SIX SAYINGS ABOUT ADAPTATIONISM

ELLIOTT SOBER

Adaptationism is a doctrine that has meant different things to different people. Some define adaptationism so that it is obviously true; others define it so that it is obviously false. I prefer to do neither. In this essay, I want to isolate and discuss a reading of adaptationism that makes it a non-trivial empirical thesis about the history of life. I'll take adaptationism to be the following claim:

Natural selection has been the only important cause of most of the phenotypic traits found in most species.

I won't try to determine whether adaptationism, so defined, is true. That's something that biologists working on different traits in different species will be able to decide only in the long run. Rather, my task will be one of clarification. What does this statement mean, and how is it related to various familiar remarks that biologists have made about adaptationism, *pro* and *con*?

EVOLUTIONARY FORCES AND A NEWTONIAN ANALOGY

Objects released above the surface of the earth accelerate downward at a rate of 32 feet/second^2. Or rather, they do so unless some force other than the earth's gravitational attraction is at work. A similar principle can be stated for the process of natural selection. *In a population subject to natural selection, fitter traits become more common and less fit traits become more rare, unless some other force prevents this from happening.*[1] With sufficient time, this transformation rule means that the fittest of the available pheno-

[1] This description of evolutionary theory as a 'theory of forces' is drawn from Sober 1984. 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

types (if there is just one) will be the only one that remains in the population. This resulting phenotype is said to be *optimal*, not in the sense that it is the best *conceivable* trait, but in the sense that it is the best of the traits *available*.

What might prevent the optimal phenotype from evolving? There are several possibilities (Maynard Smith 1978). First, random events induced by small population size can prevent fitter traits from increasing in frequency. Another possible preventer is the underlying genetics—the pattern by which phenotypes are coded by genotypes. The simplest example of this is the genetic arrangement known as heterozygote superiority; if there are three phenotypes, each coded by the diploid genotype found at a single locus, then the fittest phenotype will not evolve to fixation if it is encoded by the heterozygote genotype. Other more complicated genetic arrangements can lead to the same result. 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 per cent 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 of the available phenotype evolves. However, when other forces intrude, other outcomes are possible.

'Pure' natural selection has predictable results, but the world is never pure. For example, 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 non-selective forces also played an important role. A Newtonian analogy is useful. 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 gravitation is the only important

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.

influence on the trajectory of a falling body or if other forces also play an important role. We know that objects are not the same in this respect; the trajectory of a bowling ball differs markedly from the trajectory of a feather. In physics, we are quite accustomed to this pluralistic view of the relative importance of different forces; adaptationism raises the question of whether pluralism is also the right view to take in evolution. If organisms are almost always like bowling balls, then forces other than natural selection can be ignored if one wishes to explain and predict which of the available phenotypes found in a population evolves. If organisms are often like feathers, this idealization will be a mistake. Perhaps selection was important without its being the *only* important cause.

With this conception of what adaptationism means, I now want to consider several remarks one commonly hears—from biologists, philosophers, cognitive scientists, and others—on both sides of this controversy.

Saying number 1: 'Natural selection is the only natural process that can produce adaptive complexity.'

In his essay 'Universal Darwinism', Richard Dawkins (1983 and Ch. 2 above) updates the 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'—that is, 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's 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 'complex-

ity' and 'order' so 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 non-selective means, it is entirely unclear how non-selective 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 (1979), 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 shouting about, if both sides agree that natural selection is important, indeed indispensable, as an explanatory principle?

Dawkins's 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 Koehl 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 retention and possible modification. 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, 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). However, as we will now see, this is correct for some so-called constraints, but not for others.

I mentioned earlier that 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 programme is committed to the unimportance of such constraints. The supposition 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 does not evolve in isolation from the effect that leg structure has on vulnerability to injury. The optimality modeller 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 adaptationist will want 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 modeller 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 fruit-fly 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 naïve 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 naïvely 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 (see Fig. 5.1). 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 fact that long legs tend to be weak, 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

Leg strength

	Strong	Weak
Long	*w*	*x*
Short	*y*	*z*

Leg length

FIG. 5.1. A 2-by-2 table of fitness.

