

# 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

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

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

will tend to become prevalent is not enough to satisfy the demand for an explanation of the first appearance of such an extraordinary thing. And note that if one replies that eyes are really rather likely to arise through macromutation after all, or that one should simply look to chance to explain the first instance of the trait, then there is a sense in which one has not truly offered a selective explanation for the existence of eyes; rather, one has appealed to something like a general law of generation of organic form, or to blind chance.

Selection can explain the origin of novel trait types by causing tokens of other traits to spread (Endler 1986). Selection is creative. Consider the following case, borrowed from Neander (1995). Imagine that there are three 'genetic plans', P1, P2, and P3. P3 gives us a fully functional eye. P2 yields a slightly inferior eye, and P1 is even worse. A population exists in which all members have P1, bar a few with P2. As P2 increases in frequency in the population, then the chances of a variant arising with P3 may increase too. In case this is not clear, think of an example; if I can persuade more people to buy lottery tickets, then I increase the chances that someone will win. Similarly, if the number of genetic loci where a favourable mutation might occur increases as a result of selection, then selection can explain the first appearance of a favourable mutation of that type.

Sticking with the lottery example, although increasing the number of tickets explains why someone wins, it does not explain why Emma wins, rather than Nicole, who has also bought a ticket; increasing the number of tickets makes Emma no more likely to win than Nicole. Similarly if selection, by increasing the number of organisms with P2, explains why P3 eventually arises, it does not follow from this that selection explains why Sam first acquires the P3 mutation, rather than Suzy, who is also descended from a P2 individual. The claim that selection is creative does not straightforwardly resolve the related question (addressed by Sober 1995 and Neander 1995, among others) of whether selection explains why individual organisms have the traits they do.

Now that we have seen how selection explains adaptedness, we can also see that selection does not explain adaptedness alone (Lewens 2004). There are a number of assumptions hidden in our earlier scenario about the emergence of eyes. If increasing the number of P2 variants is to increase the chance of a P3 variant arising, it must be the case that the P3 plan is more likely to arise

from the P2 plan than from the P1 plan, for suppose that while P2 is fitter than P1, and P3 is fitter than P2, P3 is mutationally closer to P1 than to P2. If that is the case, then selection will make the emergence of the P3 plan less likely as it increases the frequency of the P2 plan. What is required for selection to have its cumulative character, whereby it leads to progressive adaptation, is for fitness orderings of phenotypes to map onto the mutational 'distances' between the plans that code for those phenotypes. That, in turn, is a requirement on the organisation of individual organisms; indeed, the familiar point that selection can cause populations to get stuck on the 'local optima' of fitness landscapes is another way of making the point that organisms may be constructed in such a way that mutations for highly functional versions of some organ may sometimes be more likely to arise from forms of low function than from forms of intermediate function.

Selection does not explain adaptedness alone, because selection has the character that makes it cumulative only when it acts on systems with the right kind of organisation. This is not the place to say what those organisational conditions might be, but it is the place to point out that this makes organic organisation an element of the explanation of adaptedness itself (Lewens 2004, Walsh 2000). We also have reason to believe that 'drift' or 'sampling error', whereby populations (especially small populations) change in ways that do not reflect the fitnesses of the traits in the population, can help to explain adaptedness. Drift can prevent populations from getting stuck on local optima, and in that sense the existence of sampling error, whereby lower-fitness forms sometimes replace higher-fitness forms, will occasionally increase the chances that the population will arrive at an adaptive peak that is higher still. So drift, also, can explain adaptedness.

## 5. DISCOVERING ADAPTATION

Let us move now from the metaphysics of adaptation to its epistemology. How can we determine whether a trait is an adaptation? One popular approach to this question once again looks back to natural theology for inspiration (Lauder 1996 gives a useful survey of these moves). It used to be thought that the good design of an organism indicated intelligent design; if good design is instead best

explained by natural selection, then good design is evidence for the action not of the hand of the divine artificer, but the hand of selection. Thus Pinker and Bloom (1990, 707) write that 'evolutionary theory offers clear criteria for when a trait should be attributed to natural selection: complex design for some function, and the absence of alternative processes capable of explaining such complexity'.

