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What is Natural Selection?

Björn Brunnander

Abstract:

‘Natural selection’ is, it seems, an ambiguous term. It is sometimes held to denote a consequence of variation, heredity, and environment, while at other times as denoting a force that creates adaptations. I argue that the latter, the force interpretation, is a redundant notion of natural selection. I will point to difficulties in making sense of this linguistic practice, and argue that it is frequently at odds with standard interpretations of evolutionary theory. I provide examples to show this; one example involving the relation between adaptations and other traits, and a second involving the relation between selection and drift.

Key words: Adaptation, Drift, Force metaphor, Natural selection

Introduction.

Ever since Darwin there has been an ambiguity in usage of the term ‘natural selection’. It is sometimes taken to denote a *consequence* of other factors; explicated in terms of differential reproduction/change in frequency due to fitness differences (Wilson 1975, p. 589; Endler, 1986, p. 4; Ridley 1993, pp. 63-64; Futuyma 1997, p. 365). On such an interpretation selection is a consequence of there being variation in (heritable) characteristics that matter in the prevailing circumstances.ⁱ However, as is well known, selection is frequently spoken of as a force that causes, creates, builds, shapes, or programs. We seem to have two different readings that I will call, respectively, *the consequence interpretation* and *the force interpretation*. These different senses frequently co-reside in the same accounts without comment, and I agree with Walsh et al. (2002) that this merits some consideration.

Darwin himself explicated ‘natural selection’ as the “...preservation of favourable individual differences and variations, and the destruction of those which are injurious...” (Darwin, 1859/1998, p. 108), in which case it is a consequence of properties of existing varieties and of environmental features. However, he also spoke of selection as that which *causes* preservation and destruction of varieties (p. 112), in which case it is presumably a label for environmental factors. He explicitly admitted to personifying natural selection as an agent of change, analogous to the role played by man in artificial selection (p. 111). In artificial selection, man is certainly an environmental factor operating on the population at

hand rather than a *consequence* of variation and environment. Now to three modern examples of this coexistence of non-equivalent notions of selection:

Evolutionary psychologists John Tooby and Leda Cosmides hold that “[w]hat is most compelling about Darwin’s approach is that the process of natural selection is an inevitable by-product of reproduction, inheritance, and mutation.” (1992, p. 51). Taking the liberty of substituting this notion of selection for tokens of ‘selection’ elsewhere in the same text yields, for instance, that biological functionality is “...traceable originally to the operation of [an inevitable by-product of reproduction, inheritance, and mutation] on reproducing systems...” (pp. 53-54), and that “...[an inevitable by-product of reproduction, inheritance, and mutation] is the single significant anti-entropic or ordering force orchestrating functional organic design...” (p. 55). It doesn’t sound entirely right to assign the ability to *operate* and *orchestrate* to an inevitable consequence *per se*, so I think we should conclude that the authors are varying their usage of ‘natural selection’.

In *The Blind Watchmaker* Richard Dawkins asks: “How could such a simple idea go so long undiscovered by thinkers of the calibre of Newton, Galileo, Descartes, Leibnitz, Hume and Aristotle?” (1986, xv-xvi). The idea is, according to Dawkins, “...that non-random reproduction, where there is hereditary variation, has consequences that are far-reaching if there is time for them to be cumulative.” (xv). It is clear that in speaking of a “simple idea” Dawkins has the principle of natural selection *per se* in mind; the fact that unicellular organisms can have descendants like us is presumably not a *simple* idea. Dawkins seems to suggest that the discovery of this principle would have impressed the pre-evolutionists in question. However, this is not all that likely. It should be noted that on standard explications, as the ones referred to above, the principle of natural selection is entirely consistent with essentialism. Assume that organisms could never deviate to any substantial degree from their ancestors. There could still be heritable variation, the differences could sometimes be connected to different abilities to cope with life, and there could be changes in frequencies that reflected such differences; thus natural selection. However, in such a world the changes would all occur within the “limits of the essence”; sometimes slightly larger individuals may be favoured, sometimes smaller, sometimes those with more fur, sometimes those with less. Since the principle of natural selection as such doesn’t specify the range of possible variation it is common ground for evolutionists and essentialists. The difference is that while the principle isn’t particularly important to essentialists, evolutionists need, or at least once needed, to *stress* it in order to show that directionality in the production of new varieties isn’t required to have new adaptations arise.