constraints of this type is irrelevant. 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: 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 ensured 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 in (B). Adaptationists such as Pinker and Bloom (1990) tend to favour 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 *Pa* rather than phenotype *Pc*? Here *Pa* is the population's *actual* present phenotype and *Pc* 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 judgements 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:

Conceivable variation	Actual variation	Variant that evolves
$P_1 \ldots P_n \ldots P_{n+m}$	$P_1 \ldots P_n$	P_1
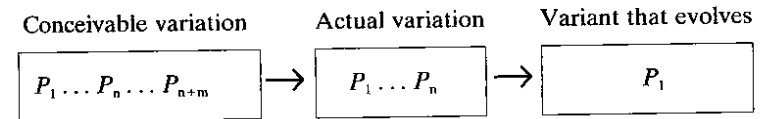
Selection is the process that is responsible for what happens in the second stage of this process. Constraints on variation, on the other hand, determine which of the conceivable variants actually are represented in the ancestral population. Presumably m is a large number; there are many variants that 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 *et al.* 1992: 147–51 for further discussion of 'limits and selections'.

In the 'spandrels' paper, Gould and Lewontin (1979) 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.[2] The chin is apparently such a trait, and the architectural selection idea of a spandrel was used as a 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 of their own. 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

[2] In Sober 1984 I discuss the difference between *selection-of* and *selection-for* in this connection.

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 stripping 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. Naïve 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 does deny that genetic constraints are important and pervasive, but it does not deny 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 do consider is sex ratio—the mix of males and females found in a population. R. A. Fisher (1930) analysed 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.[3] Given that human males have a slightly higher mortality rate than females, Fisher's model predicts that slightly

---

[3] For a simple exposition of this idea, see Sober 1993: 17.

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 can also 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 levelled, 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 ongoing debate

about whether the human language faculty is an adaptation to facilitate communication.[4] 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 (1959) advanced a falsifiability criterion for distinguishing scientific propositions from unscientific ones. This criterion entails that existence claims of the kinds just described 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 plague 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. 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 rigour.

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 non-selective factors and therefore are false.'

It is true that optimality models ignore non-selective factors that frequently or always play a role in influencing trait evolution. However, the debate

---

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

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 non-selective forces, also makes a prediction about what will evolve. 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:

$$H_1: y = ax$$
$$H_2: y = bx + cw + dz$$

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 H_1 is nested within H_2, H_2 will always fit the available data better than H_1.[5]

Hypothesis choice in science is not guided exclusively by a concern for fitting the data. Scientists do not always prefer the more complex H_2 over the simpler H_1. Simplicity also plays a role in model selection, although the rationale for the weight given to simplicity is not completely understood.[6] Typically, scientists will see how well the simpler model H_1 fits the data; only if goodness-of-fit improves *significantly* by moving to H_2 will H_1 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

---

[5] 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 H_2 is a pluralistic model in which the independent variables combine additively. This is not the mathematical form that pluralistic models of evolution must inevitably take.

[6] Forster and Sober (1994) argue that H. Akaike's (1973) approach to the problem of model selection helps explain why simplicity matters in scientific inference.

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.[7]

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. 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. The spandrels paper presents a view about this as well. Gould and Lewontin are more pluralistic than some other biologists are inclined to be. Although they concede that natural selection is the most important cause of trait evolution, they maintain that other causes have been important as well. Adaptationism asserts the more monistic view—point that natural selection is not just important—it is the only important factor; other, non-selective 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 got in the way of the evolution of some traits (e.g. because of heterozygote superiority) but not of 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

[7] In this essay 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. 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 1997.

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.[8]

REFERENCES

Akaike, H. (1973), 'Information Theory and an Extension of the Maximum Likelihood Principle', in B. Petrov and C. Csaki (eds.), *Second International Symposium on Information Theory* (Budapest: Akademiai Kiado), 267–81.

Beatty, J. (1995), 'The Evolutionary Contingency Thesis', in G. Wolters and J. Lennox (eds.), *Concepts, Theories and Rationality in the Biological Sciences*, Pittsburgh–Konstanz Colloquium on the Philosophy of Biology (Pittsburgh: University of Pittsburgh Press), 45–81.

Chomsky, N. (1988), *Language and Problems of Knowledge: The Managua Lectures* (Cambridge, Mass.: MIT Press).

