The Natures of Selection
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ABSTRACT

Elliott Sober and his defenders think of selection, drift, mutation, and migration as distinct evolutionary forces. This paper exposes an ambiguity in Sober's account of the force of selection: sometimes he appears to equate the force of selection with variation in fitness, sometimes with 'selection for properties'. Sober's own account of fitness as a property analogous to life-expectancy shows how the two conceptions come apart. Cases where there is selection against variance in offspring number also show that selection and drift cannot be distinguished in the way Sober hopes for. These issues have significance beyond the parochial matter of the coherence of Sober's system. There is no good principled answer to the question of which features of a population should count among the contributors to fitness. This means there is no non-arbitrary account of the nature of selection.

1 Evolutionary Forces

The question of whether natural selection and drift can be understood as forces has received a lot of attention in recent years, much of it sparked by Walsh, Lewens, and Ariew's ([2002]) attack on Elliott Sober's influential presentation ([1984]). Walsh *et al.* simultaneously discussed a number of issues that should have been kept apart, including topics relating to the interpretation of probability, the level at which selection acts, and so forth. In this article I want to narrow the focus, by looking at the specific way in which Sober and his defenders have understood the nature of selection and drift, and their status as forces. I will show an ambiguity in Sober's understanding of what natural selection

is. Usually he equates selection with variation in fitness; sometimes he equates selection with 'selection for properties'. The two conceptions are not the same, at least not given Sober's understanding of fitness as a property analogous to life-expectancy. Once this ambiguity is noted, it strains Sober's own defence of selection and drift as causes. I also show how Sober's understanding of the relationship between selection and drift is put under pressure by some cases that Sober himself has brought to the attention of philosophers of biology. These cases involve selection against variance in offspring number. Finally, I will build on these cases to draw a conclusion with significance beyond the matter of the internal coherence of Sober's system. We should not expect any good principled answer to the question of which elements of some evolutionary process should count among contributors to fitness, hence we should not expect any principled account of how we should understand the force of selection.

2 Selection and Drift

Let us recap the basic features of Sober's way of understanding drift and selection, as outlined in *The Nature of Selection* (Sober [1984]). We can understand the relationship between the two forces using an analogy with coin-tossing. In a series of fair coin tosses that is short, the chances of the coin landing heads all the time are higher than they are in a longer run of tosses. Sober argues that we can think of the length of the sequences as a variable affecting the chances of reaching a 50:50 ratio of heads to tails. The bias on the coin also affects these chances. A weighted coin is more likely to depart from a 50:50 ratio than a fair one. What happens in an actual population of organisms also depends both on the chances of surviving and reproducing of the members of that population, and on how large the population is. Sober is therefore able to distinguish drift understood as an unlikely outcome given some probability distribution from drift understood as a factor of variable strength affecting that probability distribution. On this view, the intensity of drift is inversely proportional to the size of the population. And the intensity of selection is proportional to variation in fitness in the population.

Suppose a fair coin is tossed 100 times, and it lands heads up 80 times. This is a fairly unlikely result. The figure is more likely to be somewhere around a 50:50 ratio of heads to tails. (This does not mean, of course, that the specific sequence of 80 heads and 20 tails, whatever it is, is more likely than any specific sequence of 50 heads and 50 tails.) But while we can agree that the observed outcome is unlikely, this does not occur because of some special interfering cause acting on individual tosses, which stops some from landing tails when they should. This is most obvious in the case where the coin is tossed just once. Here it may well land heads 100% of the time, but this does not reflect the action of some error-inducing cause—a freak gust of wind, say—which

strongly affects this individual toss. Similarly, in cases where the actual ratio of heads to tails is close to 50:50, there is no distinctive cause acting on individual tosses that ensures that the right number land heads and tails. Whether the ratio corresponds to the coin's chance of landing heads, or whether it departs from it, the causes acting on individual tosses are the same. Analogous reasoning led Walsh *et al.* to deny that drift was a cause acting on individual organisms, and to deny that drift was a force distinct from selection. But this sort of criticism does not undermine Sober's account. Sober's way of understanding the coin-tossing analogy made drift, which is inversely proportional to population size, analogous to the length of a sequence of tosses, and made no claim about whether drift acted on individuals or populations.

The moral Sober (and followers) tend to draw from these discussions is that we need to keep a firm grip on the product/process distinction when we discuss drift (or selection). Drift understood as 'process' simply measures the size of the population. So a very large population in which the less fit variant is the most successful might have lots of drift-the-product, but very little drift-the-process. Analogously, the case in which the fair coin lands heads 80 times out of 100 is one in which there is both drift-the-product and drift-the-process. I find the 'product/process' label a little clumsy here, for the size of a population is not a process. But Sober's distinction is important when it comes to introducing his conception of selection and drift as forces. Selection and drift count as forces because they can be assigned intensities, and because the alteration of these forces results in predictable differences in the probabilities of various trait distributions.

In a recent article, Sober and Shapiro ([2007]) give a brisk summary of this stance:

> Our view is that drift (the process) occurs in a population whenever the population is finite, just as the process of selection occurs in a population whenever there is variation in fitness . . .