So, what difference would the principle of natural selection have made for the pre-evolutionists Dawkins has in mind? If essentialism was in fact true then *no time in the world* could make for any significant accumulation. No thinkers, whatever their calibre, can gather that essentialism is false *merely* by grasping that change in the frequencies of types is to be expected given heritable variation in fitness. Unless your mind is set on questioning essentialism on other grounds, stumbling on the principle of natural selection will most likely not strike you as something to write home about. What these considerations indicate is that Dawkins is combining an interpretation of ‘selection’ which is consistent with essentialism, the “simple idea”, with an interpretation where the term denotes causal factors that render essentialism less likely, in which case it is *not* a simple idea.

Daniel Dennett (1995) is my third case in point. He speaks of Darwin having “...discovered the power of an *algorithm*.” (p. 50, emphasis in original). The algorithm is the principle of natural selection for which Darwin, according to Dennett, provided a “short and sweet” deductive argument. (p. 48). However, this principle could have been accepted with the same short and sweet deductive argument in a steady-state world with species means fluctuating within the limits of the essences. It simply cannot be any power on the part of this algorithm that accounts for the fact that our world is not like that; the algorithm is not powerful *in itself*. Thus, it seems that Dennett really wants something with the power to make adaptations from non-adaptations, while what he really invokes is the *per se* powerless principle that can be settled with a short and sweet argument.

So, ‘selection’ does not always stand for *differential reproduction/frequency change that reflects differences in fitness*. Then, what is the alternative interpretation? There are at least three possible *force interpretations*, but I will argue that none of them comes out as a clear and non-redundant alternative. Still, it may be held that force-talk is a harmless and convenient tool for expressing evolutionary considerations. To this I will argue that at least some contexts *suffer* from talk of selection, and random drift, as forces, and that adopting consistently the consequence view amounts to conceptual progress. One such context involves claims that adaptations are created (shaped, programmed...etc) by natural selection. The second case I will consider involves claims regarding the relation between selection and drift.

Before turning to discussing the force interpretation(s) I will present what I take to be a standard account of selection in terms of the consequence view.

A standard account of selection qua consequence.

Darwin faced a situation where evolution, to him and at least some of his contemporaries, seemed to be worthy of consideration (Darwin 1859/1998, pp. 6-17, 19-20). What was needed was an account of how this change over time happens. A constraint on such an account was that it had to be able to “save” increases in functionality. Those who accepted evolution as a fact had to find a way to explain an increase in functional complexity in a sequence of types in a lineage, each resulting from its predecessor: $T_1, T_2, T_3 \dots T_{n-1}, T_n$. Darwin’s account of natural selection deals with the question by vastly increasing the number of generations, and by pointing to variation within generations. That is, it points out that T_1 -individuals did indeed give rise to T_2 -individuals, but also to $T_{2i} T_{2ii} T_{2iii} \dots T_{2.n}$, many of which were unsuccessful at survival and reproduction. This means that the explanandum is somewhat changed. There is no longer any point in asking particularly what makes T_1 give rise to T_2 . Let T_{2v} stand for all the varieties that T_1 -individuals produce as offspring. The question must then be: How can T_1 give rise to T_{2v} ? However, prior to Darwin the question about the sources of modification was regarded as crucial because it was thought to hold the key to evolution, since some such sources were assumed to produce change tending towards increased, and more adaptive, functional complexity. That is, the explanandum was seen as a tendency to produce marginally “superior” offspring. Darwin’s account is that there is no such tendency to explain.ⁱⁱ With the Darwinian solution the question about the sources of modification loses much of its importance. Direction is explained not by the sources of modification, but by the causes of differences in survival and reproduction between individuals (Sober, 1984, pp. 147-155, captures this switch of explanandum). No notion of a directional force survives if we ask why T_1 gives rise to T_{2v} , why T_2 gives rise to $T_{3v}, \dots$ etc.

If there is variation in many respects there will presumably also be variation in respects that matter for survival and reproduction. Whatever the circumstances are they will not likely provide all varieties with equal opportunities (perhaps only a divine creator could make *such* circumstances). Thus, given that like (by large) begets like and that the units of inheritance are sufficiently non-blending, there will be changes in frequencies of types that reflect differences in abilities to cope with prevailing circumstances. On standard definitions/explications such changes *are* natural selection (to repeat those references: Wilson 1975, p. 589; Endler, 1986, p. 4; Ridley 1993, pp. 63-64; Futuyma 1997, p. 3). On this interpretation then, natural selection is something that happens as a result of the existence of individuals with heritable differences that make a difference for survival and reproduction. Given the falsity of essentialism, and thus a potential for “unlimited” accumulation, and given

time, life-friendly environments can be filled with functional complexity. Different environments will, of course, tend to support different forms. The beauty of this view is that there is no need to invoke any particular directional *force* in order to make this happen. Natural selection is something that occurs due to, roughly speaking, variation, heredity and environment, *not* something that must be *added* to make things occur, and thus not something that brings any causal impact of its own. This interpretation is the *consequence view*.

