The Negative View of Natural Selection

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Abstract: An influential argument due to Elliott Sober, subsequently strengthened by Denis Walsh and Joel Pust, moves from plausible premises to the bold conclusion that natural selection cannot explain the traits of individual organisms. If the argument were sound, the explanatory scope of selection would depend, surprisingly, on metaphysical considerations concerning origin essentialism. I show that the Sober-Walsh-Pust argument rests on a flawed counterfactual criterion for explanatory relevance. I further show that a more defensible criterion for explanatory relevance recently proposed by Michael Strevens lends support to the view that natural selection can be relevant to the explanation of individual traits.

Key words: evolution, natural selection, adaptation, causal explanation, contrastive explanation

1. The Negative View as a Problem

Can natural selection help explain why a particular organism has the traits it does? On the *positive view* of natural selection, it can: past selection for some trait can help explain why a later individual instantiates that trait. On the *negative view* of natural selection, it cannot: selection can explain the distribution and origin of trait types in a population, but it cannot explain the possession of any particular trait token by any particular individual.

The debate is more than a matter of idle curiosity.[1] The negative view, if correct, has serious implications, of which perhaps the most troubling is that it threatens to render inexplicable the *adaptedness* of an individual organism.[2] While an organism's first-order traits admit of proximate explanations in terms of their developmental history, an individual's adaptedness does not: one could know everything about the proximate causal processes by which an organism comes to develop a particular set of traits, and yet still lack an explanation for the *good fit* between those traits and the environment in which the organism lives. One could know everything about how a chameleon builds its long, sticky tongue and sharp, grippy claws and yet still be amazed when the chameleon crawls out of its egg, scales a tree and zaps a nearby insect. *Why is it so well adapted to its environment?* Purely developmental explanations seem to fall short here. Yet, if the Negative View is correct, there can be no *evolutionary* explanation of this phenomenon either, since the

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[1] To track the contours of the debate, see Ayala 1970; Cummins 1975; Wright 1976; Nagel 1977; Lewontin 1983; Sober 1984, 1995; Neander 1988, 1995a,b; Dretske 1988; Walsh 1998; Matthen 1999, 2002, 2003; Lewens 2001; Pust 2001, 2004; Forber 2005; Nanay 2005, 2010; Stegmann 2010a, b.

[2] Note that, on the Negative View, selection may still explain why *adaptations*, construed as trait types, arise in a population; it merely fails to explain, for any particular individual, why that individual has the adaptation (see Walsh 1998, Lewens 2009).

phenomenon amounts to the instantiation of a particular trait (viz. adaptedness) by a particular individual. We seem to be left with no explanation at all.[3]

The aim of this paper is reassurance. We owe the most influential argument for the negative view to Sober (1995), though Walsh (1998) and Pust (2002, 2004) have subsequently strengthened Sober's case in significant respects. Here I show that the Sober-Walsh-Pust (SWP) argument rests on a flawed criterion for explanatory relevance. I then show that a more defensible criterion for explanatory relevance vindicates the positive view. In particular, I show that natural selection is likely to be relevant in explaining the adaptedness of an individual organism.

2. The Sober-Walsh-Pust Argument

To understand the structure of the SWP argument, we first need to consider how a simple argument for the positive view fails. Consider some organism O with some arbitrary trait T inherited from its ancestors. These ancestors enjoyed a selective advantage in virtue of possessing T. Does natural selection thereby help explain why O has T? Consider the following line of reasoning:

(1) Past natural selection for T helps explain why O's ancestors reproduced successfully.

(2) Anything that helps explain why O's ancestors reproduced successfully thereby helps explain why O exists.

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[3] Walsh (2003, 2006) suggests that an appeal to *developmental plasticity* (see West-Eberhard 2003) may do the necessary explanatory work. I remain sceptical: plasticity may explain *some* adaptive phenotypes, but can hardly explain, for instance, why a chameleon is so adept at fly-catching when a no-less-plastic human baby, left to develop in the same environment, would not be.

(3) Anything that helps explain why O exists thereby helps explain why O has T.

(4) (from 1, 2, 3) Past natural selection for T helps explain why O has T.

The simple argument is plainly valid. If it is sound, the positive view is vindicated. Premise (1) seems plausible, while (2) and (3) appear to be grounded in the causal continuity of the processes involved: the reproductive success of O's ancestors led to O's conception, O's conception initiated its development, and O's development produced its phenotype. Yet it is easy enough to see that something must be wrong, for suppose that O's ancestors also enjoyed a selective advantage in virtue of possessing another arbitrary trait, X, which O does not possess and which is functionally unrelated to T. Now consider the following parallel argument:

(5) Past natural selection for X helps explain why O's ancestors reproduced successfully.