Sober's understanding of drift fits well with usage among population geneticists. Even its apparent failures turn into strengths on closer inspection. One question that is important to population geneticists concerns the chances of new favourable mutations disappearing from a population as soon as they appear. This question is answered directly by appealing to the comparative fitness of the new mutation, regardless of population size. It is easy to see why this is the case: in general, the question of how likely an individual is to have offspring that inherit its traits does not depend on how many other members there are in the population. If an individual fails to reproduce in spite of enjoying a fitness advantage, then we might indeed pinpoint this individual episode as a failure of selection. We might also be tempted to attribute it to the action of drift, in

spite of the fact that the strength of the effect does not depend on the size of the population. But interestingly, it is precisely because the strength of this effect is not measured by population size that Gillespie is uncomfortable about calling it 'drift' (Gillespie [2004], p. 92).

3 Evolutionary and Newtonian Forces

Are drift and selection forces? It is best not to phrase the question as bluntly as this. Instead, one should simply ask in what respects drift and selection resemble Newtonian forces, and in what ways they differ, paying attention all the time to the dangers of a seductive metaphor. Christopher Stephens ([2004]) has already done a good job of discharging this task, and the exploration of the force analogy has been furthered by Brandon ([2006]), but a few comments remain in order. As we have already seen, selection and drift resemble forces in virtue of their taking magnitudes, the alteration of which is systematically related to the probability that a population will change in various different ways. One disanalogy with classic Newtonian systems concerns how an evolving population needs to be altered in order to remove forces from it. In Newtonian cases, we remove forces by removing material bodies. But in a finite evolving population, we remove the force of drift by adding organisms until the population is infinite in size. Since no real population is infinite in size, the inescapability of drift gives a way of justifying Brandon's recent claim that 'drift is not a "special" force in evolution; it is the default position' ([2006], p. 325). There are further disanalogies. Drift (but not selection) differs from Newtonian forces, because if two traits of equal fitness are present in a finite population, then while population size determines the chances of one of these traits being eliminated from the population, it does not allow us to predict which one will be eliminated. In this sense, drift is a force with magnitude but no direction (Sober [1984], p. 116). In a more extended sense, as Sober and Stephens have remarked, drift does have direction, because drift has a tendency to eliminate heterozygosity. Brandon counters, quite rightly, that drift has no tendency to fix any specific homozygote ([2006], p. 325). But rather than concluding that the force analogy is false for drift we should simply say that, like all analogies, it has limitations.

We can also reason backwards from population outcomes to the presence of evolutionary forces. One begins by asking how a population should behave if particular known 'forces' are in operation. Second, one sees how the population actually behaves. If there is a mismatch, we can infer that some other additional unknown 'force' was at work. This is another way in which evolutionary forces resemble Newtonian forces, but again the analogy with Newtonian forces is at best partial. The reason is that the size of a population only makes a difference to the *probable* outcome in that population. It is consistent with the 'force' of drift being very strong (i.e., the population being small) that observed trait

frequencies might correspond to what we expect on the basis of fitness values. And it is also consistent with observed trait frequencies departing severely from what fitness values lead us to expect, that the force of drift is very weak (i.e., the population is, in fact, large). In this second case, we would have made a mistake if we inferred, from the fact that the population does not change in the way that we expect on the basis of the known strength of drift and selection, that some additional evolutionary force must have affected the population. In contrast with this, if I fire a projectile and it diverges from the path predicted by the forces I know about, then a Newtonian model gives the result that some unknown force must have been at work.

This difference has further consequences. If we consider an evolving population subject only to selection and drift, we can say which forces act, we can give them intensities, and we can say what outcomes are likely given the forces that are present. But suppose the actual change is unlikely given these forces. Sober claims that we cannot say how much of this unlikely result is due to drift, and how much to selection ([1984], p. 117). So here is another disanalogy with Newtonian forces.

There is a way to compare the causal impacts of selection and drift in situations such as this one, and thereby to bring selection and drift more closely into line with the Newtonian paradigm. It follows naturally from Sober's approach, but Sober rejects it. He says:

> When a population evolves under the impact of a suite of deterministic forces, it makes perfect sense to ask what contributions the component forces made [. . .] [W]e can estimate the relative contributions of each by seeing how the trait would evolve in a population in which only one of them is at work. (ibid.)

But we can do something similar when drift and selection are present. We cannot say with certainty what would have happened if drift had been the only force. But we can ask what would have happened if selection had been the only force. This is to ask what would have happened had the population been infinite in size. And we might conclude that any departure from what would have happened under the action of selection alone is the causal result of drift. If, for example, a population is very large, and it changes in a way that departs markedly from fitness-based expectation, then we will say that weak drift has had an unusually powerful causal influence. Note that this way of accounting means we will never judge the force of selection to have had unlikely effects: whenever something happens to a population that is unlikely given the intensities of selection and drift, it will always be drift that is responsible for the unlikely outcome. This conclusion is consonant with Sober's claim that selection is a deterministic force, while drift is indeterministic.

Why does Sober reject this way of comparing selection and drift? There is a clue in his discussion of coin-tossing:

> If a fair coin lands heads up six out of ten times it is tossed, there is no saying how much its probability of landing heads contributed to this result as compared with the fact that it was tossed only ten times. (ibid.)

But had the coin been tossed an infinite number of times, the chance of it landing heads up half the time (rather than six-tenths of the time) would have been arbitrarily close to one. On this reckoning, Sober's way of thinking about forces might lead us to say that the coin's only being tossed ten times is responsible for its landing heads once too often.