Now, since selection *is* frequently spoken of as a force we would seem to need an interpretation that makes it come out that way. Whatever that interpretation will be there is reason to believe that it must be consistent with the account of selection I presented above (more on this in the next section). This is after all just the standard view. If there is disagreement this is not about how selection works. The issue is rather: *To what aspect of the process does the term 'selection' refer?* The consequence view replies to this question by saying that the term refers to a consequence of variation, heredity, and environment that is *not* to be regarded as a force that causes evolution. Recent accounts that argue for this view are Matthen and Ariew, 2002, and Walsh et al., 2002 (there is much agreement between my general outlook and the ones presented in these papers, but my approach is different from both).

Selection as force.

The practice of speaking of selection as a force was begun by Darwin himself in his personifying of selection. Selection is spoken of, in analogy with a human breeder, as that which scrutinises (Darwin 1859/1998, p. 112), that for which varieties are visible or not. Today, selection is frequently claimed to create, build, favour, pick, shape, or install programs. It is reasonably clear that Darwin intended his way of speaking to be *consistent* with the account I presented above; selection is what follows given certain conditions, *and* it is spoken of as a force. Elliot Sober is perhaps the most well-known current exponent of the view that selection is a force (See Sober, 1984, esp. Ch. 1), and he states explicitly that he intends this to be consistent with the view that selection is a consequence (personal communication). A further indication supporting this (should you suspect that Sober misreports his views) is found in Walsh et al. (2002, p. 468). Here the authors argue against the idea that selection and drift are forces. They discuss Sober's position and conclude: "Ironically, Sober's reason for thinking that selection and drift are forces is our reason for thinking that selection and drift are appropriately statistical..." (468). This seems to be saying

that Sober's argument is consistent with the consequence view (Walsh et al. do not use this very term, but on their interpretation selection is a "mere consequence" (p. 453)).

Now, Darwin and Sober do not exhaust the class of force-speakers, but I think what has been said sufficient to assume that what is at stake is the reference of the term 'selection', not the workings of the evolutionary process. So, how does 'selection' refer to a force that causes evolution? I have been able to uncover three candidate interpretations that have some *prima facie* plausibility; (1) a wide interpretation where 'selection' denotes the whole process; (2) a narrow interpretation where it denotes environmental features; and (3) an interpretation where the term denotes (at least some) organism-environment interactions. I will discuss these alternatives in turn.

The wide reading.

A wide alternative would be to interpret 'selection' as referring to the whole process, that is, to all of the factors that yield functional complexity. This would guarantee that 'selection' stands for something with an independent causal contribution. In this sense it would also stand for something that is incompatible with essentialism since it would include the "limitless" nature of variation. As far as I can tell, this interpretation is the *only* candidate if the force interpretation is meant to rule out essentialism.

However, if the intention with this wide reading is to capture *all* factors that account for adaptive complexity it won't be able to support the commonly accepted distinction between selection and drift. This since it is likely that some complex functional structures depend on past drift fixations (I will return to this issue in Selection vs. Drift section). Furthermore, this interpretation really fails to make sense of *most* occurrences of 'selection'. Ever since Darwin selection has been spoken of as *that which* scrutinises, picks, chooses, favours, ...etc. This usage demands selection to be *separate* from mutation and heredity, something that is frequently made explicit in discussions on the impact of selection. The separation is evident in remarks such as: "Natural selection may only subtract, but mutation can add." (Dawkins, 1986, p. 206), and: "Darwin's theory of natural selection had three essential ingredients: variation, inheritance, and selection." (Buss et al. 1998, p. 534). So, we must consider a *narrower* interpretation. One way to make sense of this is to interpret 'selection' as signifying the environment, or parts of it.

The narrow reading.