Is this a good inference? Partly it depends, once again, on the strength we read into the claim that a trait should be 'attributed to natural selection'. We have already seen that if a trait promotes fitness in some population through effect E, it is highly likely that there has been selection for E. This requires only that there has been some heritable variation in past generations with respect to the performance of E. Yet some intend by adaptation not merely 'trait that has been selected for its function' but the far stronger 'trait that has been built for its function'. Hence Gould and Lewontin's worry that the usefulness of a trait in some respect does not entail, nor even make probable, the claim that the trait is an adaptation for that effect: 'male tyrannosaurs may have used their diminutive front legs to titillate female partners, but this will not explain *why* they got so small' (1979, 581).

We can also explain why Lewontin (1984) is concerned about the potentially misleading label 'adaptation'. If we stress parallels between natural selection and natural theology we are likely to think of selection as akin to a 'Blind Watchmaker' – selection as a craftsman shapes organic form to meet environmental problems. But adaptedness is not always produced by selection acting in this 'shaping' mode. One alternative is that members of a population slowly migrate until they find a habitat in which some preexisting, unchanged, trait enhances fitness. This is a natural selection explanation of sorts, for the relational trait of 'being in a better habitat' increases its frequency as the members of this population change their environments. But it is nonetheless misleading to say that the fact of adaptedness indicates selective design in this scenario, and we would be wrong to infer selective shaping, although not selection for, from the functionality of the trait.

There is a second, and more contentious, role for appeals to good engineering design in establishing the existence of adaptation. In the first mode, we know that the trait promotes fitness, and we infer

that selection explains this state of affairs. In the second mode, we infer from the structure of the trait both a likely fitness contribution and selection for that contribution. This is the way that Dennett characterises the inference from the fossil remains of *Archaeopteryx* to the joint claims that *Archaeopteryx* was able to fly, and that its wings were selected for flight: 'An analysis of the claw curvature, supplemented by aerodynamic analysis of wing-structure, makes it quite plain that the creature was well-designed for flight' (1995, 233).

It is at this point that the objection that adaptationist hypotheses are 'just-so stories' (Gould and Lewontin 1979) is most likely to rear its head. The problem of just-so stories is a problem of underdetermination – it is simply too easy to 'make evolutionary sense' of a trait by showing how it might have contributed to fitness. Consider the crest of the *Corythosaurus casuaris*, an example beautifully discussed by Turner (2000). *Corythosaurus* was a 'duckbilled dinosaur' (a hadrosaur), whose fossil remains suggest that its skull bore a curious crest, shaped like a Corinthian soldier's helmet. These crests are hollow, and air inhaled through the nostrils would have passed through the cavities of the crest on the way to the lungs. Was the crest an adaptation? If so, for what? Turner lists a variety of responses that have been tabled at one time or another for the functions of hadrosaur crests: they were weapons; they were anchors for a short trunk; they housed an olfactory system that detected predators. If we focus only on data that relate to the rough structure of the hadrosaur crest, then it seems there are very many design hypotheses that will make sense of the structure. Some will be ruled out – the crest could not have been a snorkel, for there are no holes in the crest that would permit air to be drawn in to the lungs. But many others remain, including the delightful hypothesis that *Corythosaurus*'s crest was more SCUBA than snorkel – a short-term air tank that would have enabled the dinosaur to forage underwater.

It is not only adaptationist hypotheses that face the problem of underdetermination. Maybe hadrosaur crests are not adaptations at all – perhaps a cranial crest is a side effect of selection working on some other aspect of hadrosaur anatomy, with no special function of its own. If we are to assert this we need evidence; otherwise this is a just-so story, too, albeit not an adaptationist one. Nonetheless, the historical nature of some biological hypotheses does present them, as a class, with especially acute problems of underdetermination

compared with those of nonhistorical sciences. If we have two incompatible hypotheses about hadrosaur crests, we should try hard to find some data that might discriminate between them. The problem for biology is that sometimes we can say what data we need, but these data are inaccessible. Are hadrosaur crests air tanks, predator detectors, or something else? We could tell quite easily if we could observe hadrosaurs in action, but that avenue is (and always has been) closed off to us.