(6) Anything which helps explain why O's ancestors reproduced successfully thereby helps explain why O exists.

(7) Anything which helps explain why O exists thereby helps explain why O has T.

(8) (from 5, 6, 7) Past natural selection for X helps explain why O has T.

The only difference between these arguments is the substitution of arbitrary trait X for arbitrary trait T. Yet the second argument implies that we can explain the current traits of individuals by citing past selection for completely different traits: to explain why I have an opposable thumb, I can point out that my ancestors enjoyed a selective advantage by virtue of possessing an appendix!

This information should be irrelevant, and the culprit is (3): it is not true that anything which helps explain why *O* exists also helps explain why *O* has *T*. As Sober (1995) notes, the implicitly contrastive nature of the explanandum shows how such a situation can arise:

> The fact that I have a sweet tooth explains why I order dessert in the restaurant, and why the waiter places a dessert before me. However, my taste for sweets does not help explain why I find myself facing a slice of cake rather than a dish of ice cream. The contrastive character of explanation shows how selection can explain the existence and number of offspring, without thereby helping to explain why those offspring have the traits they do. (Sober 1995, 388)

The simple argument for the positive view fails because, when we ask why some individual has the traits it does, we are asking not why O has *T simpliciter*, but why *O* has *T* rather than some alternative (or class of alternatives) *T**.[4] Because not all causes of *T*'s instantiation by *O* will be relevant in explaining why O has *T* rather than *T**, it is possible in principle for past selection to explain why some organism exists without thereby explaining its traits. This, of course, does not show that selection is *never* relevant to the explanation of trait contrasts: this stronger result requires a further argument.

To this end, Sober asks us to imagine a genealogy of uniparental organisms in which there is selection for a trait *G* against an alternative *B* (Figure 1). Sober accepts that natural selection for *G*

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[4] For discussions of contrastive explanation in general, see Dretske 1973, van Fraassen 1980, Garfinkel 1983, Lewis 1986, Sober 1994, Woodward 2003, Lipton 2004 and Strevens 2008. Strevens account will receive further attention in Section 4.

over B explains why organism 3 (henceforth: O_3) has two offspring while organism 2 (O_2) has none. He denies, however, that selection explains why organism 4 (O_4) or organism 5 (O_5) is G rather than B. Crucially, he denies this on the grounds that the following counterfactual is true:

> [I]ndividuals 4 and 5 would have had the traits they have even if organism 2 had not failed to reproduce … [and] even if organism 3 had produced more than two offspring (Sober 1995, 387).
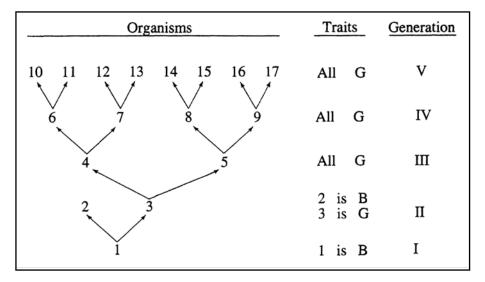

Figure 1: A genealogy of uniparental organisms (from Sober 1995).

Sober's central claim, then, is that an alternative selective regime (say, selection for B over G) would have resulted in one of two possible outcomes: either (i) O_4 and O_5 *would never have existed at all*, or (ii) O_4 and O_5 *would still have existed with the same traits they actually have*. An alternative selective regime would never, by itself, have resulted in O_4 or O_5 being B. From this, Sober infers that the selective regime does not help explain why O_4 and O_5 are G rather than B. Focussing on the traits of O_4, we can formulate Sober's argument more precisely as follows:

S1.   Selection for *G* over *B* helps explain why O_4 has *G* rather than

B only if (if there had been selection for *B* over *G*, O_4 would

have possessed *B* rather than *G*).

S2.   If there had been selection for *B* over *G*, O_3 would have either

failed to reproduce altogether or else would have produced

offspring with the same traits as its actual offspring.

S3.   (from S2) It is not true that, if there had been selection for *B*

over *G*, O_4 would have had *B* rather than *G*.

S4.   (from S1, S3) Selection for *G* over *B* does not help explain why

O_4 has *G* rather than *B*.

I do not intend to challenge the counterfactual embodied in premise S2. What I want to

challenge is the principle—embodied in premise S1—that the truth of this counterfactual implies

the explanatory irrelevance of selection. First, however, let us consider how Sober's original

argument has been modified in the light of subsequent developments.

