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1 Adaptation

Eyes have long fascinated those who study the natural world. Cleanthes – the natural theologian protagonist of Hume's *Dialogues Concerning Natural Religion* – invites his interlocutor to 'consider, anatomize the eye: Survey its structure and contrivance; and tell me, from your own feeling, if the idea of a contriver does not immediately flow in upon you with a force like that of sensation' (1990, 65). Darwin, too, counted the eye among what he called 'organs of extreme perfection'. Placing himself squarely within the tradition that runs from natural theology, through Darwin, to a certain style of modern biology, Maynard Smith writes that 'the main task of any theory of evolution is to explain adaptive complexity, that is, to explain the same set of facts that Paley used as evidence of a creator' (1969, 82). More recently still, Dawkins (1986) is impressed, also, with a force like that of sensation, by how well suited – how well adapted, that is – the eye is to its purpose. Like Paley, he thinks eyes are better pieces of work than watches, although unlike Paley he regards their artificer as blind.

An essay on adaptation could fill volumes. One might begin by asking how adaptation is to be explained. Immediately we would need to answer the prior question of what the proper definition of adaptation is, and we would also have to get clear on the nature of the diverse candidate processes – natural selection, self-organisation, macromutation, development, divine design – sometimes tabled as potential explanations. We might go on to ask in what senses adaptations are purposive, and whether they all share some single ultimate purpose, such as the proliferation of an organism's genes. Once the nature of adaptation is pinned down, we could move on to consider the questions of whether adaptation is ubiquitous or rare, and whether there might be important nonadaptive phenomena in the biological world that an exclusive concern with adaptation might lead us to overlook. In short, a thorough study of adaptation would need to address most of the topics covered in this *Companion* – teleology, the units of selection, development, and others. Here, then, I will restrict myself to brief discussions of four questions. How should we *define* adaptation, how should we *explain* adaptation, how can we *discover* adaptation, and how *important* is adaptation?

1. DEFINING ADAPTATION

In the analytical table of contents of his landmark work *Adaptation and Natural Selection*, George Williams claims that 'evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect should not be called a function unless it is clearly produced by design and not by chance . . . Natural selection is the only acceptable explanation for the genesis and maintenance of adaptation' (1966, vii). I want to take some time in the first two sections of this essay to pick these comments apart.

What, precisely, is the special and onerous concept of adaptation? As a preliminary, we should take Elliott Sober's (1984, 196) advice and distinguish products from processes. Consider an example: marriages produce marriages. This sounds peculiar, until we remember that 'marriage' can refer either to the process of getting hitched or to the blissful union that is the product of that process. Similarly, 'adaptation' can refer either to the process by which organisms become well suited to their environments, or it can refer to the organic traits that are the end results of this process. Unless I stipulate otherwise, I will be talking about adaptation as a product in this essay.

Broadly speaking, there are three quite different styles of definition of the adaptation concept. First, we could give a rough indication of what adaptation means by pointing to some of its instances – things like the eye, or the wing. Such definition by example, certainly when the examples are few, tells us little about how we should apply the concept. At this point, a second style of definition may appear. Adaptation is a concept used in modern biology, yet modern biologists sometimes define the term in an informal way that echoes natural theology's conception of organisms as designed objects. Williams gives just such a definition in the quotation we just saw: 'An effect should not be called a function unless it is clearly produced by design and not by chance'. This distinction between what an object's *effects* are and what its *functions* are makes clear sense when we are talking about tools designed by agents. A screwdriver may be good at levering lids from paint tins, but that is not what the screwdriver is *for* – that is not its function – because the screwdriver was not designed to lift lids from paint tins. Williams's definition expresses his view that adaptations are traits that are *for* something. For Williams, therefore, the question of whether some trait is an adaptation should depend on its design history. But Williams is no creationist: the design history in question is the evolutionary history of the trait.

Williams's comment explains why many biologists draw a distinction between adaptive traits and adaptations. Adaptive traits augment fitness in some way or another – we might also use Mayr's (1986) term and say that they have the property of *adaptedness*. The adaptedness of a trait is not sufficient for the trait to be an adaptation, because the trait, like the screwdriver, may not have the right kind of history.

Richard Dawkins also defines adaptation in terms of good design, and he defines design, in turn, as that which gives only the appearance of intelligence: 'We may say that a living body or organ is well designed if it has attributes that an intelligent and knowledgeable engineer might have built in order to achieve some sensible purpose, such as flying, swimming, seeing, eating, reproducing, or more generally promoting the survival and reproduction of the organism's genes' (1986, 21). For Dawkins, as for Maynard Smith, the way to define adaptation is in terms of what a natural theologian might have counted, mistakenly, as evidence of intelligence.