For the remainder of this section I will follow Turner in discussing the discovery of adaptation in the more general context of *inference to the best explanation*. Within science and without, we often infer that a proposition is true on the grounds that if it were true, it would be the best explanation of our data (Lipton 2004). Such inferences feature throughout the *Origin of Species*, for example. Time and again, Darwin says that his theory should be accepted because it offers a better explanation of diverse sets of facts than do its competitors.

To support inference to the best explanation is not to say merely that once we have a hypothesis that would make our data probable, we should believe that hypothesis. This would entitle us, for example, to infer any combination of past ecological circumstances, no matter how outlandish, just so long as they make likely the sparse structural data that we have to hand relating to fossil remains. For an explanation to be good, hence for it to command our assent, it must meet further constraints, and we can use these further constraints to illuminate some of the ways we might discriminate between alternative adaptive hypotheses, including hypotheses about *Corythosaurus's* crest.

If an explanatory hypothesis makes the data very probable, we say that the hypothesis has high *likelihood*. Immediately, it will be clear that likelihood does not handle underdetermination problems well. If several incompatible hypotheses all entail the data, then they all have equal likelihoods, so likelihood cannot be used to choose among them. And likelihood certainly is not the only thing we look for in a good explanation (although it is important). Suppose our datum is the fact that Sam has won the National Lottery. The hypothesis that Sam entered the lottery fair and square makes this datum exceptionally improbable. The hypothesis that Sam has a brother who rigged the machines makes our datum far more probable. But we do

not assume that every lottery winner is a cheat, even though such hypotheses have far greater likelihoods than the hypotheses that these individuals are legitimate winners. Is there evidence that Sam has a brother? Is there any reason to think his brother has control over the lottery machine? Without further evidence in favour of these assumptions the fact that they constitute an explanatory hypothesis with a high likelihood does not count strongly in favour of the truth of that hypothesis. Similarly, unless we have evidence in favour of the assumptions laid out in some selection hypothesis, the high likelihood of that hypothesis does not count strongly in its favour. The first lesson, then, is that as well as offering adaptive hypotheses that 'make evolutionary sense' of the traits we are interested in, we need to test the assumptions of those hypotheses directly before we put faith in them. Is there any reason to think that hadrosaurs foraged in water, so SCUBA apparatus would have been useful to them? Perhaps the crest is a musical instrument or resonator (a hypothesis much favoured today), but is there reason to think that hadrosaur hearing was good enough for the noises the crest produced to have been audible? Did hadrosaurs live in groups, in which auditory signals were therefore valuable? The answers we give to these questions can help to rule some hypotheses in, and others out.

A second way to bolster our explanatory inferences is to see whether they conform to any general pattern. Suppose we have observed lottery fixing in many cases that resemble Sam's own victory. This counts as further evidence in favour of the claim that Sam's victory was also fixed. Similarly, we can bolster selective hypotheses by looking to see whether the hypothesis of adaptation in question conforms to any general pattern. This is where the so-called comparative method can be powerful. Consider Darwin's example of the bald head of the vulture. An engineering analysis of what a bald head might be good for, coupled with knowledge of the feeding habits of the vulture, could lead us to the hypothesis that the bald head is an adaptation 'for wallowing in putridity' (1964, 197). This, after all, makes evolutionary sense of the trait's appearance. Darwin points out, however, that 'we should be very cautious in drawing any such inference, when we see that the skin on the head of the clean-feeding male turkey is likewise naked' (*ibid.*).

Suppose we conclude, on the basis of the fact that male turkeys have bald heads, that some common ancestor of turkeys and vultures

had a bald head, and that both turkeys and vultures have inherited this trait. That would undermine the claim that the bald head of the vulture has been shaped by selection to enable it to wallow in putridity, providing we think the common ancestor was clean-feeding as the turkey is. But it is consistent with this scenario that the bald head of the vulture contributes to fitness by enabling the vulture to wallow in putridity, and even that there has been maintaining selection for this effect in the recent past that explains the continued presence of the vulture's bald head. So appeals of this kind to the traits of related species in the refutation of adaptation claims makes best sense if one understands adaptation neither in the manner of Reeve and Sherman, nor in the manner of Sober, but as Gould and Vrba understand it – as a trait shaped by selection for its function.