Sober's original argument concerns one trait in one organism, and it is not obvious, on the

face of it, that the same considerations will apply for all traits and all organisms. In particular, it is

far from obvious that considerations which apply in the case of monogenic traits in haploid

organisms will extend to polygenic traits or to the traits of diploid organisms (and organisms of

other ploidies). Neander (1995) argues for an exception when traits are polygenic; Matthen (1999)

argues for an exception when reproduction is sexual. In reply to Neander, Walsh (1998) defends of

the applicability of the argument to polygenic traits; in reply to Matthen, Lewens (2001) argues that

there is nothing special about sex. I will not recapitulate these arguments here. I will simply

concede here that Sober's argument, if sound, applies to polygenic traits and to organisms of all

ploidies.

As Pust (2001, 2004) notes, Sober's original argument is invalid unless augmented with a further premise. S3 does not follow from S2 alone, because S2 leaves open the possibility that, under the alternative selective regime, O_4 still exists as the offspring of a different parent. To be valid, Sober's argument must be supplemented with the assumption that O_4 is *necessarily* the offspring of its actual parent, O_3. This assumption has been a focal point for subsequent criticism (see Pust 2001, 2004; Matthen 2002, 2003; Forber 2005). Nonetheless, to give Sober's argument the best possible chance of success, I will concede this premise too.

Putting the pieces together, the SWP argument, appropriately strengthened and generalized, runs as follows:

S1. Selection for G over B helps explain why O_4 has G rather than B only if (if there had been selection for B over G, O_4 would have possessed B rather than G).

P1. O_4 is necessarily the offspring of O_3.

S2. If there had been selection for B over G, O_3 would have either failed to reproduce altogether or else would have produced offspring with the same traits as its actual offspring.

S3. (from P1, S2) It is not true that, if there had been selection for B over G, O_4 would have had B rather than G.

S4. (from S1, S2) Selection for G over B does not help explain why O_4 has G rather than B.

W1. The same considerations apply, *mutatis mutandis*, for all trait contrasts, regardless of the complexity of the traits in question or the inheritance system of the organism in question.

Conclusion: (from S4, W1) Selection for traits does not explain the

traits of individuals.

To reiterate, I grant P1 and W1 for the sake of argument. For I contend that the protracted disputes over the legitimacy of these premises have led to the main players in the debate overlooking a central but separate issue: regardless of the status of the other premises, the argument remains of doubtful soundness by virtue of its reliance on the proto-theory of contrastive explanation embodied in S1. I want to argue that, on closer examination, this proto-theory turns out to be highly questionable.

3. Contrastive Explanation in Focus

As a preliminary remark, let me emphasize that, in attacking S1, I am not attacking a straw man: a reliance on an S1-type premise is not a dispensable feature of Sober's presentation. On the contrary, S1 (or else a very similar principle) is explicitly assumed by all recent defenders of the negative view. For Walsh (1998), to ascertain whether natural selection can explain the traits of individuals, we must ask "would altering just the selective regime alter [an individual's] genotype?" (1998, 257). Walsh argues that, since it would not, the selective regime is irrelevant. For Pust (2004), the claim that natural selection explains why an individual possesses some trait "presupposes … that some appropriate change in the selective regime would have resulted in the same individual's having a different trait" (2004, 766). Ulrich Stegmann (2010a) considers an organism x which possesses some trait A rather than an alternative trait B. He concedes, as Sober does, that natural selection helps explain why x's mother survived to reproductive age, but asks, "is it true that if the mother had died before reaching reproductive age, then x would have B instead of A?" (2010, 65). Because this counterfactual is false, he argues, the selective regime is irrelevant in explaining the

contrast (see Nanay 2010 and Stegmann 2010b for further discussion of this pivotal counterfactual). The centrality of S1 to the SWP argument is evident in all these cases.

To see why S1 is dubious, consider a more general claim of which it is a special case, the "simple counterfactual criterion" (SCC) for explanatory relevance:

SCC: *C* rather than *C** helps explain *E* rather than *E** only if: (if *C**

had occurred, then *E** would have occurred).

Counterexamples to SCC arise whenever the non-occurrence of *E** is guaranteed by more than one causal factor. Suppose I want to get to London to Paris, but my arrival is blocked by two independent factors: there are leaves on the line in London and the train drivers are on strike in Paris. The causal explanation of why I end up stuck in London, rather than successfully reaching Paris, will make reference to these factors, yet both will fail to satisfy SCC. For if the train drivers had been working, rather than striking, I would *not* have reached Paris, owing to the continuing presence of leaves on the line. And if the leaves had been cleared promptly rather than being left to pile up, I would *not* have reached Paris, owing to the continuing drivers' strike. Both factors fail to satisfy SCC because the *non-occurrence of E* is overdetermined*. In such cases, SCC is overly stringent: when we want to explain *E* rather than *E**, causes can fail to satisfy SCC yet gain explanatory relevance via their role in helping to ensure the non-occurrence of *E**.