This sounds silly, and the reason why it sounds silly cements a further suspicion one might have about regarding selection and drift as forces. When tossing a fair coin, it is odd to think of its fairness as a deterministic force, which guarantees that it lands heads up 50% of the time, so long as other forces—such as a short run of tosses—do not interfere. Yet this is exactly how Sober thinks of selection. Instead, one could think of the coin's fairness as an indeterministic factor, giving the coin a probability of landing heads that varies depending on how many times it is tossed. This, I take it, will be the sort of thing that propensity theorists of chance are likely to say. Mellor, for example, characterizes chances as dispositions to produce limiting frequencies (e.g., [2005], p. 50).[1] But if a coin's fairness is a disposition to produce some hypothetical frequency of heads in the limit, that same disposition also confers probabilities on alternative frequencies of heads and tails in shorter runs of tosses. In the same way, one might think of selection as an indeterministic force, which gives a population a probability of changing that varies with the population's size. Sober's own reason for refusing to compare the causal efficacy of drift and selection makes it clear that when he claims that selection is a deterministic force, this is not intended to amount to a fundamental metaphysical truth. Rather, it is an artefact of a particularly valuable way of comparing populations, by reference to their size and their variation in fitness, understood as two independent variables. As he puts it:

> . . . the decomposition of an evolutionary process into its deterministic and stochastic components may seem rather contrived. Could one not just as easily construe coin tossing as having two components, one 'deterministic', the other 'stochastic'? [. . .] The reason is to facilitate comparison among different populations. ([1984], p. 115)

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[1]   Mellor argues persuasively that, strictly speaking, we should think of propensities as properties of coin tosses, not of coins themselves: we should focus on a fair toss, rather than a fair coin. This complication has relevance to the propensity account of fitness, but I will not pursue the issue in this paper, and the complexities it introduces do not undermine the point made about the deterministic nature of selection.

Sober also agrees with the view that we should see force talk in evolutionary theory as an analogy, to be judged by how useful it is. Selection and drift are, as Sober himself stated in his original 1984 discussion, similar to Newtonian forces in some ways, and dissimilar in others. Acknowledging several differences, Sober says of force-talk that 'nothing much hangs on this terminology' ([1984], p. 117). So we should read Sober as defending a deflationary view of evolutionary forces: it simply mistakes Sober's intentions to attack him by claiming that the analogy with Newtonian forces is less than perfect. The preceding discussion is valuable because it allows us to isolate two central elements of Sober's account of drift and selection that are suitable targets for attack. Sober believes that selection and drift are *distinguishable causes* of evolutionary change. In Sections 4 and 5 of this paper I raise problems for Sober's effort to show that selection is a cause. In Section 6 I raise problems for the specific manner in which Sober seeks to distinguish selection from drift.

4 Is Natural Selection a Cause?

Although I have shown some sympathy with the view of natural selection and drift as forces, I have hedged up to this point on the question of whether they are causes. It is obvious that the claim that natural selection is a cause does not entail that it is a force akin to Newton's forces. Plenty of causes—the genetic and environmental causes of disease, for example—bear only a distant analogy to Newtonian forces in terms of their comparability. What may be less obvious is that the claim that natural selection and drift are analogous to Newtonian forces in various respects does not entail that they are also causes. Consider, for example, the contributions the sides of a rectangle make to the rectangle's area. If the shorter side is increased by some unit, this has a greater influence on the area of the rectangle than if the longer side is increased by the same unit. One might say, I suppose, that the area of the rectangle can be attributed to the influences of two independent forces, and that changes to the shorter side exert a greater force on the overall area than changes to the longer side. Admittedly, the analogy with forces is weak, but one might see these 'influences' as sufficiently force-like to make talk of 'forces' appropriate here—after all, for Sober force-talk is licensed simply by the fact that it enables us to compare populations, and we can also make comparisons in the context of rectangles. Yet suppose we are talking not about the sides of a rectangular cornfield, but the sides of an abstract geometrical rectangle. I take it that no one will think that the lengths of the sides of such a rectangle cause the rectangle's area. Similarly, even if one agrees that population size and fitness differences have a force-like relationship with respect to changes in trait frequencies in a population, it does not follow that they must be understood as causes of those frequency changes. Indeed, if I am right that Sober's defence of the force view should be regarded

as deflationary in style, we should not expect it to lead in any straightforward manner to more metaphysically loaded conclusions about the causal status of drift and selection.

A number of recent articles have argued that natural selection and drift are causes, on the grounds that selection explanations and drift explanations satisfy Woodward's ([2003]) manipulability criterion for causal explanation (e.g., Reisman and Forber [2005]; Sober and Shapiro [2007]). The manipulationist argument works like this. We define natural selection as a force (or factor, fact, influence, or whatever) that exists whenever there is variation in fitness in a population. The existence of variation in fitness then makes probable some further population change. Alter the variation in fitness, and one alters the likely later state of the population. One comparative fact—individuals of one type being better able, on average, to survive and reproduce, than individuals of another type—causes another comparative fact—the increase in frequency of individuals of the first type. We equate drift with population size. This can be manipulated, too, and once again these manipulations result in predictable differences in population composition. Since both the selection and drift can be manipulated in ways that have systematic impacts on population outcomes, both selection and drift are causes.