For a third way to strengthen our adaptive inferences, let us return to the lottery case. Suppose we think that Sam cheated in winning the lottery. This claim will lead us to make certain predictions about what else we should observe. One prediction that issues from our hypothesis might be that someone Sam knows will have been in the London area (where the lottery machines are located) on the weekend when the lottery was held. If this prediction turns out to be right, then it provides only the weakest evidence in favour of our hypothesis. On the other hand, we might make a more detailed prediction of the same type: a member of Sam's family will have been lurking in the television studio where the machines are kept at the precise time of the lottery. If CCTV evidence shows this prediction to be true, then we will be far more confident of our hypothesis. In general, we should be more confident of an explanatory hypothesis if its fine-grained predictions turn out true than if its more hand-waving predictions turn out true. Here, then, is a final way, championed in a series of papers by Orzack and Sober (e.g., Orzack and Sober 1994), for us to increase our confidence in the truth of plausible adaptive explanations. We should demand that our hypotheses yield rigorously quantified predictions. Such predictions might include detailed engineering specifications of what structure some trait ought to have, on the assumption that it has a certain function. This, roughly speaking, is Rudwick's (1964) *Paradigm Method* for determining the function of fossils. But Orzack and Sober point out that we can also make quantitative predictions at the level of the population, by specifying the exact frequency of

trait distributions we should expect to find under some functional hypothesis.

## 6. ADAPTATION AND ADAPTATIONISM

Although I have concentrated for most of this essay on adaptation, I want to close with some words about *adaptationism*. The problems we have looked at so far concern what adaptations are, how we should explain their appearance, and how we can tell when we have found one. The varieties of adaptationism all assert, in one way or another, that adaptation is of special importance for biology. Needless to say, that is an ambiguous claim, and various writers have made efforts to distinguish the varieties of adaptationism, producing estimates from two forms through to seven (e.g., Godfrey-Smith 2001, Lewens 2002, Lewens forthcoming).

It will serve our purposes well enough here to distinguish four types of adaptationism:

*Empirical adaptationism* – most traits are adaptations.

Nature is, in some sense, ‘well designed’.

*Methodological adaptationism* – regardless of the actual level of design quality in nature, or the prevalence of adaptations, the best way to investigate nature is to assume that all traits are adaptations.

*Explanatory adaptationism* – the proper business, or the most important or interesting business, of evolutionary biology is the explanation of adaptation.

*Epistemological adaptationism* – biologists have methods that are good enough to establish fairly decisively the truth and falsehood of most hypotheses about adaptation.

I include the fourth in my list of forms of adaptationism only for historical reasons. One of the favourite criticisms of antiadaptationists has been that hypotheses of adaptation are frequently ‘just-so stories’. We saw in the last section how evolutionary historical hypotheses of all kinds – not just the hypotheses about adaptation – can be subject to underdetermination problems, and we looked at ways to enrich our inferential practices when trying to overcome these problems. Even so, antiadaptationists have historically been

sceptical of the methods by which we test hypotheses of adaptation; conversely, a strand of adaptationism has incorporated a greater optimism about such methods. I now set this fourth form of adaptationism aside.

Let me say a little about the other three kinds of adaptationism, beginning with empirical adaptationism. I phrased this as the view that nature is well designed. But what does that mean? There are several options for how to explain this. At the strong end of the spectrum we might take adaptationism to be the view that all traits are the best ones possible. Even here we run into problems (what is the meaning of 'possible'?), but we are likely to dismiss this version of the hypothesis as false, even obviously so. After all, much of the evidence against intelligent design uses the imperfection of organic traits for their apparent purposes as evidence. At the weak end of the spectrum is the view that natural selection has been involved in some way in the history of most traits. This threatens to turn out trivially true. An effort to give an interesting reading to the hypothesis of adaptationism comes from Sober and Orzack: 'Natural selection has been the only important cause of most of the phenotypic traits found in most species' (Sober 1998, 72). What this means is that the fittest available phenotypes are always the only ones present in populations. Take a population of moths, in which some are well camouflaged, others are poorly camouflaged, and none has (or has ever had) chemical secretions that kill birds instantly. If the poorly camouflaged moths end up the only ones in the population, then this result counts against adaptationism, for a better available variant did not reach fixation. If moths with deadly chemicals fail to reach fixation, then this does not count against adaptationism, for such moths were never available to be selected from.

