Pruning the Tree of Life

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ABSTRACT

Some (eg. Elliott Sober) argue that natural selection does not explain the genotypic
and phenotypic properties of individuals. On this view, natural selection explains
the adaptedness of individuals, not by explaining why the individuals that exist
have the adaptations they do, but rather by explaining why the individuals that
exist are the ones with those adaptations. This paper argues that this 'Negative'
view of natural selection ignores the fact that natural selection is a cumulative
selection process. So understood, it explains how the genetic sequences that
individuals inherit and that are responsible for their complex (and co-adapted)
adaptations first arose in the gene-pool.

> How have all those exquisite adaptations of one part of the organisa-
> tion to another part, and to the conditions of life, and of one distinct
> organic being to another being, been perfected? . . . All these results . . .
> follow inevitably from the struggle for life.
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> Darwin, *Origin of Species*, 1859, Ch. III

1 Introduction

Darwin showed that natural selection can explain how all those 'exquisite
adaptations' of plants and animals came about, or so you might have
thought. But this is a misunderstanding of contemporary neo-Darwinian
evolutionary theory, according to some, and it isn't the Creationists I have
in mind. Most notably, Robert Cummins [1975], Elliott Sober ([1984],
Ch. 5), and Fred Dretske [1990] have argued that natural selection can't
explain why you and I have eyes and ears, why a rooster crows, or why
spiders spin their webs.

On first hearing this view, some think it sounds crazy, but it can be
glossed to seem like just good plain common sense, or basic biology at
least. Here's the gloss. The view is that natural selection is not a positive
force that creates adaptations because natural selection has to be

distinguished from mutation and inheritance, and it is these that explain our eyes and ears, the rooster's crow and the spider's web. On this view, random mutations create genetic plans, and natural selection chooses between them—not by creating the good ones, just by destroying the bad ones. Usually, having put it like this, the view that at first seemed crazy seems almost banal instead: if that's what they mean, you might think, they are right, obviously. None the less, I am going to argue that the initial reaction is closer to the mark. The view isn't crazy, but it is wrong.

The plan is simple. I begin by clarifying the controversy (in Section 2). Much of the real work is done here, for finding our way through this debate requires that we see how certain distinct explanatory issues are related. Then I outline the arguments against the claim that natural selection explains our adaptations (in Section 3), starting with some that crop up casually but frequently in discussions on the topic, and then focusing on Sober's, for his is by far the most developed. Finally, I give my reply (in Section 4).

I agree with Sober that there is something 'irreducibly population level' about selectional explanations. He is right that natural selection does not explain changes in populations by aggregating explanations of changes to individuals. But he is mistaken when he denies that natural selection cannot explain the properties of individuals. It can, I argue, by explaining changes in populations. I also argue that Cummins, Sober, and Dretske are, in effect, committing something like the inverse of the gambler's fallacy. The gambler's fallacy involves treating a single-step selection process as if it were a cumulative selection process, and I'll argue that they are treating a cumulative selection process as if it were a single-step selection process.

2 What the controversy is about

The purpose of this next section is to clarify just what's at issue, but toward this end it begins with what's not at issue. First, let's table some basic biology with which we can all agree in the context of this debate. There are three main points, the first concerns the nature of inheritance, the second concerns the nature of natural selection, and the third concerns the nature of mutation.

(i) Inheritance is a matter of transmitting traits from generation to generation. *The more likely it is that an offspring will resemble its parent with respect to a given trait, the more heritable that trait is.*[1] This transmis-

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[1] This is not the population genetic sense according to which inheritance depends partly on the variance of the trait in the population—e.g. in this sense, the human heart has low heritability because it is almost universal. (I am grateful to Kim Sterelny for this point.) The simpler notion will serve our purpose here, however.

sion need not be genetic, but we'll only be interested in genetic inheritance in this paper. Genes can be passed on from generation to generation unaltered, and they can have a stable effect on the physiology or behaviour of an organism across a range of environments.

(ii) Genetic evolution occurs when there is a change in the genetic composition of a population over generations, and natural selection is one of the major forces of genetic evolution. Defining natural selection is not an easy task, but for present purposes it suffices to say that *natural selection is the non-accidental differential replication of available variation.* Differential replication of genotypes can be due to accident (such as deviations from the statistical limiting case during fertilization, for example), but it can also be caused by the adaptive or maladaptive consequences of some genes. Selection generally occurs when a gene confers an advantage or disadvantage on the individual carrying it (in the environment in which the selection occurs) by producing physiological or behavioural changes that increase or decrease its viability or fecundity—that is, by making it more or less likely to survive and reproduce. The general rule is that (*ceteris paribus*) if a gene, G_1, confers a greater advantage than gene, G_2, G_1 will increase relative to G_2 in the population's gene pool, and so genetic evolution by natural selection will occur.

(iii) Besides natural selection, there are other factors involved in evolution, such as mutation, migration, genetic drift, and environmental change. And it's mutation, along with inheritance and selection, that is the focus of interest here. *A mutation is a random change to a gene or gene sequence*—random, not in the sense that, when a mutation occurs, its occurrence is as probable as any other outcome, but in the sense that *whether it occurs is entirely independent of whether it would be adaptive that it occur.* Mutations often produce no physiological change at all (for numerous codons can code for the same amino acid), and most that do are disastrous (for random changes to a complex organized/intricate system are more likely to disrupt it than improve it), so only a minute fraction produce beneficial changes. When they do, it's purely fortuitous that they do.[2]