It is hard to square Williams's claim that adaptation is a special and onerous concept for modern evolutionary biology with all these covert uses of what appear to be natural theological notions in the definition of that concept. If adaptation could be defined only as something that the superstitious would take as evidence for a designer, then the best thing for modern biology to do would be to eliminate the adaptation concept altogether on the grounds that it is part of a natural theological worldview we no longer share. Because

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few, if any, biologists or philosophers could tolerate the elimination of the adaptation concept from biology, a move to a definition in the third, more formal, style is widely preferred.

2. HISTORICAL DEFINITIONS OF ADAPTATION

Formal definitions of adaptation tend to divide into historical and nonhistorical varieties. A formal definition that is endorsed by many philosophers (although not by so many biologists) is Sober's (1984, 208):

> A is an adaptation for task T in population P if and only if A became prevalent in P because there was selection for A, where the selective advantage of A was due to the fact that A helped perform task T.

One of the reasons why a definition like this is attractive is that it promises to tidy up Williams's claim that adaptations are the result of design rather than chance. What is required, if this claim is to be made respectable, is some evolutionary process that can play the role of design. Sober achieves this by defining adaptation as the product of a natural selection process, a process that can be distinguished from the mere chance appearance in a population of the trait in question.

Sober's definition leads to some awkward results, especially if assessed by its success in grounding the notion that adaptations are produced by design. First, a trait can be an adaptation for some task even when the first occurrence of the trait is an entirely fortuitous affair that has nothing to do with selection. This is a consequence of the definition of 'selection for' a property. Suppose a pair of wings arises, fully formed and fully functional, in a population of flightless foxes. These wings help their prodigiously lucky bearer to catch chickens more effectively than other foxes, and as a result the flying fox is far fitter than its fellows. Baby foxes inherit the wings of their parents, and wings soon become prevalent in the population. In this (intentionally absurd) scenario, there is selection for flying in virtue of the fact that wings increase their frequency in the population because they allow flying. Hence wings are adaptations for flying by Sober's definition, even though the metaphors of selection designing, building, or shaping the trait are hard to apply. This is hardly a fatal objection to Sober: modern biology can get by perfectly well

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with an adaptation concept that jars some of our intuitions about when it is appropriate to speak of 'design' or 'shaping'. Even so, we will see that for some biologists, adaptations are understood as traits that have been (in some sense) shaped, built, or modified by selection, not merely traits whose frequency has increased because of selection.

Sober's definition helps us to make some sense of Williams's claim that adaptations are not products of chance, but in doing so it causes problems for Williams's follow-up assertion that selection is the only permissible explanation of adaptation (a claim that Richard Dawkins [1996] also makes). It makes that second claim true, but vacuously so. It is hard to portray Darwin's intellectual breakthrough as the realisation that adaptation is best explained by natural selection, if adaptation is simply defined as a product of a selection process. Fisher (1985, 120) makes the point forcefully: 'Defining the state of adaptation in terms of its contribution to current fitness, rather than origin by natural selection, is essential if natural selection is to be considered an explanation of adaptation.'

Fisher's argument can be resisted. We can keep hold of Sober's definition of adaptation while rephrasing our understanding of Darwin's breakthrough in more particularist terms: Darwin realised that natural selection could explain the organisation of eyes, wings, instinctive behaviours, and many other specific traits. None of these claims is vacuously true, even if the general claim that natural selection is the only explanation of adaptation is. We might also consider replacing Williams's general assertion with the rephrased claim that selection is the only permissible explanation of adaptedness, where adaptedness is defined nonhistorically in terms of a contribution to fitness. Whether this revised claim is true would require further assessment, but it seems clear that it is not trivially true.

There are other problems that have driven some biologists (e.g., Reeve and Sherman, 1993) to prefer nonhistorical definitions. Consider a trait that becomes prevalent in a population by chance, but that is subsequently maintained at a high frequency in the population because of its superior fitness compared with alternatives. Sober's definition denies that the trait is an adaptation, for selection has not made it prevalent, even though maintaining selection does subsequently explain why it remains prevalent. Conversely, Sober might have to accord the status of adaptation to traits that have spread through a population in virtue of some effect, but that have not had that effect for several generations. We might have to say that the human appendix is an adaptation for digestion. Yet these kinds of traits are more usually thought of as vestiges, not adaptations.