Given mutation (taken widely as the source of variation) and heredity, it is *environmental factors* that favour or disfavour varieties, and so cause frequencies to change. This interpretation gets good support from exercises of substitution. Here are a few examples from the philosophical literature on selection: Francisco Ayala writes that natural selection “...favored genes and gene combinations increasing the functional efficiency of the eye.” (Ayala 1970, p. 6) , Karen Neander that blood-pumping hearts were “...favored by natural selection.” (Neander 1991, p. 168), and Elliott Sober claims that selection “...may account for why particular organisms survive and why they enjoy a particular degree of reproductive success.” (Sober 1984, p. 152). Here we can substitute ‘environment’, ‘prevailing circumstances’ or the like for ‘natural selection’. Consider also Dawkins’ claim that selection *subtracts*; it seems straightforward to interpret this as claiming that *environmental factors* subtract from the existing variation. This usage is clearly in line with Darwin’s personifying application of ‘natural selection’, modelled on the breeder scrutinising his herd; the breeder does indeed favour traits, and does indeed account for why individuals “enjoy a particular degree of reproductive success”.

I think there is an entirely clear sense in which environmental factors can be said to favour or disfavour traits. However, a basic problem with this interpretation is that it seems utterly redundant. With the notion of natural selection Darwin, and Wallace, did *not* add to the array of factors that may impinge on individuals and determine their fates. Selection and drift are not to be lined up alongside gravity, wind, fog, and properties of visual systems to account for why someone fell off a cliff (see Matthen and Ariew, 2002, pp. 62-65, and Walsh et al 2002, p. 67, for discussion). Rather than focusing on environmental factors *per se* Darwin and Wallace pointed to a consequence of there being individual differences in coping with such factors. Given this, there is no reason why the narrow reading of ‘selection’ should be needed. We have plenty of ways to talk about environmental features, but we do not have plenty of ways to designate changes in frequency that reflect differences in fitness.ⁱⁱⁱ We talk in general terms of selective regimes, ecological stresses, environmental conditions, or the like, and we also speak more specifically of predators, climate, mates, and so on. I find it simply odd to insist that ‘selection’ should be used to refer to environmental features *per se*. Now, I doubt that anyone would explicitly argue for such an interpretation. Should there be those who intend it seriously they should be concerned about the prevalence of definitions not consistent with their views. The fact that such concern is totally absent indicates that people are not really committed to this interpretation.

The interaction reading.

The third and last alternative I will consider is one that holds that ‘selection’ denotes, not environmental features *per se*, but rather environment-organism *interactions* (henceforth E-O interactions). These interactions are then what causes traits to spread.

One question for the interaction reading is whether E-O interactions, rather than environmental factors *as such* need to be invoked. Consider cases where some trait is said to be *favoured by* selection, or when a change is held to be *due to, effected by, caused by* selection. In such cases it seems that nothing is left out if we speak of environmental factors as exhausting the causes of change. This is a very general point. In saying that someone was injured by a car we presuppose properties of bodies and refer to the car as the cause. It is certainly true that the injury is due to a car-body *interaction*, but while invoking such interactions as causes may be *permitted* in current practice, it is not *mandatory*. I fail to see a substantial difference in outlook between, on the one hand, invoking a factor F as cause while presupposing another factor G and, on the other, invoking the F-G *interaction* as cause. In any case, and returning to the evolutionary issue, there seems to be nothing missing if we hold environmental features *per se* to be the causal relata. Given the existing range of variation, including the mechanisms of inheritance, we can account for the proliferation of a trait as something caused by environmental factors. So insisting that ‘selection’ denotes E-O interactions does not establish the need for such usage to point to evolutionary causes.

I stressed in the previous section that Darwin and Wallace did *not* discover a formerly unknown cause of individual success or failure. Nor did they discover a formerly unknown kind of organism-environment *interaction* for which they needed a term. They pointed to the aggregated *consequences* of generally well-known interactions. Still, even if ‘selection’ does not denote an *additional item* in the causal inventory of our world we may still find it useful to have a term that refers to some aggregate of causal factors. We presumably do such things all the time, and the habit is not controversial. So, for instance, it seems quite acceptable to speak of *high-risk behaviour* in some context, referring to a wide variety of risk-taking manners. However, it seems less acceptable to claim that ‘high-risk behaviour’ denotes a *force*.