This is all common enough ground in this debate (if there are disagree-

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[2] Or at least highly fortuitous. The *rate* of mutation can be controlled to some extent. Cells have procedures for checking that a DNA sequence has replicated correctly—an advantage given that most mutations are disastrous. But some mutation is required for 'evolvability' and in some circumstances evolvability can be improved by an increased mutation rate. Certain *kinds* of mutations could also be favoured. For example, some virus protect a central core of their genetic material with a sheath, but leave the outer ends exposed, increasing their chance of collecting segments of genetic material from the host with whom they have co-evolved over millions of years. The ends contain gene sequences similar to the host's, which the virus seems to employ to counter activity by the host's immune system.

ments over details, they need not concern us in this context). We are all agreed, then, that heritable variations can arise through random genetic mutation, and that natural selection selects between these variations. What is at issue then? Roughly speaking, the issue is whether natural selection, none the less, partially explains our adaptations. But it's important to be clear about what this amounts to, and it will help if we distinguish between three different explanatory tasks, each of which could be described as explaining why the creatures that exist have the properties they do. So, consider, for example, the question: '*Does natural selection explain our opposable thumb?*' (Sober's example). There are three different questions that this could be taken to be asking.

First of all, it could be asking about the development of particular individuals, such as you and I, and about the causal influences that shaped our own ontogenetic development of thumbs. A complete answer would *include* a description of a causal process that starts with our conception, and our inheritance of our genome from our parents, and that describes our embryonic development, where cells differentiate and organs and limbs (including thumbs) are formed, on through our post-natal growth as children through to maturity. I'll call this the *Individual Development Question*. It asks: *how or why does a particular individual develop his or her particular opposable thumb?*

Second, it could be asking how or why beings with opposable thumbs prospered and persisted in the human (or pre-human) population. To simplify matters, suppose that, once upon a time, there were two kinds of individuals in an ancestral (pre-human primate) population—one kind with opposable thumbs, the other without—and also suppose that those with opposable thumbs had more offspring because of their opposable thumbs, and that we are their descendants. We could be asking why the one kind of creatures (those with thumbs) prospered and persisted, rather than the other kind (those without). I'll call this *the Persistence Question*. It asks: *how or why did the genetic plan for an opposable thumb prosper and persist in the human population, once it arose?*

Third, it could be asking how or why a genetic plan for opposable thumbs arose in the human species (or their pre-human ancestors) in the first place. Granted that you and I inherited a genetic plan from our parents that specified opposable thumbs, and granted that the genetic plan, once it arose in the human population, prospered and persisted, so that almost all humans do inherit such a plan, the third question asks further: how did the genetic plan originate? This is the modern equivalent of Paley's question, for he too wanted to know how the blueprint for our adaptations arose. Of course, Paley argued that the best explanation was

Divine Design. To remind ourselves of this, I'll call this question the *Creation Question* (but I use the word 'creation' broadly, to include Divine Design, but also to include non-intentional and even completely accidental processes as well). The Creation Question asks: *how did the genetic plan for an opposable thumb originate in the human species (or its ancestors)?*

This said, which question is the focus of controversy? It's basically the third question. Some say that natural selection cannot answer the Creation Question (even partly)—I'll call this the *Negative View*—and some say that it can answer the Creation Question (partly)—I'll call this the *Positive View*. Cummins, Sober, and Dretske are proponents of the Negative View, while I am defending the Positive View (see also Mayr [1963], Ayala [1970], Dawkins [1986]). The bulk of this paper concerns the Creation Question therefore. But notice that, while neither the first or the second question are the *focus* of controversy, they are infected by the controversy to some extent. It's worth seeing how the contagion spreads.

Cummins, Sober, and Dretske often seem to talk as though it's really only the first question—the Individual Development Question—that is their concern. For example, Sober says:

> Natural selection does not explain why I have an opposable thumb (rather than lack one). This fact falls under the purview of the mechanism of inheritance (Cummins 1975). There are only two sorts of individual level facts that natural selection can explain. It may account for why particular organisms survive and why they enjoy a particular degree of reproductive success. But phenotypic and genotypic properties of individuals—properties of morphology, physiology, and behavior—fall outside of natural selection's propriety domain ([1984], p. 152).

Reading this passage in isolation, it is tempting to suppose that Sober is merely concerned to emphasize that natural selection has limited bearing on the ontogenetic development of the individual. But this is not his main concern, as will become clear later (in Section **3**).

With respect to the first question, we can allow that there is an important way in which the role of natural selection in explaining individual traits is limited. Natural selection cannot alter our genes once we've inherited them from our parents. Of course, if my genetic plan is sufficiently disadvantageous, and I am non-viable as a result, then I'll disappear and my genetic plan (or this instance of it, anyway) will disappear with me. Similarly, I might survive a near-fatal childhood accident because of my dexterous opposable thumb, and I might survive to mature and reproduce as a result. But natural selection cannot otherwise, *post-conception*, alter our

particular genetic plan or its contribution to our particular ontogenetic development.[3]

The first question is nevertheless controversial in so far as a *complete* answer to the first question includes an answer to the third question too. That is, a complete explanation of our individual development of our individual opposable thumbs includes an explanation of how the genetic plan specifying opposable thumbs, which we individually inherited, first arose in the gene pool to which we belong.[4] It is because Sober believes that natural selection does not explain *this* kind of fact that he believes that natural selection does not explain (beyond destroying it or preserving it entirely) an individual's development of an adaptation either.