5 An Ambiguity in Sober's Account of Selection: Variation in Fitness versus Selection-for

The manipulationist account requires that we put some constraints on admissible variables on which one might intervene. The manipulationist will want to deny, I presume, that an abstract geometrical rectangle's area is caused by its length or width. So the manipulationist must deny that length and width are appropriate targets for intervention. The question of exactly how this might be achieved is not something I will discuss here. But it does seem that the manipulationist defence of the causal efficacy of the force of selection is difficult for Sober to follow in its basic format, because Sober denies that fitness is a causal property. Sober believes that fitness is not itself a causal disposition, but instead is a summary of other causal dispositions, dispositions that make a difference to the ability to survive and reproduce. This is why Sober says that fitness is like *life-expectancy* ([1984], p. 95). On Sober's view, life-expectancy is the result of an actuarial calculation that takes into account death from all *potential* causes—whether they act or not—to yield an overall probabilistic expectation for longevity. Similarly, fitness is the result of an analogous calculation that takes into account possibilities of death and of reproduction at all potential ages to yield an overall probabilistic expectation for reproductive output. In this paper I will assume that Sober's argument for the non-causal nature of fitness is a good one. The worry is that if fitness is not a causal property, and

selection is variation in fitness, it is hard to see how selection could be a causal force.

In response to this, Sober and Shapiro ([2007]) say that 'Walsh, Lewens, and Ariew ([2002], p. 466) equate selection with variation in trait fitness; as a result they focus exclusively on selection-of and neglect the concept of selection-for. But selection-for is where the causal action is'. At times, it also seems that Sober and Shapiro equate selection with variation in fitness, so it is unclear whether they regard this equation as an error. (Recall their comment that 'the process of selection occurs in a population whenever there is variation in fitness'.) The most charitable interpretation, also suggested by Sober's own earlier work, is presumably that while he and Shapiro say that selection occurs 'whenever' there is variation in fitness, they do not mean to equate selection with variation in fitness. Whatever the proper exegesis, I will show that the two concepts are not extensionally equivalent.

Sober's argument for viewing fitness as a property akin to life-expectancy turns on the thought that even if a trait makes a positive contribution to fitness, it does not follow that the trait causes the success of the organism in question. Here is an example that Sober used back in 1984:

> Suppose an organism has a certain chance of surviving predation and another of surviving a disease. Suppose, further, that, as it happens, the individual is attacked by a predator and escapes but is never exposed to a disease. That is, exposure to a disease is a possibility that is never actualised. In this case, to cite overall fitness as a cause is to blend together a true account of what the actual cause was with an irrelevant account of what the cause might have been, but was not. ([1984], p. 91)

Sober's line of thinking helps to show us that selection understood as variation in fitness is not equivalent to selection understood as 'selection for properties'. Consider a case rather similar to the one Sober presented us with. In every year, a population has equal high chances of being affected by malaria, cholera, and smallpox. The three diseases are equally deadly for those whom they affect. Suppose that there are two types within this population. The Cholpoxes are resistant to cholera and smallpox, but not to malaria. And the Mals are resistant to malaria, but not to cholera and smallpox. Since, for Sober, fitness is akin to a measure of life-expectancy, we can take it that this is a case in which the Cholpoxes are fitter than the Mals—we should expect the Cholpoxes to do better. But in fact, over two or three generations, malaria strikes regularly but cholera and smallpox never do. This situation is, of course, unlikely—we should expect cholera and smallpox to strike, it just turns out that they do not. (If the chances of these diseases striking were in fact very low, it would not be legitimate to count resistance to them as significant contributors to fitness.) Under these circumstances, where only malaria ends up striking, the Mals might go to

fixation in spite of the fact that they are less fit than the Cholpoxes. I take it that Sober counts this as an instance where there is selection for malaria-resistance, but not for cholera or smallpox resistance. Fitness, as Sober says, is a summary of valuable dispositions, many of which turn out to be unactualized, and hence play no role in the actual fate of the Cholpoxes.

In their recent paper, Sober and Shapiro seem unsure as to whether Sober was right to deny that fitness is a causal property. They say that Sober made the mistake of thinking that a disposition does not cause its manifestation. They argue, for example, that fragility can be a cause of breaking, even if it is comparatively uninformative to say that the vase broke because it was fragile. As we will see, there remains a difference between the conception of selection as variation in fitness, and the conception of selection as 'selection-for', even if Sober and Shapiro are right that fitness is a causal disposition. If they are right about the causal character of fitness, they might still argue that variation in fitness—and hence selection in this sense—can be a cause, albeit not the same cause as selection in the sense of 'selection-for'. This option remains a difficult one for Sober to embrace, because a general concern with the explanatory relevance of dispositions was not Sober's only reason, or even his primary reason, for denying that fitness could be a cause. The problem that led Sober to deny that fitness was causal was that Sober regarded fitness as a summary of an organism's dispositions which may, or may not, be manifested. Sober's argument was that the genuine causal properties are whichever lower-level dispositions are manifested, and as a result actually explain survival and reproduction of the organism in question. Perhaps recalling this, Sober and Shapiro repeat Sober's 1984 assertion that while *selection-of* is not a cause, *selection-for* is: 'In any event, even if fitnesses are causally inert, it doesn't follow that natural selection is too. The distinction between the concepts of *selection-of* and *selection-for* explains why' ([2007], p. 253).