This consideration suggests that the application of SCC in biological contexts might lead to errors if it is possible for the non-instantiation of a particular trait by a particular individual (e.g, the non-instantiation of *B* by O_4) to be overdetermined in the same way that my non-arrival in Paris was overdetermined. In fact, such scenarios are not merely possible: they are biologically commonplace.

Suppose, for instance, that we want to know why an individual moth, *M*, has dark rather than pale colouration. After investigating, we find that colouration is inherited, and that *M*'s parents both possessed the dark allele rather than the pale allele. Any reasonable criterion should allow for the obvious explanatory relevance of parental genotype to offspring phenotype. Suppose, however, that there was extremely strong selection against pale colouration, such that, *if M's parents had possessed the pale allele, they would never have survived to reproductive age*. As a result, it is *false* that, if *M*'s parents had possessed the pale allele, *M* would have possessed pale colouration. Not-*E** (i.e., the non-instantiation of pale colouration by the offspring moth) is overdetermined by two independent factors (namely, the parental genotype, and the strong selection against the pale allele) in exactly the same way that my non-arrival in Paris was overdetermined by two independent factors. The information that *M*'s parents possessed the dark allele rather than the pale allele consequently fails to satisfy SCC. Hence, either SCC is defective in this context, or parental alleles are genuinely irrelevant to the explanation of offspring traits. The latter possibility seems sufficiently absurd to warrant a preference for the former.

If SCC is defective here, however, it will be defective in many other biological contexts too. For it will be defective whenever not-*E** (i.e., the non-instantiation of the contrast trait) is overdetermined by two independent factors. Not-*E** will be overdetermined in this fashion whenever (i) the actual trait in question was inherited by the organism from its parents, and (ii) there was strong selection against the non-instantiated contrast trait, such that, if the organism's parents *had* possessed the alternative allele, the organism would never have existed at all. Whenever these conditions are satisfied, SCC will entail, absurdly, that parental genotypes are irrelevant to the explanation of offspring phenotypes. Of course, it will also entail that *natural selection* is irrelevant to the explanation of offspring phenotypes. Indeed, as the SWP argument points out, natural selection will in general fail to satisfy SCC. At this point, however, I think we might legitimately

start to wonder whether this result is owed more to the defectiveness of SCC than to the genuine irrelevance of natural selection.

4. A better relevance criterion

The SWP argument relies on an assumption regarding the nature of contrastive explanation that has evaded scrutiny in the ensuing debate. I have argued that this assumption (namely, that contrastive-explanatory relevance can be captured by a simple counterfactual criterion) is extremely dubious: SCC is defective in many biological cases. This is a reason to doubt the soundness of the SWP argument, but it is not in itself a vindication of the positive view. To defend the positive view, we need to find a better criterion for explanatory relevance, and we need to show that it *does* allow for the relevance of selection to the explanation of individual phenotypes.

To find such a criterion, we can turn to a recent account of contrastive causal explanation that succeeds where SCC fails: that of Strevens (2008, ch. 5). Strevens articulates his account in the form of the following four-step procedure:
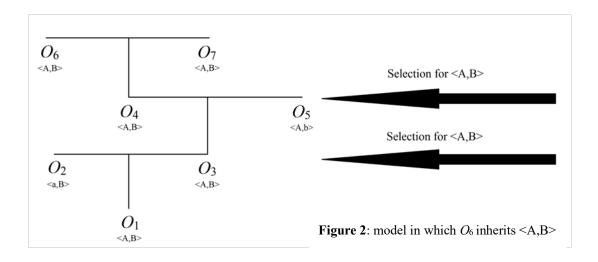
> Your task is to explain why e rather than f occurred, or for short, e-not-f. You proceed by constructing separate causal explanatory models for e and f that satisfy the following conditions:
>
> 1. The model for e is veridical; it is a (noncontrastive) standalone explanation for why e occurred.
>
> 2. The model for f is veridical except for one or more states of affairs that you might call the *switching events*. The model falsely represents the switching events as not having occurred.
>
> 3. Each of the switching events appears in the model for e. They are therefore difference-makers for e.