Cummins also argues that natural selection does not explain the characteristics of individuals. His main interest is in the explanatory role of talk of functions, and he is responding to Larry Wright's claim that functions generate legitimate teleological explanations in contemporary biology. Simplifying somewhat, Wright argued that the function of a trait is that which it does, the doing of which it was selected for. It was supposed to follow from this that a trait's function explained its presence in an organism (Wright [1973]). But Cummins vigorously opposed this suggestion; he argued, in effect, that the fact that the koala's pouch has the function of protecting baby koalas (and was adaptive because of this) does not explain why koalas have pouches. Why not? Because natural selection does not explain the adaptations of individual organisms, or so Cummins says.[5]

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[3] If natural selection explains an individual's survival, then it also explains many other traits of the individual as well, as Kim Sterelny points out to me. For example, it could also explain why I am well-fed, and so why I have some stored fat, strong bones, and good muscle tone. However, I am uncomfortable with the claim that natural selection explains an individual's survival or death (or any of these things). I would concede less to the explanatory power of natural selection here than either Sober or Cummins does. Natural selection *supervenes* on many such instances of individual survival (and reproduction). I am therefore inclined to say that *they* explain *it* (and that neither is the cause of the other). But since this issue is not important for what follows, I'll leave it hanging.

[4] I make this, and one or two further points, in a less well-developed treatment of this topic, in my [1988].

[5] Dretske's conclusion follows on from this, but takes us even further afield (see my paper, 'Dretske and his Modest Theory of Innate Content'). He is concerned with the explanatory power of the content of mental representations (often called 'the Soprano Problem'). How do the semantic properties of a state, as opposed to its physical properties (non-redundantly?), causally explain its effects? For example, how does our desire for ice-cream, *qua* desire *for ice-cream*, not *qua* neuro-physiological state, causally explain our going to the freezer? Dretske [1988] argues that content does have a special role in explaining behavior: but this is not true of innate content, he says. He argues that the content of a mental representation is determined by its function, and that when this is determined by natural selection, as in the case of any representation that occurs prior to learning, the content it underwrites can't explain behavior. Why? Because natural selection can't explain adaptations. Amongst other things, it can't explain why an individual is 'wired' to behave in a certain way in a certain context (see esp p. 92). I doubt that Dretske needs such a strong claim, a point he later acknowledges in a more cautious discussion of this topic ([1990], p. 829).

In my view, the most interesting (and charitable) interpretation of Wright reads him, for specifically biological functions, as making a claim that applies directly to types of traits, and only indirectly and derivatively to individual tokens (Neander [1991] (a) and esp. (b)). That is, he should be read as suggesting that past adaptive effects of ancestral marsupial pouches explain why present marsupials (koalas included) have pouches. But Wright was unclear on this score, and Cummins is too. He runs his discussion of Individual Development and Creation Questions together and the reader is obliged to disentangle them, in the following crucial passage for example:

> One sometimes hears it said that natural selection is an instance of negative feedback. If this is meant to imply that the relative success or failure of organisms of a certain type can affect their inherited characteristics, it is simply a mistake. The characteristics of organisms which determine their relative success are determined by their genetic plan, and the characteristics of these plans are utterly independent of the relative success of organisms having them. Of course, if s is very disadvantageous to organisms having a plan specifying s, then organisms having such plans may disappear altogether, and s will no longer occur. We could, therefore, think of natural selection as reacting on the set of plans generated by mutation by weeding out the bad plans: natural selection cannot alter a plan, but it can trim the set. Thus we may be able to explain why a given plan is not a failure by appeal to the functions of the structures it specifies ... But this is not to explain why, e.g., contractile vacuoles occur in certain protozoans, it is to explain why the sort of protozoan incorporating contractile vacuoles occurs (pp. 750–1).

What Cummins needs to establish, to target the most interesting interpretation of Wright, is that natural selection does not answer Creation Questions. For if natural selection does partly explain how the genetic plan for pouches originated in the marsupial gene-pool, then it also partly explains how an individual koala subsequently inherits said genetic plan and develops said pouch, just as Wright requires it does.

We have seen that the Individual Development Question, while not central to the controversy, is infected by the controversy. The same is true, although to a lesser extent, of the Persistence Question. With respect to this question, all parties to this debate agree that natural selection can explain why traits prosper and persist in a population once they have originated. Our opposable thumb, for instance, was probably selected because of the additional dexterity it provided which allowed us to make and grasp tools, which improved our ability to feed and defend ourselves. We can also all agree that (as Cummins and Sober point out) Persistence

Questions can be answered without answering Creation Questions. The Persistence Question, given above, presupposed that there already were primates with opposable thumbs, and it simply asked why they, rather than the primates that lacked them, were the kind of creature that prospered and persisted.

What is controversial is whether natural selection answers Creation questions *as well as* Persistence Questions, or whether it answers Persistence Questions *instead of* Creation Questions. Sober argues that natural selection answers Persistence Questions *instead of* Creation Questions, and his claim follows smoothly from the Negative View. This is worth dwelling on, because it reveals—as Sober stresses—how really radical the Negative View is.

It is often thought that when Darwin described the operation of natural selection he answered Paley's Creation Question: how did all those natural complex systems, so wondrously well adapted for their purpose, originate? Darwin's role in the demise of Natural Religion is normally described as follows. In his *Natural Theology* [1802], Paley, who was a major influence on the young Darwin, argued that the complicated adaptations of living systems were too wildly improbable, considered as the result of random natural forces. He also argued that a better explanation of such adaptations, one which renders them probable, was Divine Design. Despite Hume's previous critique of other versions of the Argument For Design, in his *Dialogues Concerning Natural Religion* [1779], Paley's argument remained highly influential, until intellectual opinion was swayed by the publication of Darwin's *Origin of Species* [1859]. What Darwin did, as the story is normally told (and as I am happy to tell it) is *propose an alternative explanation of the complex adaptations of living systems*, showing that they are even more probable, considered as the result of natural selection. (Natural selection allows for systems that satisfice, and explains the imperfections as well as the perfections.)