The case we have been discussing exposes a potential ambiguity in Sober's conception of selection. In some places, he seems to equate selection-the-cause with variation in fitness. In other places he wants to equate selection-the-cause with selection-for. The two conceptions of selection can come apart, because fitness can range over unactualized dispositions. This was Sober's main reason for denying that fitness is a causal property. To see how they come apart, consider that in the case we have been discussing, there is variation in fitness. By hypothesis the Cholpoxes are fitter than the Mals. This should lead Sober to say that the force of selection is present, and that it favours the Cholpoxes. But this means only that the superior fitness of the Cholpoxes compared to Mals leads one to expect, probabilistically, that the Cholpoxes replace the Mals. The problem, however, is that the components of the Cholpoxes' fitness which contribute to this expectation—cholera-resistance and smallpox-resistance—are unactualized dispositions. There is selection for malaria-resistance, but not for

cholera- or smallpox-resistance. If selection-the-cause is identified with variation in fitness, then the force of selection favours the Cholpoxes. If selection-the-cause is identified with selection-for, then the force of selection favours the Mals. Sometimes it appears that Sober does indeed equate selection-the-cause with selection for: '. . . natural selection—that is, selection for characteristics—is one of the causes of evolution' ([1984], p. 101). This is not equivalent to a view that equates natural selection with variation in fitness.

Sober might object to this accusation of ambiguity in various ways. Perhaps the most likely reaction, strongly suggested by Sober's earlier work, is for him to argue that he has always held the following consistent position. Selection understood as variation in fitness, and selection understood as selection-for are indeed different conceptions. It is selection-for that is the causal process, not selection understood as variation in fitness. But it is selection as variation in fitness, not selection-for, that plays the role of a force in population genetics.[2] So, Sober tells us that: '. . . natural selection—that is, selection for characteristics—is one of the causes of evolution . . .', and at the same time he notes that 'fitness differences among organisms or traits do not by themselves reveal which properties are selected for and which are selected against' ([1984], pp. 101–2). He might then construe the case outlined above as one in which the force of selection does indeed favour the Cholpoxes, but this force is not one with causal efficacy. Selection for malaria-resistance, on the other hand, is a causal factor that results in the Mals going to fixation in spite of the force of selection.

This interpretation of Sober's stance brings him closely into line with the superficially contrasting positions advocated by Walsh *et al.* ([2002]), and Lewens ([2004]). These authors argued for a distinction between 'the force of selection' and 'selective forces'. The latter were equated with the sorts of ecological factors—insecticide, sunshine, predation—that cause the deaths of some individual organisms while leaving others intact, and which thereby cause changes in the composition of evolving populations. Walsh *et al.* and Lewens argued that these 'selective forces' could not be identified with 'the force of selection' discussed in population genetics, and explored in Sober's account of evolution as a theory of forces.

Sober might instead argue with the way the example is set up, by claiming that because there is no selection for smallpox- and cholera-resistance, in fact the Mals are fitter than the Cholpoxes. This, it seems to me, undermines Sober's characterization of fitness as akin to life-expectancy. Our only reason for excluding smallpox and cholera resistance from our reckoning of fitness is that they play no causal role in the life and death of the Cholpoxes. In effect, we are equating fitness with the sum of *actualized* dispositions affecting survival

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[2]   I am grateful to an anonymous referee for encouraging me to pursue this interpretation of Sober.

and reproduction, and in so doing we undermine Sober's primary reason for denying that fitness is causally efficacious. The same goes for the response that since malaria strikes regularly, but cholera and smallpox do not strike at all, it cannot be the case that the Cholpoxes are fitter than the Mals. By hypothesis, the three diseases are equally likely to strike, it is simply that malaria is the only one that ends up striking. If we make the determinants of fitness range only over efficacious causes, rather than probable (but non-efficacious) causes, then we move away from a conception of fitness as analogous to life-expectancy.

The distinction between selection understood as variation in fitness and selection understood as selection-for is, I think, undeniable. Does it undermine Sober's account of the relationship between selection and drift? Let us assume that Sober opts for an equation of the population-genetic force of selection with variation in fitness. I have already suggested that Sober's own stance is most plausibly construed as one that denies causal efficacy to this force in cases such as the one under discussion, while instead crediting selection-for with causal efficacy. On this view, the Cholpoxes are fitter than the Mals, in virtue of their greater expected longevity. So here is a case where the force of selection favours the Cholpoxes. Sober, remember, thinks that natural selection is deterministic. Since the Cholpoxes do not go to fixation, it must be because of the action of a competing evolutionary force that opposes the force of selection. The only candidate force one might turn to here is drift. If we continue to interpret Sober's position as one that denies that the force of selection is a causal one, then presumably the force of drift is also non-causal. And yet, both forces explain the trajectory taken by the population. If Sober is to preserve his manner of distinguishing selection from drift he must claim that, had the population been infinite in size, then the relevant dispositions of the Cholpoxes and the Mals would not have been unactualized. The presence of drift explains why there is no selection for cholera- or smallpox-resistance, hence it explains why the Mals replace the Cholpoxes, and it also explains why the force of selection does not have the result one would anticipate.

