Perhaps adaptationists have often ignored questions about constraints and have confused the issue of current utility with the question of historical origin. The spandrels paper is aimed at correcting these mistakes. These negative remarks are quite consistent with the idea that thinking about optimality is a useful – indeed, an indispensable – heuristic for formulating hypotheses that are worthy of test.

It is a quite separate matter what role natural selection has played in the history of life.

pluralistic than some other biologists are inclined to be. Although they claim that natural selection is the most important cause of trait evolution, they maintain that other causes have been unportant as well. A more monistic viewpoint would be that natural selection is not just important – it is the *only* important factor; other, nonselective, processes may safely be ignored. This raises a substantive question about the history of life that must be decided on a trait by trait basis. For example, it is perfectly possible that genetics has gotten in the way of the evolution of some traits (e.g., because of heterozygote superiority) but not others. And perhaps there has been sufficient time for optimal phenotypes to evolve in some contexts, but not in others. And random events may have been an important influence in some populations, but not in others. These issues are not settled by affirming the importance of natural selection in explaining the vertebrate eye; nor are they settled by pointing out how often adaptationist thinking has been sloppy. Just as feathers and bowling balls differ with respect to the forces that importantly influence how they fall when released above the earth's surface, so different traits in different populations may differ with respect to which evolutionary forces significantly influenced their evolution. Even after all reasonable methodological *caveats* are given their due, adaptationism as a claim about nature remains a conjecture with which to reckon.

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Notes

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¹ It is controversial whether there really are laws that govern evolutionary processes. Beatty (1995) has recently argued that there is no such thing. I disagree, and hope to spell out my reasons on another occasion.

² This description of evolutionary theory as a "theory of forces" is drawn from Sober (1984).

³ More precisely, a trait increases in frequency precisely when its fitness (\bar{W}) is greater than \bar{w} . If p is the frequency of a trait in generation i , and p' is its frequency in generation $i+1$, then the "replicator dynamics" I am describing says that $p' = p\bar{W}/\bar{w}$.

⁴ Selection can produce evolution only if the traits under selection are heritable. It makes no sense to talk of selection "alone" producing an evolutionary outcome if this means that it does so without heredity. Rather, the right way to understand the principle I describe in the text is that selection can be expected to lead to the evolution of fitter traits when like phenotype produces like phenotype. Departures from this simple rule of heredity can impede the ability of natural selection to lead fitter phenotypes to evolve, as explained below.

⁵ On the other hand, it must be admitted that some self-described adaptationists often hold that the range of variation available for selection to act upon is quite rich; for example, see Dawkins (1982, p. 32). This thesis about variation sometimes surfaces in debates about adaptationism in a manner that may be illustrated by an example suggested to me by Paul Bloom. Consider two hypotheses about how the human language faculty evolved:

(A) An ancestral human population contained a vast number of language structures; natural selection eliminated all but one of these. Thus, the present language faculty is the fittest of the alternatives that were available.

(B) Due to constraints on the physical form of human beings and their ancestors, there were just two phenotypes represented in the ancestral population: no language faculty at all and the language faculty that human beings now possess. The latter was fitter than the former in the evolution of our species, and natural selection insured that this fitter phenotype was the one that evolved.

Under both hypotheses, natural selection caused the fittest available phenotype to evolve. However, natural selection seems to be “doing more work” in (A) than it does in (B). Adaptationists such as Pinker and Bloom (1990) tend to favor hypotheses that resemble (A), whereas anti-adaptationists such as Chomsky (1988) advance claims that resemble (B).

Does the difference between (A) and (B) represent a disagreement about the “power” of natural selection? Consider the following type of question:

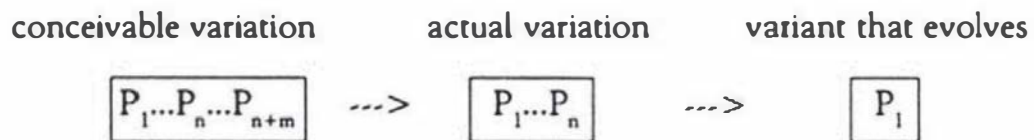
Why does this population now have phenotype P_a rather than phenotype P_c ?

Here P_a is the population’s *actual* present phenotype and P_c is a *conceivable* phenotype that the population now does not possess. Selection will be the answer to more of these questions if (A) is true than it will if (B) is true. And constraints on variation will be the answer to more of these questions if (B) is true than it will if (A) is true (on the assumption that there are finitely many conceivable variants). However, neither of these judgments allows one to compare the power that selection and constraints *actually* exercised. I see no way to answer the following question:

If (A) is true, which was the more important cause of the phenotype that evolved – selection or constraints?

and the same holds for the parallel question about (B).