But Sober says that this misdescribes the dialectic of the situation. When Darwin explained the wondrous adapt*edness* of living things, he did so, not by explaining why *the creatures that exist have the adaptations they do*, but rather by explaining why *the creatures that exist are the ones with those adaptations*. Contrary to a popular misconception, Darwin answered Persistence Questions, but not Creation Questions, Sober claims (Sober [1984], Ch. 5.2, esp. p. 150). Darwinian natural selection, in answering Persistence Questions, changed our conception of the propositions that needed explaining, according to Sober. It follows that, by answering Persistence Questions, *Darwin rendered any special answer to the Creation Question* (*beyond that of random natural forces*) *otiose*! Sober is right to stress how revolutionary this transition is—or rather, in my view, would be.

Radical as the Darwinian revolution was, I don't agree that it was *this* radical. Natural selection does, of course, answer Persistence Questions. But it doesn't answer Persistence Questions *instead* of Creation Questions: it answers Creation Questions *by* answering Persistence Questions. Or so I will argue (in Section **4**).

In sum. According to the Negative View, natural selection can only explain the distribution of an adaptation in a population (why creatures with that adaptation prospered and persisted). It cannot, according to the Negative View—even partly—explain the phylogenetic development of adaptations (that is, it cannot answer Creation Questions). So it doesn't partly explain an individual's development of an adaptation either (unless by explaining the individual's survival). I disagree. But so much for claims and counter-claims, let's look at the arguments.

3 Arguments for the Negative View

The Negative View has intuitive appeal for many people. Before turning to the more developed defence of it that Sober offers, and the addition to this that Dretske contributes, I'll state three far simpler arguments (or tools of persuasion, if that seems too generous a name) that people often find persuasive, at first blush. These are not seriously developed anywhere in print, as far as I know, although they are sometimes used in passing. But they litter informal discussion of this topic so frequently, it is best to set them out in bold black and white, and assess them in that stark light. Despite the far greater sophistication and subtlety of Sober's defence, I think a similar mistake underlies all of these arguments. This section outlines the arguments, the next (Section **4**) gives my reply.

(i) Some seem to think that the Negative View is Just Basic Biology. It's Just Basic Biology that evolution by natural selection is a two-part process, the argument goes: first there is the random generation of heritable variation through mutation, and then there is the natural selection of pre-existing variations by differential replication. So, the theory *just says* that natural selection doesn't create variations, that it's the mutations that do that. And it *just says* that natural selection merely selects from amongst the variations that happen to arise.

(ii) The same people are also often in the grip of certain metaphorical pictures. For instance, natural selection works like a sieve, they say. On this picture, genetic plans are thrown into the sieve of natural selection, where they are tossed around against the hazards of life, and as a result some genetic plans (on average the most adaptive ones) but not others (on average the less adaptive ones) make it through into the next generation.

Both adaptive and maladaptive genetic plans are in at the start; sieving just sorts the one from the other.

Common and especially *garden* metaphors are popular. Cummins, for instance, recommends that we 'think of natural selection as reacting on the set of plans generated by mutation by weeding out the bad plans: natural selection cannot alter a plan, but it can trim the set.'[6] The most popular metaphor is probably that of natural selection *pruning* the tree of life. It goes like this. Picture the tree of life. There it stands spreading out from the primordial slime: phylum branching into classes, classes into families, families into genera, genera into species, and all over leafy with individuals at the growing tips. Then picture natural selection pruning the less promising shoots and branches. A snip here, a twig drops, some sawing there, a branch comes crashing down. Just like us pruning the apple tree, the pruning merely removes growth, *for what is retained was there before the pruning began.* So, the metaphor suggests, natural selection did not create the tree of life: it just determined which branches were removed and which remained.

(iii) Thoughts about counterfactuals also seem to lead to the Negative View. I think the central thought is this. What matters to our existing, and having the adaptations we do, is that our lineage exists. That is, what matters is that your parents begat you, and my parents begat me, and their parents begat them, and their parents in turn begat them, and so on. Crucially, it doesn't seem to matter what other creatures do or don't exist besides. So there could have been, *in addition*, all the creatures that natural selection actually eliminated doing their share of begetting besides. The idea is that there is a nomologically possible world where we (or our counterparts) co-exist with all the creatures that natural selection actually eliminated, and, if so, this shows that natural selection was inessential to the creation of us and our adaptations.

Of course, this possible world would need to be enormous to cater for so many appetites, it is conceded. To eliminate natural selection, we have to render inapplicable the Malthusian principle—that if unchecked, a population will expand beyond the resources available to feed it.[7] But

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[6] Cummins makes much of the protozoans in what he describes as a 'hint'. He describes two different species of protozoan, a sea-water and fresh-water variety, both of which have a contractile vacuole. The vacuole has a function for the sea-water protozoans, but not for their fresh water cousins, and is, if anything, slightly maladaptive in their case. Why Cummins thinks this is significant for the present debate is obscure, however, because the Positive View doesn't entail Adaptationism. That is, if natural selection did partially explain adaptations, it would not follow that natural selection must result in perfectly well-adapted creatures. (See e.g. Gould [1980].)

[7] 'Even slow-breeding man has doubled in twenty five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny' (Darwin, [1859], p. 117).

supporters of the Negative View might say that this only shows that, given our limited resources, natural selection answers Persistence Questions. Given the limited resources of our planet, it might be argued, there was a struggle for survival, and the fittest on average won out, so the better adapted lineages prospered and persisted in preference to the less well adapted. In other words, limited resources caused the various different kinds of creatures to compete for existence, but that competition didn't *create* the different kinds of creatures: they were a precondition for it, it was not a precondition for them.[8] Or so supporters of the Negative View are apt to claim.