This response is more promising than one might think. Its plausibility depends on the plausibility of the counterfactual 'Had the population been infinite in size, then the relevant dispositions of the Cholpoxes and the Mals would not have been unactualized'. In the situation we have described, cholera and small-pox are both *likely* to strike the population, it's just that they don't. On the one hand one might say that the counterfactual is implausible. We imagine a much larger population, but hold fixed the non-appearance of cholera and smallpox. Under these circumstances, even as the population gets larger, cholera and smallpox still fail to strike. Perhaps, though, the counterfactual is plausible. As we consider a larger population, we consider a larger spatial and temporal slice of the environment. It therefore becomes less plausible that the diseases in question—which must be likely to strike if resistance to them can be reckoned

as an element of fitness—fail to appear. Once the population is infinite in size, their appearance is guaranteed. This verdict even gets support of a kind from the practice of population genetics, which assumes that so long as selection is the only force in operation—an assumption that requires in turn that the population is infinite in size—fitnesses can be treated deterministically. On this interpretation, the counterfactual *must* come out true; if it is not true, our initial reckoning of fitness was erroneous.

The difficulty one has in deciding on the plausibility of the crucial counterfactual is an artefact of our understanding of drift as a force that diminishes 'in the long run'. The problem is that this notion is ambiguous between a mere increase in population size at a time, and an increase in population size during an extending time period. We understand fitness in dispositional terms—it tells us the expected reproductive output of some trait in the long run. It therefore follows that as the run gets longer, we approach the expected reproductive output. In a situation in which reproductive output falls below expectation because the environment does something unlikely, we can safely suppose that in the long run the environment will fall into place and behave according to expectation. This notion of what happens 'in the long run' involves a temporal extension of the environment as much as it involves a numerical extension of the population. After all, we can also imagine a population increasing in size while the environment still fails to act in the anticipated manner. If we focus on population size, rather than population persistence over time, then we obscure the conceptual link that a lengthening time sequence establishes between the expected reproductive output and the actual reproductive output.

6 A Second Problem: The Determinants of Fitness

Sober's own work ([2001]) has drawn attention to interesting cases, originally discovered by Gillespie ([1974]), in which a trait can be favoured, apparently by selection, even though all members of a population have identical expected numbers of offspring (and grand offspring). Sober uses these cases to illustrate the problems of always thinking that fitness can be identified with a propensity to survive and reproduce. He uses a simplified example in which individuals can have one of two reproductive strategies. Suppose that reproduction is asexual, and that offspring resemble parents perfectly. Type A individuals have two offspring in each generation. Type B individuals all have an equal probability of having either one offspring or three. The expected number of offspring of both types is therefore two. Sober shows that in spite of this, so long as the population is finite in size, type A—which has narrower *variance* in offspring number—will reliably increase its frequency.

One might naively think this result is contingent on the existence of some predator, for example, that finds it easy to consume either one or three offspring,

but not two. Or perhaps it is because a parent finds it easier to look after two offspring regularly, rather than alternating between one and three. But this is to make the mistake of thinking that the causes of long-run success must be ecological, and if either of these reasons were correct, then we would, in any case, be wrong to characterize both types as having the same expected number of offspring. In fact, the reasoning behind the success of the A type compared to the B type is purely mathematical in nature.

Sober works through his example of so-called 'within-generation variance' in offspring number in the following way. In the first generation, imagine there are just 2 As and 2 Bs in the population. Whatever happens, there will be 4 As in the second generation. How many Bs will there be? Each one has a 50% chance of having either 1 or 3 offspring. So there is a 25% chance that there will be 2 Bs, a 50% chance that there will be 4, and a 25% chance that there will be 6. Crucially, the number of offspring the Bs have also makes a difference to the overall population size, hence to the frequency of A. The overall population size can be 6, 8, or 10. So the expected frequency of As is given by a weighted average of 4/6, 4/8, and 4/10. We end up with an expected frequency of A of 0.52, and an expected frequency of B of 0.48. We should expect A to increase its frequency.

Sober uses this example to make the important point that fitness understood as expected offspring number will not always suffice to predict fluctuations in trait frequencies. In this case, the As and the Bs have the same average number of offspring, yet the As, with lower variance, are favoured. If our theoretical interest in the fitness concept is that it should reflect the chances of a trait going to fixation, then it needs to incorporate information that goes beyond expected reproductive output (Frank and Slatkin [1990], p. 255). As Sober's example shows, even if two types of organism have the same expected number of offspring, variance in offspring number can make a difference to fixation probabilities.

Sober looks at several other examples in his 2001 paper, all of which indicate the need to take a flexible approach to the understanding of fitness. There are occasions, for example, when we need to use the *geometric mean* of offspring number, calculated over time, rather than the arithmetic mean, if we are to predict the change in composition of a population. But the case we have been examining in more detail has special implications for Sober's general framework for thinking about selection and drift. This is because, as Sober points out, Gillespie's mathematical treatment of within-generation variance calculates a trait's fitness in such a way that 'The strength of selection for the variance component is inversely proportional to population size' (Gillespie [1974], p. 602). It is therefore a case where, as the population increases in size, the expectation that type A increases in frequency compared to type B gets lower. The case undermines Sober's view of the nature of drift and selection in two

ways. First, the two forces are linked in this sort of case: by altering the intensity of drift (i.e., by making the population smaller) one thereby alters the intensity of selection. Sober might reply by saying that this is a case in which two distinct forces are controlled by the same variable. There is nothing especially unusual in this: distance between particles can affect both gravitational force and electrostatic force, without the two forces becoming one. The plausibility of this reply is limited in the evolutionary domain, partly because Sober's argument for viewing selection and drift as distinct forces turns on the usefulness of this approach in comparing alternative situations. It is because we can alter the prospects for a population in two distinct ways—either by changing the population size while leaving fitnesses the same, or by changing the fitnesses of its members while leaving population size the same—that it is useful to think of selection and drift as independent forces. So if selection itself turns out to vary with population size, it seems there are cases where this sort of comparison has limited value. This brings us to the second way in which the case under consideration undermines Sober's general picture. Irrespective of what the case says about the relationship between selection and drift, it undermines Sober's characterization of selection itself. On Sober's usual understanding of selection as a force, we should expect it to be most efficacious in large populations, where the force of drift is small. The intensity of selection is not itself supposed to be dependent on population size, but its action may be swamped by the strong force of drift that exists in small populations. Drift, on the other hand, is meant to get weaker as the population gets larger. In the case under consideration, selection gets weaker as the population gets larger.