On Orzack and Sober's view, the adaptationist hypothesis could be true even if the range of available variation for selection to act on turns out to be very highly constrained. Indeed, adaptationism would be true at a possible world where the laws of nature dictate that only two kinds of entity exist, both make copies of themselves, and the type that is more fecund replaces the less fecund type. Yet there may be nothing much like good design at this world – no 'organs of extreme perfection'. This makes clear the difficulty of finding a reading of the adaptationist hypothesis that satisfies our intuition that if adaptationism is true, then natural selection is

a powerful force. Certainly in the dull world I just described selection seems to have very little power.

Adaptationism is sometimes better understood as a heuristic rather than an empirical hypothesis. It is a recommendation for how to go about investigating nature in a fruitful manner. Once again, we could catalogue many variant forms of methodological adaptationism ranging from the boringly sensible advice that sometimes it is useful to test hypotheses of the form 'X is an adaptation for E', through to the implausible insistence that nothing that is of value in biology can be discovered unless one tests hypothesis of the form 'X is an adaptation for E'. What is important to note is that versions of methodological adaptationism can be useful even if one thinks that adaptation is not ubiquitous. The adaptationist heuristic is useful when the failure to establish an adaptationist hypothesis suggests to us that selection is not responsible for the aspect of organic form we are investigating.

Explanatory adaptationism tells us that, in some sense or another, the proper business of evolutionary biology is the study of adaptations (for this reason I have elsewhere called it 'Disciplinary Adaptationism' [Lewens forthcoming], but for the sake of clarity I will stick with Godfrey-Smith's terms here). John Maynard Smith is an adaptationist of this kind, as is Richard Dawkins, who writes that 'large quantities of evolutionary change may be non-adaptive, in which case these alternative theories may well be important in parts of evolution, but only in the boring parts' (Dawkins 1986, 303).

Sterelny and Griffiths (1999, 228) worry that there may be some kind of vacuity in explanatory adaptationism. The problem stems, once again, from the widely accepted definition of adaptation as 'trait selected for some function'. If explanatory adaptationism includes the claim that adaptation is always explained by selection, then this aspect of the position is, indeed, trivial under this definition. But this does not make the general claim that biologists ought to busy themselves with adaptations vacuous. The standard definition of adaptation leaves open a variety of questions that one might try to answer, none of which is trivial, and not all of which are about adaptation. Which are the adaptations? Which traits are adaptations for what? Which traits are functionless? Which organisms are descended from which others? An exhortation to focus on questions of the first two types is not vacuous.

The fact that evolutionary biology contains questions that are not about adaptation saves explanatory adaptationism from vacuity, but this only generates new problems for the position. How could we argue against someone who says that an evolutionary biologist's proper business is to determine genealogical relationships among species, regardless of which traits might be adaptations for what? One might reply by saying that explaining how selection shapes traits for their functions is important because it is necessary in the struggle against creationism. These 'well-designed' traits are just the ones that, absent a good selection explanation, will be used as evidence by intelligent design theorists. But first, this would only establish adaptation as the most important part of biology if we agreed that intelligent design was so threatening that its defeat should be the discipline's primary goal. And even if we were to inflate intelligent design in this way, it still would not undermine the importance of tracing lines of descent between species. This project, too, is centrally important in undermining creationist arguments.

We arrive back at the beginning, then, with natural theology. Explanatory adaptationism is merely a statement of explanatory interests, interests that we should not feel compelled to share, but whose salience is derived from Anglo-American biology's roots in natural theology. This conclusion is ironic: far from expressing enmity between modern biology and natural theology, explanatory adaptationism is testimony to the fellowship between the two traditions.