Perhaps defenders of force-talk argue that ‘selection’ denotes causal factors, even if those factors are not forces (I take this to be Sober’s position (personal communication), and Christopher Stephens (2004) seems to fit this description as well). But even this position is problematic. If ‘selection’ really refers to some aggregate of causal interactions it would be

good to be able to say *which interactions* belong to that aggregate. Consider Darwin's own claim that natural selection is the "...preservation of favourable individual differences and variations, and the destruction of those which are injurious..." (Darwin, 1859/1998, p. 108). Intuitively this may seem to capture the notion of selection qua E-O interactions, and thus to support such an interpretation. But, which preservation and which destruction? "Fitness-blind" factors will sometimes happen to preserve favourable variations or destroy injurious forms, and such interactions should presumably not count as selection, at least not if the selection-drift distinction is to be upheld. It is quite reasonable to take Darwin to refer to an expected population-level consequence of variation in fitness rather than to some subcategory of interactions consisting of the selection-events.

As long as we stick with human breeders there may be a fact of the matter which of their interventions are motivated by the *intention* to favour some specific trait. Perhaps it seems as if things should be as clear in nature at large. I think this is mistaken. When intention is excluded from the picture, the question of which interactions constitute selection comes to lack determinate answers (see Matthen and Ariew, 2002, pp. 62-65, on the elusiveness of definitions of 'selection' and 'drift' in terms of individual-level interactions). Evolutionary biology at large neither provides determinate answers to such questions nor needs to. For instance, Tinbergen et al. (1962) gathered evidence for the hypothesis that eggshell-removing behaviour among gulls was due to the fact that eggshells drew the attention of predators. His investigation is generally considered as corroborating a selectionist hypothesis. But the success of his investigation did not require an answer to the question: *which* individual events were selection-interactions? We need to ask: How can that *not* be a problem for evolutionists? A good answer, I think, is that 'selection' does not denote a specific subclass of interactions, so there is no need to provide criteria for membership in that subclass.

We have the following situation: There is no obvious need to invoke E-O interactions rather than environmental factors as such in order to account for evolutionary causation. The question as to whether a particular individual interaction is an instance of selection is left without interpretation. If we want to keep the distinction between selection and drift, there is no current proposal that helps us to determine which E-O interactions constitute selection. It is not a case of "merely" lacking a reliable method, we lack an interpretation of the question itself. It is clear that evolutionary biology can thrive just the same. These considerations make me doubt the interaction reading of 'selection', *and* doubt that biological practice supports such an interpretation.

To sum up the discussion so far: We do have a reasonable account according to which ‘selection’ denotes a consequence of heritable variation and environment. It may sound non-standard and odd to say that changes *are*, or *constitute* selection (or drift), rather than that they are *caused by* selection (or drift). Still, this is entirely in keeping with prevailing explications and it remains to be shown that something is missing in such formulations. We do not have a clear, non-redundant proposal according to which ‘selection’ denotes a cause of evolution.

Now, my discussion so far has presupposed that force-talk belongs at the serious end of the scientific repertoire. However, one may deny this. Perhaps force-talk is just an informal but convenient and timesaving manner of speaking of somewhat unspecified aggregates of evolutionarily relevant factors. In what follows I will question even this claim. I will argue that force-talk is less useful than commonly thought; much talk of selective forces fails to map onto any reasonable interpretation at all. Force-talk sometimes masks conceptual oddities, and is likely to breed a dim understanding of evolutionary matters.

First a note on exposition: When I use the terms ‘selection’ and ‘drift’ in what follows I intend a consequence interpretation; the former stands for changes in frequencies to the extent they reflect differences in fitness, the latter for frequency changes to the extent they are random with respect to fitness.^{iv} When speaking of what *causes* changes I will talk of environmental factors, prevailing circumstances, and the like. Since force-talk is prevalent in discussions of the making of adaptations I will, in relating to these discussions, sometimes use the terms according to this practice. I will then write “selection (force)” and “drift (force)”. This is not to be seen as an endorsement of this practice but merely as a device to relate to prevailing expositions.

Adaptations and dysfunctional traits.

Only those who survive and reproduce will give rise to new variation, and survival and reproduction are determined by interactions with the environment. Given differences in fitness, “sieving” will tend to be non-random. Given “limitless” variation, *prevailing* or *recurring* circumstances can make for *accumulation* of useful structure. This dependence on environment is what makes for claims about the powers of natural selection (force). An important underlying assumption is that a particular structure is not equally close to any other structure from a developmental point of view. A mutation yielding an individual of the trait type T_n might be more probable with a T_{n-1} -parent than with a T_{n-2} -parent.^v So, if the environment is such that T_{n-1} replaces T_{n-2} , this increases the probability of a mutation producing T_n . We may apply this same consideration to earlier events in the chain, spelling

out the dependency of current forms on past environments. No mutation will make an eye in a world where there are no proto-eyes, so eyes owe their existence to environments favourable to increasingly complex proto-eyes.