Consider the following two stage process:



Selection is the process that is responsible for what happens in the second stage of this process. Constraints on variation, on the other hand, determine which of the conceivable variants actually are represented in the ancestral population. Presumably m is a large number; there are many variants that one can conceive of that are not actually represented in ancestral populations. If so, selection effects a reduction from n variants to a single trait, whereas constraints explain why only n of the $n + m$ conceivable variants are actually represented. However, it would be a mistake to compare the “power” of selection and of constraints by comparing the magnitudes of these two reductions. It is impossible to be very precise about how large m is; and a little imagination will make m so big that constraints always turn out to be more “important” than selection. This is a hollow victory for anti-adaptationism, since it turns on no empirical fact. See Wright, Levine, and Sober (1992, pp. 147-151) for further discussion of “limits and selections.”

⁶ In Sober (1984), I discuss the difference between *selection-of* and *selection-for* in this connection.

⁷ For a simple exposition of this idea, see Sober (1993, p. 17).

⁸ Pinker and Bloom (1990) and the accompanying commentaries on their target article provide an indication of current division of opinion on this issue.

⁹ The two models will fit the data equally well in a case of zero dimensionality – when the best estimate of values for the parameters c and d is that $c=d=0$. Note also that $H2$ is a pluralistic model in which the independent variables combine additively. This is not the mathematical form that pluralistic models of evolution will take.

¹⁰ Forster and Sober (1994) argue that H. Akaike's approach to the problem of model selection helps explain why simplicity matters in scientific inference.

¹¹ In this paper I have not discussed the way in which the units of selection problem affects how adaptationism should be formulated. The optimal phenotype for an *organism* need not be the optimal phenotype for a *group* of organisms. This point was already visible in Figure 2b; in this example, running fast is good for the organism but bad for the group. Although it is more or less a matter of definition that the fittest phenotype evolves under pure natural selection, it is a substantive question in cases like the one depicted in Figure 2b what that fittest phenotype will be. For an introduction to the units of selection problem, see Sober (1993); for discussion of how the units of selection problem connects with the issue of adaptationism, see Sober and Wilson (forthcoming).

Figure 1

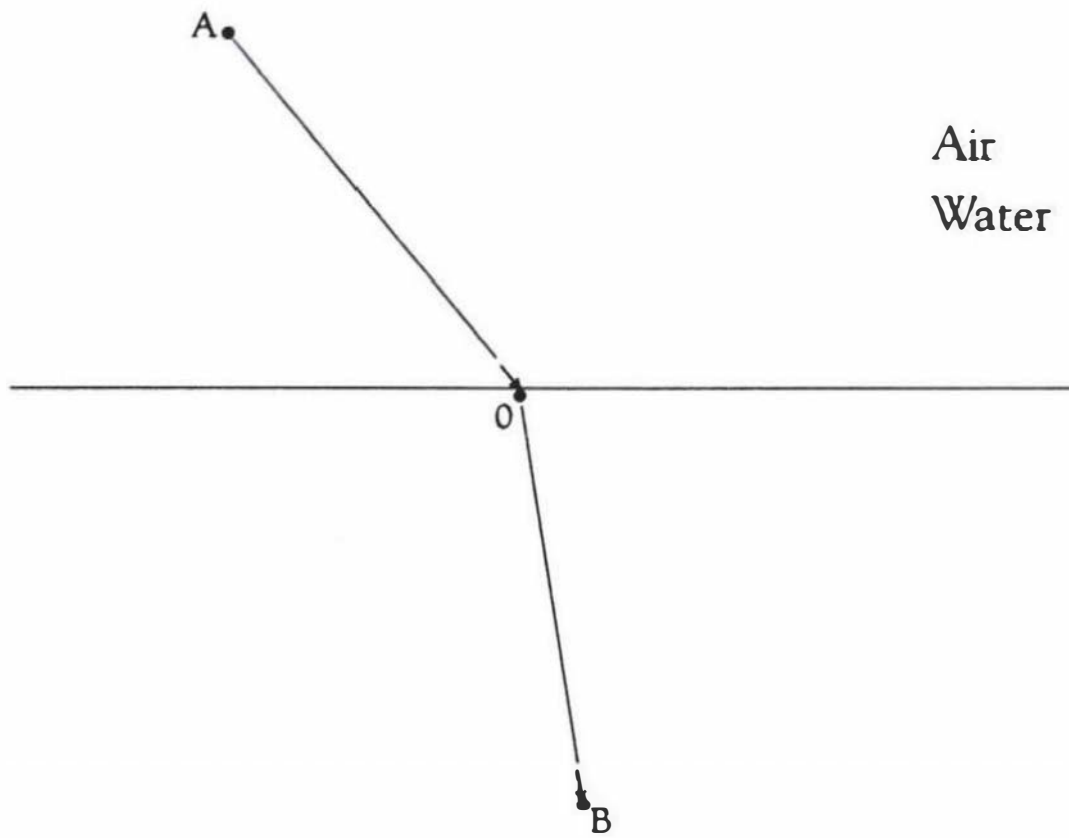


Figure 2