Dawkins, R. (1982), *The Extended Phenotype* (San Francisco: Freeman).

——(1983), 'Universal Darwinism', in D. S. Bendall (ed.), *Evolution from Molecules to Man* (Cambridge: Cambridge Universiy Press), 403–25; reproduced as Ch. 2.

——(1986), *The Blind Watchmaker* (London: Longman).

Fisher, R. A. (1930), *The Genetical Theory of Natural Selection* (New York: Dover; 2nd edn. 1958).

Forster, M., and Sober, E. (1994), 'How to Tell When Simpler, More Unified, or Less *Ad Hoc* Theories Will Provide More Accurate Predictions', *British Journal for the Philosophy of Science*, 45: 1–36.

Gould, S. (1980), *The Panda's Thumb* (New York: Norton).

——and Lewontin, R. (1979), 'The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme', *Proceedings of the Royal Society, London*, B205: 581–98, repr. in E. Sober (ed.), *Conceptual Issues in Evolutionary Biology* (Cambridge, Mass.: MIT Press; 2nd edn. 1994), 73–90.

Hamilton, W. (1967), 'Extraordinary Sex Ratios', *Science*, 156: 477–88.

Kingsolver, J., and Koehl, M. (1985), 'Aerodynamics, Thermoregulation, and the Evolution of Insect Wings—Differential Scaling and Evolutionary Change', *Evolution*, 39: 488–504.

Krebs, J., and Davies, N. (1981), *An Introduction to Behavioral Ecology* (Sunderland, Mass.: Sinauer).

Lewontin, R. (1978), 'Adaptation', *Scientitic American*, 239: 156–69.

[8] My thanks to André Ariew, Paul Bloom, Alain Boyer, and Steven Orzack for useful comments on earlier drafts. I am also grateful to Hudson Reeve and Paul Sherman for calling my attention to the detailed agreement that links Reeve and Sherman 1993 and the ideas summarized here, which are presented in Sober 1993 and Orzack and Sober 1994 in more detail. The present article is excerpted from 'Evolution and Optimality—Feathers, Bowling Balls, and the Thesis of Adaptationism' (*Philosophical Exchange*, 26(1996): 41–57).

Lewontin, R. (1980), 'Adaptation', in *The Encyclopedia Einaudi* (Milan: Einaudi); repr. in E. Sober (ed.), *Conceptual Issues in Evolutionary Biology* (Cambridge, Mass.: MIT Press, 1st edn. 1984), 235–51.

——(1990), 'How Much Did the Brain Have to Change for Speech?', *Behavior and Brain Sciences*, 13: 740–1.

Maynard Smith, J. (1978), 'Optimization Theory in Evolution', *Annual Review of Ecology and Systematics*, 9: 31–56; repr. in E. Sober (ed.), *Conceptual Issues in Evolutionary Biology* (Cambridge, Mass.: MIT Press, 2nd edn. 1994), 91–118.

Orzack, S., and Sober, E. (1994), 'Optimality Models and the Test of Adaptationism', *American Naturalist*, 143: 361–80.

Pinker, S., and Bloom, P. (1990), 'Natural Language and Natural Selection', *Behavior and Brain Sciences*, 13: 707–84.

Popper, K. (1959), *The Logic of Scientific Discovery* (London: Hutchinson).

Reeve, H., and Sherman, P. (1993), 'Adaptation and the Goals of Evolutionary Research', *Quarterly Review of Biology*, 68: 1–32.

Rose, M., and Charlesworth, B. (1981), 'Genetics of Life History in *Drosophila melanogaster*', *Genetics*, 97: 173–96.

Sober, E. (1984), *The Nature of Selection* (Cambridge, Mass.: MIT Press; 2nd edn., Chicago: University of Chicago Press, 1994).

——(1993), *Philosophy of Biology* (Boulder, Colo.: Westview Press; Oxford: Oxford University Press).

——and Wilson, D. (1997), *Unto Others—The Evolution of Altruism* (Cambridge Mass.: Harvard University Press).

Williams, G. C. (1966), *Adaptation and Natural Selection* (Princeton: Princeton University Press).

Wright, E., Levine, A., and Sober, E. (1992), *Reconstructing Marxism: Essays on Explanation and the Theory of History* (London: Verso).

PART II

DEVELOPMENT