4. The model for f is in some sense the most plausible story as to how

f might have occurred. (Perhaps it is the model instantiated in the

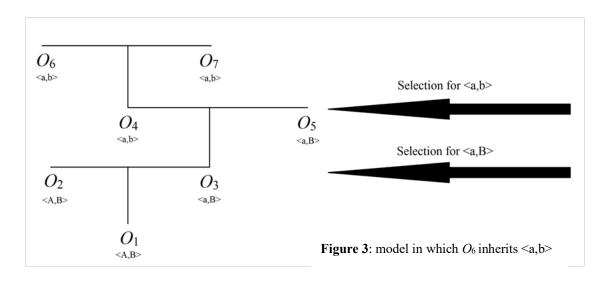closest possible worlds in which f occurs). (Strevens 2008, 175)

Strevens's procedure for explaining E rather than E^* differs markedly from the simple procedure suggested by SCC. SCC instructs to consider whether, if a cause-variable were tweaked, E^* would have ensued: if it would not have done, SCC condemns the cause-variable to explanatory irrelevance. As we have seen, this procedure is far too stringent: following it rigidly would lead us to miss straightforwardly relevant causes. Strevens's procedure is virtually a mirror image: first we construct a plausible scenario in which E^* ensues, then we look for differences between the actual and counterfactual courses of events. We look, in particular, for the "switching events" needed to turn the former into the latter. Streven's procedure copes far better than SCC when not-E^* is guaranteed by multiple factors. The most plausible counterfactual scenario in which I successfully travel to Edinburgh is one in which the weather is permissive and the train drivers compliant. The "switching events", the events one would have to change to turn the actual course of events into the contrasting scenario, are the snowfall and the strike. In this case, Strevens's procedure delivers the intuitively correct results.

We can apply Streven's procedure to show how a selective regime can be relevant in explaining the traits of individuals. Consider a population of haploid, asexually reproducing organisms. Let us focus on two loci and four genotypes: <A, B>, <A, b>, <a, B> and <a, b>. The first generation in the model contains one individual, O_1, of type <A, B>.

Figure 2: model in which O_6 inherits <A,B>

The actual course of events is represented by Figure 2. In actuality, <A, B> is fitter than <A, b> and <a, B>. The actual outcome of the process is unsurprising: new genotypes appearing in the population are selected against; and, three generations later, everyone is still <A, B>. Now consider one individual in this generation, O_6, and a particular contrastive explanandum: why does O_6 possess <A, B> rather than <a, b>?

To apply Strevens's procedure, we consider the most plausible model of how O_6 might have ended up with <a, b>. This is, of course, a model in which the relevant mutations do appear in O_6's lineage. But it is *also* a model in which the selection pressures are different; for, had they been the same, the mutations would not have been passed down to O_6 (indeed, O_6 would never have existed). There are therefore multiple switching events: mutations which in fact failed to occur would have needed to occur, and selection pressures which actually obtained would have needed to be different (Figure 3).

Figure 3: model in which O_6 inherits <a,b>

This case demonstrates that, if Strevens's model of contrastive causal explanation is on the right lines, there is at least one scenario in which natural selection is relevant in explaining the traits of individuals. But how widely will such considerations apply? In broad terms, we can see that they will apply for any contrast T-rather-than-T^* such that any plausible model for the possession of T^* by the individual concerned involves a change to the actual selective regime. Such a situation will typically arise because: (i) T is prevalent in the actual population, (ii) the intermediaries between T and T^* would be strongly selected against under the current selective regime, and (iii) T^* could not plausibly have appeared without such intermediaries. It is not difficult to come up with contrasts that meet this relevance criterion: one simply has to think of contrasting traits that are likely to be separated from an actual trait by a deep valley of unfit intermediaries. If we ask, for instance, why a particular insect resembles a stick rather than a leaf, why a particular fish has gills rather than lungs, or why a particular bat has fur rather than feathers, then selection for those traits—and selection against any mutations in the direction of the contrasting alternative—will qualify as switching events. Strevens's relevance criterion vindicates the positive view in such contexts.

There is a particular kind of trait contrast for which these considerations seem especially salient: that of being adapted to a particular environment E rather than to an alternative environment E^*. When we ask why some particular organism is adapted to E rather than E^*, it seems highly

likely that any plausible model for the contrasting outcome will involve a change to the selective regime. This is because, more or less by definition, *E* will select against any mutation that makes an organism less adapted to *E*. Hence, unless the selective regime imposed by *E* is exceptionally weak or *E* and *E** are exceptionally similar in their demands, the selective forces will need to be different in the contrast model for adaptedness to *E**. This gives us reason to suspect that Strevens's procedure vindicates the positive view precisely where we need it most: in the explanation of an individual's adaptedness to its particular environment.

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