These considerations point to a symmetry that I believe is generally overlooked. The role of prevailing (recurring) environmental conditions in making traits possible is *not* limited to the making of *adaptations*. If T_{2V} stands for the totality of non- T_1 - varieties springing from T_1 , then we must say that all the types T_{2V} are accounted for in the same way by past circumstances. At a given time, all tokens with a common ancestry owe their existence to the reproductive success of those common ancestors. This dependency on past circumstances is thus *not a difference-maker* between adaptations and many other structures, including “spandrels” (traits that are not part of any adaptation but that result from developmental necessity as adaptations develop) and dysfunctional traits. Prevailing circumstances do not “build” or “produce” adaptations by different means than they “build” or “produce” the *mutant cousins* of adaptations. A single mutation can be enough to make a complex organ, such as the eye, severely deformed and dysfunctional. A particular kind of dysfunctional eye is still a morphologically unique structure, the existence of which would be a miracle had not past environments been favourable to a long line of increasingly complex proto-eyes. Perhaps we are disinclined to marvel at severely dysfunctional organs, but it takes our universe as much time and effort to create such structures as the ones we do marvel at.

The reason I claim that the symmetry in question is overlooked is that it is hard to reconcile with strongly intentional formulations of evolutionary claims; such claims as: adaptations have been *created by*, or *programmed by* selection (force), or that they are *responses to adaptive problems*. I take it for granted that we intend to deny purpose in evolution. I also assume that locutions as the ones mentioned are intended as ways of speaking about the causal history of traits. If so, I would be entitled to claim that my organ O was programmed by natural selection (force), or that O is a response to an adaptive problem posed by a challenging environment, even if O happened to be severely deformed. The very same “programming sequence” of challenging environments that accounts for the existence of well-behaved tokens accounts for my O. My hunch is that evolutionists do *not* intend traits such as William’s syndrome or harelip to be regarded as programmed by natural selection (force). But as far as causal history is concerned, they are. Having a harelip depends on having successful ancestors with (ordinary) lips. Here is an example to support my hunch: Evolutionary psychologist David Buss claims that the evolutionary process yields three products; adaptations, by-products, and noise (2004, p. 38). Adaptations are “fashioned by the process

of selection.” (p. 40). Noise products, however, are the result of mutation, sudden changes in environment, or developmental accidents (p. 41). It appears that on this view, the success of ancestors won’t count as contributing to a current token if it is “deviant” from an adaptive point of view. But it should be obvious that no factors in the world can *undo* the dependence of a current harelip on the past circumstances in which lips thrived.

If we were to adopt the consequence view and thus think in terms of the cumulative impact of past environments, it would be obvious that all variation, from the highly adaptive to the utterly dysfunctional, is on a par as regards their successful ancestors. Then, if the purpose-invoking expressions in use are intended as causal accounts of the existence of current traits, such expressions must apply to deviants as well. It is doubtful whether talk of programming and such is at all tempting given the consequence interpretation. This view is less friendly to the inclination to think in terms of purpose.

Of course, adaptations *are* special, but as for their *effects* rather than as for the factors that make them. There is indeed a distinction between traits/effects that account for the establishment of particular varieties, and traits/effects that are negligible in this respect (it should be obvious that this consideration does not separate all *token* adaptations from all *token* non-adaptations). However, the current point is that this is *not* a distinction between traits that have been created, programmed, or exquisitely moulded by prevailing environmental features, and traits that haven’t. At least not if such expressions are *really* about non-purposive causal history.

5. Selection vs. Drift.

To repeat, it is the dependency of traits on (past) environments that underlies claims about the causal role of natural selection (force). Environmental factors cause traits to increase in frequency and this affects the probabilities of certain new varieties arising. As Karen Neander puts it: “Selection does more than merely distribute genotypes and phenotypes,...by distributing existing genotypes and phenotypes it plays a critical role in determining which new genotypes and phenotypes arise.” (Neander, 1995, p. 585). So, environments have such a role to play, but we shouldn’t treat this as something characteristic of instances of *selection* in particular. All that is required for increasing the probability of a trait T_n arising, given that T_{n-2} is at fixation (and assuming that T_n is more probable given T_{n-1} than given T_{n-2}), is that T_{n-1} increases in frequency. *It does not matter whether the change reflects differences in fitness or not.* Ever since Sewall Wright (1932/2004) it has been accepted that drift fixations *can* make

possible the evolution of structures in a lineage that would not have arisen otherwise. As for such cases, the argument that Neander applies to selection (force) would apply to drift (force).