(iv) Finally Sober's argument. This appears in his book, *The Nature of Selection* ([1984], Ch. 5, esp. 5.2). It is there embedded in a discussion of the general nature of explanation, but most of this will have to go unmentioned here. None of it is critical to the disagreement between us, however, for Sober doesn't have any especially stringent requirements on explanation—this is not what leads him to argue that natural selection doesn't explain adaptations.[9]

But one thing he does stress, and that I should mention, is that explanation is relative to contrast classes determined by pragmatic features of the context. (When we ask why Betty went to the party with John, we might be asking why Betty went to the *party* with John—e.g. rather than to the theatre—or we might be asking why Betty went to the party with *John*—e.g. rather than with Bill.) Sober argues that the Darwinian revolution involved a subtle change in the contrast classes relevant to the explanations that biologists seek. Natural selection, he says, explains why a population is composed of individuals with a certain trait (as opposed to different *individuals*). It does not explain, he says, why the individuals of which a population is composed have this trait (as opposed to a different *trait*; see esp. p. 150).

Sober (following Lewontin [1983]) makes a distinction between two kinds of explanation: developmental and selectional (Sober [1984], pp. 148–55). What seems essential is that *developmental explanations* explain the properties of populations by explaining how the individuals in a population acquire certain properties, while *selectional explanations* explain the properties of populations by explaining how a population comes to be composed of individuals with certain properties.

To illustrate this distinction, Sober gives the following example (p. 149). Suppose that all of the children in a room read up to the third grade level. A

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[8] I am grateful to Nick Agar for helping me to see that this argument could be extended in this way (he does not endorse the argument, by the way).

[9] In fact, Sober sees himself as having less stringent requirements than most, and in important relevant respects. See fn. 11, this paper.

developmental explanation could explain how each child changed by explaining how each child developed the ability to read at that level and then aggregating these individual explanations. It could explain how all the children in the room acquired the ability, by describing how each of them went to school, and so on, without explaining why there are only children of this kind in the room. In contrast, we could give a selectional explanation. Perhaps it was a condition on entry into the room that the children could read up to the third grade level. This explanation treats the children as static; it assumes that they already have the ability when they enter the room, and that they don't lose it subsequent to entry. So, by hypothesis, it doesn't explain how each child acquired the ability, it presupposes it instead. The selectional explanation only explains why those children that have the ability are the ones that are in the room.

The moral that Sober draws from this example is that developmental explanations can explain the development of a trait in individuals, whereas selectional explanations can only explain the distribution of individuals with that trait in a population. Selectional explanations are, says Sober, 'irreducibly population level' explanations. They are not aggregations of explanations at the individual level, and they do not explain the phenotypic or genotypic properties of individuals.

Notice that a Lamarckian explanation of evolution is developmental. Cultural evolution can be Lamarckian in the sense that properties acquired through one's lifetime can be inherited by one's offspring (convert to Catholicism in your teens, and you increase the probability of your children being Catholic). In such explanations, the individuals themselves change. On a Creationist theory, neither population nor individual changes its essential properties, but Creationism is intended to explain why a population has individuals of a certain kind by explaining why its individuals have the properties they do (God made them or their ancestors—e.g. Adam and Eve—that way). A population level fact can thus be explained by an individual level fact.

Natural selection, in contrast, explains changes in a population by explaining changes in the composition of the population. The genetic composition of the population changes over time because there is variation amongst us, and some of us leave more of our genes behind. Explanations that appeal to natural selection are selectional explanations in the relevant sense, says Sober, so they can only explain the distribution of adaptations—that is, why individuals with those adaptations prosper and persist.

Sober summarizes his conclusion in the following passage:

> The frequency of traits in a population can be explained by natural

selection, even though the possession of those traits in the population cannot. This reflects the fact noted earlier that selectional explanations, unlike developmental ones, do not explain population level facts by aggregating individual level ones. Selection may explain why all the individuals in the room read at the third grade level, but not by showing why each individual can do so (Sober [1984], p. 152).

(v) Finally, it is worth mentioning Dretske's neat example, intended to further illustrate Sober's claim. It shows that the logic of Sober's example is not an accident of the particular example he employs. Dretske gives the example of Clyde the clock collector. Clyde has a rather peculiar taste in clocks—he only collects clocks that lose ten minutes a day whenever the humidity is over ninety degrees. One of the clocks is called 'Ben'. Question: why does Ben lose ten minutes a day (when the humidity is over ninety degrees)? As Dretske says, there will be some internal state in Ben that causes the hands to slow down when the humidity is high. Perhaps, the oil used to grease Ben's cogs turns tacky when the humidity is high. If so, the causal antecedents of Ben's running slow include the manufacturer putting the oil there, the oil itself and its properties, and, of course, the humid conditions. But crucially, Dretske stresses, Clyde's selective collecting does not explain why Ben runs slow when the humidity is high.

These are the main arguments for the Negative View. The final section gives my reply.

4 Cumulative selection and Sober's strictures

Much of what Sober says in this context is true and important. There is an interesting distinction to be drawn between two kinds of explanations along the lines Sober suggests: some explanations explain changes to populations by explaining changes to individuals, and then aggregating those explanations. Others are, in a sense, 'irreducibly population level', for they explain changes to populations by explaining changes in the composition of the population. Moreover, when we explain evolution as being due to natural selection, this explanation is basically of the latter kind. As Sober says, '[p]opulation change isn't a consequence of individual change but of individual stasis plus individual selection' (Sober [1984], p. 150).

However, Sober overstates his conclusion. While all of this is true, it just doesn't follow that natural selection cannot explain the phenotypic or genotypic properties of individuals. *Even if natural selection does not explain change in a population by explaining changes to individuals, it can still explain why individuals have the properties they do by explaining*

changes in populations. The rest of this paper is devoted to defending this claim.