Now, admittedly, Sober might argue that some forms of *density-dependent selection* also make population size a contributor to fitness, hence it is not at all anomalous to find a case where selection varies with population size. Whether this really helps Sober is unclear, for it does not allow him to rebut the apparent entanglement of drift and selection. In any case, in typical cases of density-dependent selection, conspecifics form an important part of the environment. As the population increases in size, so the nature of the selective environment changes in virtue of (for example) the chances of bumping into another member of the species increasing. As Sober himself notes, in the case of selection against variance the situation is quite different. It is not a case in which overcrowding is a feature of the environment that is causally relevant to the success of individuals. Selection against variance is a case in which the strength of selection appears to vary with population size for reasons that are quite different to those that underlie standard models of density-dependent selection.

As we consider how Sober might respond to these worries, a second issue presents itself, which raises more general problems for our understanding of natural selection. In typical discussions within population genetics, the concepts

of fitness and of selection are intimately tied together—so intimately that they are practically synonymous. If the relative fitness of trait X is greater than that of trait Y, this entails that selection favours X over Y; and if selection favours X over Y, then the relative fitness of X exceeds that of Y. In the case we have been discussing, type A individuals are just as well suited to their local environments as type B individuals, at least if we measure this relationship using expected offspring number. So why should we understand fitness in a way that makes type A fitter than type B in the above example? Why not say that they are equally fit, but that for demographic reasons that have nothing to do with fitness, selection, or drift, we can nonetheless predict that A will probably replace B? This sort of move would enable Sober to reinstate his manner of distinguishing the force of selection from the force of drift. Indeed, Sober might claim that because his own manner of distinguishing selection from drift appears to work well in what we might think of as paradigmatic cases, we can use its success to justify a refusal to regard the success of the As compared to the Bs as a case of selection at all.

Sober does not take this route, presumably out of deference to biological use. Gillespie thinks selection favours the As, so Sober does, too. Sober might then fall back to a weaker position, which offers a way of distinguishing selection from drift that works in central cases, but that fails to account for some unusual cases of selection. And one might think we can defend Sober's decision to view the success of the As over the Bs as a case of selection in spite of its failure to conform with his general account of what selection is by appealing to the theoretical motivation for making variance part of fitness. If we want fitness to reflect fixation probabilities for a trait, fitness must incorporate variance. We might transform this theoretical motivation into a plausible principle: whenever we can be confident that type A is likely to increase in frequency with regard to type B, we should judge A to be fitter than B. One might also think this principle gains justification from other episodes in evolutionary biology where the notion of fitness is broadened. Fisher argued on more than one occasion that one should measure fitness not by expected number of offspring, but by expected number of grand offspring (Fisher [1930]). Such a measure of fitness appears in his discussion of the maintenance of 50:50 sex ratios, and in his discussion of runaway sexual selection. A trait that makes no difference to an organism's expected number of offspring, but which does make a positive difference to its expected number of grand offspring, is one we should expect to increase in frequency over time. It is thus reckoned as the fitter trait, presumably because we can reliably expect it to increase. This is what makes it legitimate to explain the disposition to produce male and female offspring in equal measure as a trait that is maintained by natural selection.

Perhaps, then, whenever we find some factor that makes a trait likely to increase its frequency, we should count this factor as one of the determinants of

the trait's fitness. But Sober himself is opposed to this principle, and with good reason. Sober thinks that it is a mistake to use fitness as a summary of all those factors that can make one trait likely to replace another. This is a lesson Sober draws from heterozygote superiority, among other cases. Here the homozygote may be lethal—homozygotes may have no offspring at all—but owing to facts about sexual reproduction, homozygotes will nonetheless appear in subsequent generations. The facts that determine how likely a trait is to proliferate, or to be maintained, in a population, include facts relating to how the trait is inherited. In the interests of explanatory transparency, Sober wants to separate facts relating to fitness from facts relating to inheritance. Sober also points out, as we saw earlier, that in small populations heterozygosity tends to be reduced. Sober takes this to show that drift tends to eliminate heterozygosity, not that in small populations there is selection for homozygosity. Once again, the decision to regard this as a case of selection would obscure important explanatory facts.

For these reasons, Sober and Shapiro object to Matthen and Ariew's ([2002]) recommendation that we use fitness as a summary of our overall expectation that one trait will outcompete another. But Sober's decision to characterize the increase in frequency of low variance in small populations as an example of selection reminds us that descriptive detail is in tension with the desire to generate a manageable explanatory vocabulary. This trade-off makes it difficult to come up with any non-arbitrary answer to the question of which factors should, and which should not, be counted among admissible determinants of fitness.