The view that selection (force), but not drift (force), is capable of “designing” structures is a recurring theme in discussions aiming to make clear the evolution of adaptations. Now, before turning to examples we have to consider Sewall Wright’s idea of how drift fixations can make a difference. He envisaged the possibility that an adaptation can develop stepwise from a prior state even when some immediate mutational steps make for *decreased* fitness. The reason such immediate forms *could* be established is that fitness differences underdetermine outcomes in particular cases. If such a Wrightean sequence occurs the resulting adaptation is dependent for its existence on this random “walk” through lower relative fitness. I will call such adaptations *drift-dependent*. I don’t think there is any disagreement that Sewall Wright pointed out a *possibility*. Considering the sheer number of adaptations around I would think it generally agreed that *some* of them must be drift-dependent, whatever the methodological difficulties involved in detecting such dependency in particular cases.

The Wrightean scenario has consequences for how to characterise the relation between selection and drift. But many of the proposals we are offered seem not to take it into account. So, for instance, Stephen Jay Gould claimed: “I accept natural selection as the only known cause of ‘eminently workable design’...” (1997, p. 57), and Buss et al. say “Natural selection ... is the only known causal process capable of producing adaptation.” (1998, p. 542). John Tooby and Leda Cosmides claim:

The conspicuously distinctive cumulative impacts of chance and selection allow the development of rigorous standards of evidence for recognizing and establishing the existence of adaptations and distinguishing them from the nonadaptive aspects of organisms caused by the nonselectionist mechanisms of evolutionary change...(1992, p. 62).

This remark seems to point to two distinct forces producing their separate outcomes, and if the outcome is adaptation then selection (force) made it. This is simply mistaken. Traits established at random with respect to fitness may be *part of* the functional complexity of organisms and thus not separate structures, conspicuous in virtue of a “chancy” appearance. For all we know many of the complex adaptations we focus on could be drift-dependent. Looking closer at the “design properties” won’t give us the answer in such cases since the

result of the random fixation(s) is the *existence* of the adaptation rather than a lack of “design” in it.

Richard Dawkins is explicit about the possibility of Wright’s scenario. He says: “Random drift may make it easier for selection to do its job by assisting the escape from local optima...., but it is *still* selection that is determining the rise of adaptive complexity.” (Dawkins, 1983/1998, p. 31, emphasis added). I do not understand this insistence on the division of labour *given* the concession to Wright. It strikes me as an outright contradiction. *If* an adaptation is drift-dependent *then* the events involved in the drift fixation *were* involved in determining the rise of that adaptive complexity.

We seem to lack a reading that would render it true that natural selection (force) is the *only known cause* of functional design. Adopting the consequence view we should say that adaptations are, given mutation and heredity, the result of the cumulative impact of past environments *regardless* of whether all the crucial fixations reflected differences in fitness. I have no doubt that the majority of fixations of phenotypes leading to a complex adaptation *do* reflect such differences, but this is hardly a requirement for being a step in the construction of an adaptation. The claim that only selection (force) can account for adaptive complexity doesn’t translate to anything defensible.

Accepting the consequence view, we should say that variation in functionality tends to *yield* selection rather than drift. *Cumulative* drift is simply an improbable consequence in a world where fitness tends to vary. In light of this, consider the following passage by Tooby and Cosmides:

It would be a coincidence of miraculous degree if a series of ...function-blind events, brought about by drift, by-products, hitchhiking, and so on, just happened to throw together a structure as complexly and interdependently functional as the eye..... For this reason, nonselectionist mechanisms of evolutionary change cannot be seen as providing any reasonable alternative explanation for the eye or for any other complex adaptation. Complex functional organization is the signature of selection. (1992, p. 57)