First of all, note that Sober's restrictions on the purview of selectional explanations do not apply to *every* explanation that could be classified as 'selectional', if by 'selectional explanation' we mean just any explanation that appeals to *some* kind of selection process. (The name for this kind of explanation is therefore misleading.) As Dretske points out, if the manufacturer of Ben had, for some reason, wanted Ben to run slow when the humidity was high (so that he could sell the clock to Clyde, perhaps), then Ben's manufacturer might have chosen the oil that turns tacky for that very purpose. In that case, a selection process—that is, an *intentional* selection process—would partially explain why Ben runs slow and would qualify as one of the causal antecedents of Ben's having the property of running slow when the humidity is high.

Of course, *natural selection is not an intentional selection process, but neither is it the kind of selection process to which Sober's strictures apply. Sober's strictures don't apply to cumulative selection processes either.*

The distinction between a cumulative selection process and a single-step selection process is made explicit by Richard Dawkins ([1986], Ch. 3). Sober also employs it (Sober [1993], Ch. 2). Here is how I think the distinction should be made. Both kinds of selection involve a randomizing mechanism that randomly generates possible outcomes, and selection from (or sorting of) those possible outcomes. For example, a coin toss randomizes outcomes by making the epistemic probability of heads or tails even, and then when the coin lands, one outcome rather than the other is made actual or is selected. What counts as random and what counts as being selected can be a prag-matic matter (but I won't explore this point here). Single-step selection can involve numerous repetitions of these random/select sequences (hereafter R/S sequences), and cumulative selection must involve numerous repetitions. The difference between the two is not in the number of repetitions, but rather in the *relationship between the repetitions. Crucially, in a cumulative selection process, an R/S sequence can leave its mark, altering the probable outcome of future sequences, while in a single-step selection process, one R/S sequence is isolated from the next, and cannot alter the probable outcome of future sequences.*

This is in the spirit of Dawkins' use of the distinction, but it is not how he draws the distinction himself. He says:

> The essential difference between single-step selection and cumulative

selection is this. In single-step selection the entities selected or sorted, pebbles or whatever they are, are sorted once and for all. In cumulative selection, on the other hand, they 'reproduce'; or in some other way, the results of one sieving process are fed into subsequent sieving, which is fed into . . . and so on. The entities are subjected to selection or sorting over many 'generations' in succession. The end product of one generation of selection is the starting point for the next generation of selection, and so on for many generations ([1986, p. 45).

This way of drawing the distinction won't do, and it's instructive to see why. Sober's famous selection toy would count as a cumulative selection device on this definition (see Sober [1984], p. 99), but none of the claims Dawkins makes on behalf of the *power* of cumulative selection can be made on behalf of this toy. I'll explain.

Sober's selection toy is a clear cylinder, devided horizontally by a series of sieves that become more and more fine-grained toward the bottom. Into the top of the toy, balls of different sizes and colours are placed, the toy is shaken, and the balls fall toward the bottom. All and only the smallest balls are green, and since getting to the bottom is deemed getting selected in this case, and only the smallest balls can pass through the smallest holes, only the small green balls get selected. The distinction that Sober is illustrating is this: while there was selection *of* both green balls and small balls, the balls were selected *for* being small, not for being green—because it was their being small, not their being green, that *caused* them to be selected.

(Note, by the way, that 'what something was selected for' concerns the property that was causally efficacious in the selection process, and that the notion is, therefore, an explanatory notion. Sober has no quarrel with the claim that a trait, X, was selected for Z-ing by natural selection, nor with the claim that this can, in some sense, explain X—the quarrel is with what it explains about X: i.e. it explains why individuals with X are prevalent, but it doesn't explain why any of these existing individuals have X, says Sober.)

This toy illustrates the selection of/for distinction beautifully, but it does not illustrate a cumulative selection process at all (nor did Sober suggest it did). It does qualify as a cumulative selection device on Dawkins' criteria, however. The balls are subjected to several sortings, and the product of one sorting is fed into the next, as Dawkins requires. But this is no cumulative selection device, *because the series of sieves is inessential to the final selection.* The small green balls have the same chance of getting to the bottom, and of getting to the bottom alone, as they would have if there were only a single sorting through the most fine grained sieve. My manner of making the distinction abides

better by the *spirit* of the distinction that Dawkins employs, therefore. For it is the power of cumulative selection processes to alter the probability of final outcomes that rightly impresses him. To see this power, take a look at the example that follows (it is a variation on Sober's).

Imagine a lottery machine—a cage, with 30 white balls inside, each with a different number on it, from 1 through 30. At the bottom of the cage are seven holes into which the balls fall. Each 'try' consists in the balls being whooshed about until all the holes contain at least one ball. Then the numbers are read off the balls in the bottom of the holes. People have bought tickets on which they have written seven different numbers, from 1 through 30. And you become a millionaire (and can philosophize your days away on a tropical island paradise) if your ticket matches the balls in the holes: you need the same numbers in the same order. So if your ticket reads, for example, '29, 8, 16, 3, 22, 30, 19', the ball in the first hole has to read *29,* the ball in the second hole has to read *8,* and so on.

Alas, your chance of winning is negligible indeed. With one ticket and one try, it is a very meagre $1/30^7$ or $1/656,100,000,000$. Moreover, if we were to give you, say, forty tries, instead of just one, your chance of winning on each toss would be exactly the same: i.e. $1/30^7$. You wouldn't want to put a down-payment on the yacht on these kinds of odds. The crucial point is that, *in a single-step selection process, earlier R/S sequences don't alter the probable outcome of later R/S sequences.* Those who commit the gambler's fallacy fail, in effect, to recognize that random/select sequences are causally isolated in this way. But not all selection processes are of this kind.