These problems are not fatal to Sober either – the obvious solution is to keep a historical definition, but one that looks only to quite recent selection history, including selection that maintains the frequency of a trait in virtue of one of its effects. Sober himself considers some analogous moves to weaken the original definition while retaining its historical element (1984, 198). Although a revised definition of this form upholds a conceptual distinction between being an adaptation for E and promoting fitness by E-ing, very few actual traits, so long as they are inherited, will fall into the latter category without also falling into the former. The revised historical definition helps to ground a function/effect distinction that non-historical accounts will have trouble maintaining, but the satisfaction of this desideratum may seem like a philosophical indulgence when viewed from the perspective of biological inquiry, especially once we see how rarely the conceptual distinction will make any practical difference. The biologists Endler and McClellan prefer to use adaptation to indicate current contribution to fitness on just these grounds:

> It is important to distinguish between traits that were always selected for one function ('adaptations') from those which were originally selected for another function and by chance can be used in a new way ('exaptations' for the new function). We use adaptation in both senses because as soon as a new function for a trait occurs, natural selection will affect that trait in a new way and change the allele frequencies that generate that trait. (1988, 409)

This comment is likely to mislead, because the historical definition of adaptation preferred by many philosophers is not the same as that of Gould and Vrba (1982), whose distinction between adaptation and exaptation Endler and McClellan are referring to here. Gould and Vrba's definition of adaptation, like Williams's, appeals not just to selection for some property, but to a stronger notion of shaping, or structural modification, consonant with the everyday concept of design. An adaptation, for Gould and Vrba, 'was built by natural selection for the function it now performs' (53). 'Exaptations', on the other hand, have not been shaped by selection for the tasks they now perform. A definition of adaptation in terms of recent (maintaining) selection will make almost all exaptations for some function adaptations for that same function. Some philosophers have questioned the coherence of the adaptation/exaptation distinction (e.g., Dennett 1995, 281); however, providing we can make sense of the contrast between being shaped for a function and being selected for a function, and providing our definition of adaptation appeals to shaping, this scepticism is premature.

3. NONHISTORICAL DEFINITIONS OF ADAPTATION

Reeve and Sherman have articulated the most thorough defence of a nonhistorical definition of adaptation:

> An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment. (1993, 9)

Why insist that an adaptation must be the fittest of a set of variants? Which variants go into that set? To answer these questions, we need to look at the primary goal of Reeve and Sherman's definition, which is to develop a concept suitable for answering questions about what they call 'phenotype existence'. They distinguish these kinds of questions from those about 'evolutionary history'. Students of phenotype existence ask 'why certain traits predominate over conceivable others in nature, irrespective of the precise historical pathways leading to their predominance, and then infer evolutionary causation based on current utility'. Practitioners of evolutionary history, on the other hand, 'seek to infer the origins and phylogenetic trajectories of phenotypic attributes, and how their current utility relates to the presumed functions in their bearers' ancestors' (2).

There are two slightly different rationales for appealing to a range of conceivable variants in defining adaptation. The first has to do with establishing the selective history of the trait (i.e., 'evolutionary causation'). The second has to do with establishing the trait's causal contribution to survival and reproduction (i.e., its 'current utility'). Beginning with the first rationale, Reeve and Sherman want the claim that a trait is an adaptation to be evidence for, rather than (as it is for Sober) synonymous with, any further claim about evolutionary causation. If a trait is fitter than all the hypothetical alternative traits we are considering, then the chances are it also outcompeted the actual alternative traits in the population. It is therefore likely that selection explains its presence. That is why we should exercise restraint in the hypothetical alternatives we include in the considered set – they need not include all and only actual competitors, but they should reflect likely competitors: 'A suitable choice requires only that the set contains phenotypes that might plausibly arise' (Reeve and Sherman 1993, 10). Reeve and Sherman's insistence that a trait be recognised as an adaptation only if it is the *fittest* of the phenotype set is not obligatory given the goals of this kind of evolutionary research: a trait can make a significant contribution to fitness – including the greatest contribution among actual variants present and past – even when some other plausible trait might have been better still.