It is true that *if* a sequence of fixations was, step for step, random with respect to fitness, it would be a miracle if the result was functional complexity. But is this the right miracle to focus on? It would presumably be miraculous if eyes arose from non-eyes in just a few mutational steps *even if* the fixations were non-random. In order to avoid the miraculous we

will have to assume that *very many* random mutational steps are involved. But then, what is the probability that any accumulated structure involving hundreds or thousands of mutational steps has a history of all and only “function-blind” events? Well, this depends on the nature of variation. If new varieties were, at best, equally fit as prevailing ones then fixation by drift would be standard. A wide variety of forms would have the same very low probability of arising through cumulative drift. On this scenario we would have to assume that there is a sequence of equally fit varieties ever since the primeval soup, and we certainly don’t assume that. Besides, why *would* the production of novelty be inherently constrained to yield (at best) equally fit varieties if indeed mutations are supposed to be random as regards fitness? The appearance of fitter varieties is a common enough phenomenon of life on this planet on an evolutionary time-scale. All who accept evolution will take the actual occurrence of functional complexity to establish that much. If we are facing a structure that is the accumulated result of thousands of mutations, the probability that *all* the fixations involved were random with respect to fitness is *very* close to zero. So while it is indeed true that the functional complexity of the eye would be miraculous *if* all mutations on the way were fixed randomly, it would *already* require “a coincidence of miraculous degree” to have such a long sequence of phenotypic accumulation be fixed randomly.

The very idea that drift is something that *could* operate exclusively in the long run is reasonable only on the assumption that fitter varieties hardly ever arise. So, removing natural selection (force) is quite simply *pondering the probability of the outcome given that fitter varieties never appear*. It is certainly a truism for non-creationists that the construction of complex adaptations require fitter varieties to appear frequently enough on an evolutionary time-scale. Force-talk gives us the “opportunity” to state this truism by saying: “Drift is incapable of producing complex adaptations, only selection can.”

Adaptations do not arise because a design-sensitive force rather than an indifferent one is operating, they arise because variation is “unbounded”, and because there is time. The cumulative selection of fitter varieties is the trivial consequence of this “unboundedness” and not an independent cause that needs to operate in order to make adaptations rather than messy biological nonsense. I find that much that is said about selection and drift using force-talk fails to make sense in terms of a standard understanding of evolutionary theory. The consequence view offers relief from highly non-transparent claims about the evolutionary process, and thus amounts to conceptual progress.

6. Concluding remarks

I hold that whatever linguistic practice we prefer it should be a deliberate choice reflecting judgements of theoretical virtues. We seem to have a fairly clear account according to which ‘selection’ denotes a frequent consequence of heritable variation and environmental effects, and we seem to need the term for that purpose. As far as I can tell this is the *only* clear, non-redundant account there is. Saying that adaptations, but not dysfunctional traits, are created, shaped, or programmed by natural selection (force) is coherent only on a truly purposive view of evolution. Moreover, the force interpretation seems to encourage a distorted view of the relation between selection and drift. It doesn’t make sense to claim that only selection (force), and not drift (force), can make adaptations. If there generally is heritable variation in fitness then changes will tend *not* to be entirely random in that respect. Thus such variation tends to *yield* selection rather than only drift. Given a “limitless” nature of variation, complex adaptations may result, but they may be drift-dependent.

Something is wrong with force-talk. This linguistic practice frequently fails to make sense in terms of what I take to be a standard interpretation of evolutionary theory. Perhaps one could devise a variety of force-talk which eliminates these oddities. However, this would still require a change in actual practice, and it is not clear that we would be saving anything of value.

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Notes:

ⁱ The difference between defining it as differential reproduction and defining it as change in frequency will not, as far as I can tell, matter for my present purposes. It will be a consequence of variation and environment on both counts, on the latter also of heredity.

ⁱⁱ This is admittedly a somewhat modernised version of Darwin since he himself held it open that some variety of inheritance of acquired characteristics had a part to play.

ⁱⁱⁱ It would perhaps be more to the point to speak of *effects* on frequencies rather than changes in frequencies. I do not wish to commit myself to the idea that there must be changes in frequencies in the population in order for there to be selection. We could consider the impact of different factors on a population separately. For instance, status quo could result if the “fitness-sensitive” effects of predation were nullified, during the period under scrutiny, by the “fitness-indifferent” effects of

lightning. This status quo would still partly be accounted for by differences in fitness; counterfactually, if there hadn't been differences in fitness as regards predation frequencies *would* have changed due to the skewed impact of lightning.

^{iv} I am, for convenience, disregarding other processes such as differential mutation rates and migration. The question whether *all* changes that are random with respect to fitness can be labelled 'drift' won't be crucial for my account.

^v This might seem to be inherent in the subscripts used, but these are only supposed to mark order of appearance in the lineage.

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