Now imagine that we are allowed to rig the lottery machine. This time, just like before, the first try takes place, and again we check to see whether the numbers on the balls match the numbers on your ticket. But now we are allowed to fiddle with the machine in the following way. If any of the numbers match after any try, the matching balls stay in the holes, and are not tossed in subsequent tries. So suppose that after the first try, the selected balls read, '14, 2, 16, 30, 12, 19, 28'. Since the number on the third ball matches the third number on your ticket—i.e. *16*—we are allowed to hold that ball in the third hole, so that it isn't tossed in subsequent tries. Now in the second try, we only need to match a further six numbers (and the probability of getting a complete match on your second try is now $1/30^6$). Your chance of becoming a millionaire has exponentially increased! (With a further match on, say, the third try, the probability of matching all of your numbers on the fourth try becomes $1/30^5$, and so on). The crucial point is that, *in a cumulative selection process, earlier R/S*

sequences can alter the probable outcome of later R/S sequences. They can leave their mark. This machine is the gambler's dream machine: the mistake the gambler makes is, in effect, to suppose that an ordinary lottery operates somehow along these lines.

A cumulative selection process can exponentially increase the probability of a particular outcome (e.g. a sequence of numbers) relative to its probability as the result of a repeated single step selection process (i.e. a purely random process). Now Sober agrees that evolution by natural selection is a cumulative selection process,[10] and that it can exponentially increase the probability of an adaptive gene sequence arising. But Sober doesn't seem to notice that this undermines the Negative View. Denying that it does undermine the Negative View might seem to involve an outright contradiction, but while such a denial cannot be sustained, the contradiction is not as outright as I might have just made it seem.

For one thing, natural selection *on its own* is not a cumulative selection process. Recall that this paper began by distinguishing between natural selection, on the one hand, and mutation (and inheritance) on the other hand. The cumulative selection of genetic evolution involves selection *and* mutation (and inheritance) combined. That these *combined* are a powerful positive force the Negative View does not deny. The implications of Dawkins' distinction (for *this* debate, as opposed to the Creationism debate, which both he and Sober are addressing when they focus on the nature of cumulative selection) might also be obscured by Dawkins' tendency to equate selection with sorting or sieving: 'the results of one sieving process are fed into subsequent sieving,' he says, and he says similar things over and over again. Thus, while Dawkins is explicitly concerned to emphasize the positive power of natural selection as a 'creative' force (it is the Blind Watchmaker), he also employs the very metaphors that obscure, rather than reveal, the role that natural selection, *per se*, plays in the cumulative selection process—and this is the key to our puzzle: natural selection doesn't just sort and sieve.

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[10] There are differences between it and the rigged lottery, of course, but while these differences need to be addressed in the Creationism debate, they needn't much concern us here. The most important difference is that evolution by natural selection is not preprogrammed in the way that the rigged lottery is. It is not rigged in favour of any *particular* adaptive outcome. Each step along the way, a modification is favoured only if it *itself* is the most presently adaptive alternative currently available. It is not enough for it to be a step in the right direction. (See Denton [1985], for a pro-Creationist perspective on this, but see also Dawkins [1986], Ch. 4.) Sober does talk as though 'developmental explanations' are of preprogrammed development ([1984], p. 153–4), but note that this is not a feature of his main example (i.e. the developmental explanation of the children in the room).

In the context of this debate, Cummins, Sober, and Dretske focus on what happens when mutation is followed by selection, but seem to ignore *what happens when selection is followed by further genetic recombination and mutation: preceding selection can dramatically alter the probability of subsequent gene sequences occurring.*[11] Consider the following evolutionary story.

Suppose we begin with a population of 100 haploid individuals, all of whom have two genes—A_1 and B_1 (that is, both of these genes have gone to fixation). Now suppose that two point mutations occur, one after the other, in different individuals. First, an instance of A_1 mutates into A_2, then in another individual, an instance of B_1 mutates into B_2. Let's also suppose that A_2 is more adaptive than A_1, but that B_2 is less adaptive than B_1 unless combined with A_2. So in order of fitness, the alternative possible combinations are $A_2, B_2 > A_2, B_1 > A_1, B_1 > A_1, B_2$. Question: how probable is it that the most adaptive genetic sequence—that is, A_2, B_2— will arise? Answer: it depends, amongst other things, on how far A_2 has spread in the population before B_2 arises. Consider the extremes. If A_2 has gone to fixation by the time B_2 arises (*ceteris paribus*), the probability of the combination occurring is 1. In contrast, if there has been no selection of A_2 by the time B_2 arises, so that there is still just the one instance of A_2 (or worse, if through genetic drift, A_2 has disappeared altogether), the probability will be much smaller. The more disadvantageous B_2 is without A_2 (supposing that A_2 has survived at all) the smaller the probability will be. Again, consider the extreme case—if A_1B_2 is lethal, the probability will be zero.

So, yes, evolution by natural selection is a two stage process. There is the random generation of variation by means of mutation, and there is selection from amongst the pre-existing variation by means of non-accidental differential replication. But it doesn't follow that mutation, *and*

[11] We can sometimes *infer* that E is probable, given C, and yet C is not the cause of E. (Notoriously, I can infer that the flag-pole is a certain height, given the length of its shadow, but the length of its shadow is not a cause of its height and nor does it explain its height.) But I am arguing that selection can causally increase or decrease the probability of a gene sequence. As already remarked, Sober takes 'selection for' to be a causal notion ([1984], pp. 97–104). In addition, notice that he argues that explanations don't have to 'say what the cause is' (ibid., pp. 139–42) (contrary, e.g. to Salmon [1971]). It's enough, he persuasively argues, if they delineate a set of possible causes, one of which is the actual cause. It could be argued against Sober that there is no difference in kind here, as opposed to a difference in degree (of specificity). Virtually all 'saying what the cause is' leaves the actual instantiation of the cause under specified to some degree. I might learn that Billy's ball broke the window without learning about its precise trajectory, for example (let alone learning about its sub-atomic constituents). None the less, there is a sense in which Sober's claim stands, interpreted as a difference in degree. Note that it supports the Positive, not the Negative View, however.

not natural selection, explains the creation of genetic sequences and the adaptations they give rise to. It only looks that way if we focus on one isolated mutate/select sequence, but we have no business to be focusing on an isolated sequence in this way. Many, often millions, of such sequences are involved in producing adaptations like our opposable thumbs, our eyes and ears, the rooster's crow and the spider's web. And these sequences are far from being causally isolated from each other. Mutation alters the outcome of subsequent selection, which in turn alters the outcome of subsequent random generation of new gene sequences, and so on, and so forth.