The second reason for appealing to a range of conceivable variants in defining adaptation has considerable metaphysical interest, especially as a case study in the problems of causation. On the nonhistorical approach, to ask whether human eyes are adaptations is to ask whether they make a causal contribution to fitness, and if so, what that contribution is. It might seem that there is no need to specify a set of alternative possible eyes in order to answer this question; we need only consider the question 'What would we be like without eyes?' The problem is that this question has many plausible answers. We might say that vision is so important that if we had no eyes, we would have some other kind of sensory apparatus instead. If we say this, we will say that eyes are not adaptations for providing sensory information, for we would do just as well in that respect without eyes. Alternatively, we might say that if we had no eyes, we would be dead, as a result of infection in our empty eye sockets. If we say this, we will say that eyes are adaptations for preventing infection reaching the eye sockets. Both answers seem silly, but such silliness seems to result from asking, without constraint, 'What would we be like without eyes?'

These problems about how to say what the causal contribution of some part is to a whole are not specific to biology. Consider my laser printer. Our inclination is to say that the ink cartridge contributes to the workings of the whole by dispensing ink. But what allows us to say this? After all, it is not true that the only thing that would be different if my printer had no cartridge is that it would dispense no ink. Paper would not pass through the printer, either. If we understand counterfactual conditionals in the manner of David Lewis (1973a), then counterfactuals are made true by states of affairs at the nearest 'possible worlds' where the counterfactuals' antecedents are true. Roughly speaking, a possible world is a way things might have been. The statement 'Were Beckham to have got the penalty, England would have won Euro 2004' is true just in case those nearest worlds (i.e., the worlds most similar to way things actually are) where Beckham gets the penalty are also worlds where England wins Euro 2004. Now the nearest world at which my printer has no cartridge is, presumably, one where I have removed the cartridge to shake it, or some such. At this world, the printer will not function at all. Are we to say, then, that the function of the ink cartridge is to enable paper to pass through the printer?

Comparing actual eyes with a clearly specified set of alternative traits seems to be a good way of circumventing these problems for causal analysis. One might wonder, though, exactly what the role is of specifying alternatives in the determination of a trait's causal contribution. This method is somewhat at odds with contemporary counterfactual views of causation (e.g., Lewis 1973b). According to these theories, causation is indeed bound up with ways the world might have been, but we determine, say, the causal impact of a brick's flight through a window not by specifying alternative flight paths, but by specifying which actual event, or which actual fact, we are interested in understanding causally, and asking what would have been the case had that event not occurred, or had that fact not obtained. On this view, alternative flight paths follow from a specification of the fact or event of interest to us; the specification of alternatives is not a preliminary to causal analysis of some fact or event.

Generalising this method to the analysis of systems, the first step to determining a causal contribution of a part to a system is not the specification of alternative possibilities for what the part might have been like; rather, it is to specify what aspect of the part we are interested in. The effect of this is to move us away from asking blunt questions about the causal contributions of parts (organs, for example, in biology), and towards asking questions about the contributions of traits understood as finely specified facts about systemic organisation. In the case of the printer, we can ask, for example, what the effect of the cartridge's having ink at such and such density might be. Immediately we dismiss the world where the printer has no ink cartridge as irrelevant to answering our causal question; the nearest world where the ink density is different is not one where there is no ink cartridge at all. So one of the roles for specifying a range of alternative traits is to draw out, through comparison, the aspect of the trait under consideration that we are interested in. Note that we need not suppose that any actual printer cartridge has existed with ink at a different density for an appeal to such counterfactual circumstances to have legitimacy in causal reasoning. That is why, to the extent that Reeve and Sherman's phenotype set is supposed to focus attention on specific aspects of actual traits by positing ways the world might have been if the trait had been different in those respects, they are quite right not to insist that membership of the set be restricted to actual traits.

4. EXPLAINING ADAPTATION

Does natural selection explain adaptation? We have already seen how this question runs into the definitional problems of the earlier sections. If adaptation should be defined as a product of selection, then the claim that selection explains adaptation is secured by definition alone. Let us ask, instead, whether selection explains adaptedness – understood as contribution to fitness – while withholding judgement on the question of whether we should opt for a nonhistorical definition of adaptation itself.

Our first job is to distinguish the question of whether selection explains the spread of traits from the question of whether selection explains the origin of traits. In the first section I gave the example of a wing that arises fully formed through macromutation, and that then spreads through a population. In this scenario, selection explains why the trait increases its frequency, and it also explains the increase in adaptedness of the population, but it does not explain the appearance of the first wing token. If selection never explains the origin of trait types, then Darwin's innovation is not as great as it seems. People like Paley were puzzled at how such things as eyes could come to exist at all; the response that once one eye exists, eyes