Sober's 2001 paper defends his view that fitness 'is both an ecological descriptor and a mathematical predictor' ([2001], p. 309). We can use fitness (and hence selection) in an expansive, mathematically predictive way, to give an overall summary of a trait's fate in a population. In general Sober frowns on this usage, for he thinks it obscures causal facts that we should want to keep distinct for explanatory purposes. As we have seen, Sober thinks we should mark a distinction between facts about likely number of offspring and facts about inheritance. Why not keep an equally tight distinction between facts about likely number of offspring and facts about variance in offspring number? Why not insist equally stringently on using fitness, and hence selection, to cover only the first type of fact? Part of the problem underlying these questions is that there are always lower-level distinctions between causal processes that some explanatory projects may wish to make explicit. Darwin took efforts to distinguish, both conceptually and empirically, between those traits that aid in the struggle for existence, and those traits that instead aid in the struggle for mates (see, for example, Darwin [1877/2004], p. 244). He thought this distinction was important enough that he reserved 'natural selection' for explaining traits of the first sort. This conceptual division is less pressing in a modern climate that groups both

kinds of traits together on the grounds that they increase reproductive success. Even so, modern biologists typically recognize sexual selection as a special form of selection. If one is interested in using fitness to mark explanatorily important distinctions then one might, in theory, exclude factors that contribute to sexual selection from the determination of fitness.

This presents Sober with a dilemma. On the one hand, he wishes to construe natural selection narrowly, in a way that enables it to be contrasted with other 'forces' that might increase a trait's frequency. This is how he opposes Matthen and Ariew. But at the same time he wants variance to count as an element of fitness, hence of selection. Why construe natural selection as broadly as this, but no more broadly? Explanatory fine-grained-ness will not do as an answer.

There are lots of factors that contribute to the expected change in frequency of a trait. Is there any non-arbitrary way to say which of them count as determinants of fitness, and which should be construed as the contribution of migration, mutation, transmission, or other factors? There are two extreme positions that one might turn to for principled answers. One is that of maximal breadth. This is the view of Matthen and Ariew, which involves taking fitness as a summary of expected frequency change. This in turn makes such processes as mutation and migration, in addition to inheritance, elements of selection. Obviously, this position offends those who are sensitive to how most biologists actually describe things.

The other extreme position is that of maximal narrowness. But quite what this position involves is unclear. One option (Sober's) distinguishes selection from (e.g.) mutation, migration, and drift, but allows selection to encompass cases of difference in expected reproductive output and cases of difference in variance in offspring number. Another, more narrow position than this one, would reserve 'selection' for factors contributing to expected offspring number, while giving other factors, such as difference in variance, a different label. And there is an even narrower position that distinguishes natural selection from sexual selection. If the reason for advocating narrowness lies in the idea that our terms should enable us to carve up distinct causes in informative ways, then it is not clear that we will hit any natural bedrock for an appropriate position of maximal narrowness. I conclude that no good argument has yet been made for this position.

In answer to the question 'What is natural selection?' it seems there are two good answers. One is Matthen and Ariew's position of maximal breadth. This position is metaphysically principled, but it is let down by its poor performance when measured against biological use. The stronger answer is to say that as far as metaphysics goes, demarcating the contributors to fitness (and therefore selection) is an arbitrary matter. We can choose to carve our causes narrowly or broadly, and no biological fact will settle the matter of how broad we can

get before it becomes inappropriate to speak of fitness and selection. As a matter of fact, it seems that biologists count facts about variance, but not facts about inheritance, mutation, or migration among the determinants of fitness. This is consistent with there being no interesting principle that determines which factors are bundled into fitness, and which are left to non-selective forces.

7 Conclusion

Two major points have been made in this paper. They both issue from an investigation of Sober's influential framework for thinking about selection and drift as forces. The first is that there is a distinction between 'selection-for' and the 'force of selection', which renders defending the causal character of the latter problematic. The second is that when we focus on the 'force of selection', we see that it has an arbitrary or conventionalist character, deriving from the fact that there is no principled way to determine which of the many factors that make a difference to a trait's chances of increasing its frequency should be included among contributors to the trait's fitness. These two points are not unrelated. The biologist can attend to the specific ecological episodes that result in the demise of some individuals, and the successes of others. Alternatively, she can move away from this focus on causal interactions between individuals and their environments, with a view to understanding trends in trait frequencies in populations. One initial way to do this involves assigning probabilistic expectations for the likely number of offspring that different types of organism will have. This move introduces Sober's non-causal notion of fitness, understood as a property analogous to life-expectancy. The limitation of this concept, as Sober notes, is that there are predictable trends for traits in populations that this notion cannot capture, and which can instead be captured by factors relating to (among other things) expected numbers of grand offspring, or variance in offspring number. So once the move to fitness as expected offspring number is made, it seems that the explanatory project of understanding changes in trait frequencies justifies an expansion of the fitness concept to include these additional factors. Indeed, perhaps the biologist should simply cut to the chase, and define fitness—and selection with it—as an overall expectation for a trait's frequency change in a population. The problem is that this seems to result in a conception of fitness that is too inclusive for the purposes of explanation: it would count mutation and migration among the determinants of fitness, and thereby among contributors to selection. One wants an account of these concepts that is inclusive enough without being too inclusive. But once the biologist embarks on the project of understanding trait fluctuations in populations, there is no good principled account that will tell her how she should perform this balancing act.

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