Natural selection can also alter the probability of subsequent point mutations. If there is a small chance of an individual instance of G_2 mutating into G_3, the more instances of G_2 there are, *ceteris paribus*, the larger the chance there is of one instance of G_3 arising. Usually, the matter is a little more complicated, but the basic principle is the same. Suppose again that we have 100 (haploid) individuals, all of whom have gene G_1 at the start of the story. Suppose also that there is a mutation of G_1 into G_2, so that 99 individuals then have G_1 and just 1 individual has G_2, and that then there's selection of G_2 because it happens to be more adaptive than G_1. To keep things simple, let's suppose it goes to fixation (so that all 100 individuals then have G_2). So far, just as the Negative View maintains, mutation creates variation, and all natural selection does is choose between them. But now consider what happens next. Suppose that, for any arbitrary instance of G_1 or G_2, and for some third allele, G_3, the probability of the G_1 mutating into G_3 is less than the probability of the G_2 mutating into G_3. If so, the selection of G_2 (here, its going to fixation) increased the probability of G_3 occurring, and if G_3 occurs as a result— contrary to the Negative View, and in accordance with the Positive View— natural selection explains its occurrence.

Perhaps no real gardener has ever been guilty of using the Pruning the Tree of Life metaphor to defend the Negative View. Gardeners know that annual pruning doesn't merely eliminate old growth, it also channels and directs new growth. The elephantine bush, the bonsaid oak, the espaliered pear, and the standard rose are not a proper part of the plants that would have stood in their place, had they never been pruned. Just so, the tree of life would not have had all of its actual branches, just plus some more, if there had been no natural selection.

A possible world in which we (or our counterparts) exist alongside all of the creatures that natural selection actually eliminated seems nomologically possible only if we focus on local causes. My parents can beget me if there are resources enough, no matter what other creatures exist besides. This is true. But once we look further, the apparent coherence of

this 'possible' world disintegrates. How—without introducing Divine intervention or massive accident, which would vitiate the point of this possible world example—how are the weak and the slow, the moribund and the crippled, the myopic and the blind, the immune deficient and the outright infertile—how are they supposed to do their share of begetting? Is the hungry fox supposed to sit by patiently while the crippled antelope rears its offspring? Does the temperature and rainfall somehow locally correspond to the optimal growing conditions for each individual seed, no matter where it happens to fall, or what other seeds or plants it happens to fall near? And even if there were a solution to this problem, there are others.

What is essential for our existing, and for the evolution of our adaptations, is just that our lineage exists. True. But for this to be true, our ancestors needed to go forth and multiply, *just as much as they did, and with the mates they did.* The numbers matter, and who mates with whom matters, for they affect which gene sequences arise. For our ancestors to have been as fecund as they were, given that in this actual world there *are* limited resources, natural selection had to occur. Moreover, for them to mate with the mates they did, they mustn't have mated with anyone else instead, including any of the creatures that natural selection actually eliminated. Which brings me to my last point.

Natural selection is crucial for speciation, which is in turn crucial for the further development of harmonious co-adaptations, as the biologist, Ernst Mayr, has argued ([1963], Ch. 2). Natural selection usually eliminates hybrids because they tend to be less robust than more central cases. The same can occur with the offspring of individuals from diversified varieties within a species where speciation is incomplete. Once speciation has occurred, the isolated gene pool that is the species is protected from the harmful flow of genes from other gene pools. Genes from the same gene pool can then form further harmonious combinations of traits—they can be co-adapted by natural selection, as Mayr says.

Mayr does not consider the awful prospect of the 'possible' world where we (or our counterparts) co-exist alongside the creatures that natural selection actually eliminated. But I imagine he'd agree that extinction is the ultimate isolating mechanism: there is no surer way to prevent X from mating with Y than Y's not existing. Without the elimination of some variation in genotype and phenotype, all the 'gaps' between species would be filled. There could be no speciation, and therefore no species, and if we had inter-breeding life forms at all (but I doubt that life would become so complex) we'd have just one big inter-breeding population: not so much a tree of life, as a slime of life, I suggest. And as a consequence, a precondition for the substantial harmonious co-adaptation of traits—the

'exquisite adaptation of one part of the organization to another part'—would not be in place.

5 Conclusion

I distinguished three different explanatory tasks: (i) explaining the ontogenetic development of individuals, (ii) explaining why genotypes prosper and persist in the gene pool, and (iii) explaining how those genetic plans arose in the first place. While distinct, these three explanatory tasks overlap. Explaining a particular individual's phenotypic or genotypic properties—(i)—involves explaining how the genetic plans he or she inherited arose in the first place—(iii). This is partly explained by which mutations occurred when and how they randomly combined and re-combined, but that, in turn, is partly explained by explaining why pre-existing genotypes prospered and persisted—(ii). Previous selection alters the base from which further genetic sequences are randomly generated and thus changes the probability of certain genetic sequences arising. It's true that natural selection does not explain change in a population by aggregating explanations of changes in individuals, and that, *in this sense*, explanations that appeal to natural selection are irreducibly 'population level'. But it isn't true that natural selection can't explain the properties of individuals. It can: by explaining how the genetic plans the individuals inherited first arose.

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