DO ELLIOTT SOBER'S ARGUMENTS FOR GROUP SELECTION REALLY ACCOUNT FOR THE CAUSAL EFFECT OF NATURAL SELECTION?

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The way Elliott Sober conceives group selection implies two claims: a) that natural selection is a cause; b) that natural selection can act at multiple levels of biological organization and that these multi-level selection processes are distinct or independent from one another. However, a comparison of multi-level selection processes with the distinction between selection and random drift allows us to assert that, if we conceive group selection as Sober does, the possibility of accurately quantifying the contributions to evolutionary change of two selective processes acting at different levels is an essential step needed in order to properly distinguish between them. However, Sober's endorsement of the Price approach to measuring group and individual selection contributions makes it impossible for him to support, at the same time, both of the claims indicated above. He is thus forced either to admit an essential interconnectedness between selective processes acting at different levels, or to deny that evolutionary change is causally determined by natural selection.

Keywords: E. Sober – Multi-level selection – Distinguishable effects – Causation – Price equations – Contextual analysis – Interconnectedness

1. Introduction. A recent debate in philosophy of biology has addressed the problem of the causal nature of natural selection, giving way to the formulation of a number of distinct positions that could be named, following Glennan's (2008) classification, the individualistic (Bouchard and Rosenberg 2004, Rosenberg and Bouchard 2005 and, in a different manner, Brandon 2005), the dynamical (Millstein 2006, Shapiro and Sober 2007) and the statisticalist (Matthen and Ariew 2002, 2005, 2009 and Walsh et al. 2002) interpretations of the causal status of natural selection. It should however be noted that this debate has been sparked by Matthen and Ariew's 2002 paper that criticizes Sober's (1984) comparison of evolutionary processes with Newtonian forces. But, since Sober is one of the most diligent proponents of multi-level selection – and especially of group selection –, it seems to me that multi-level selection should not be seen as a neutral problem with respect to that of the force-interpretation or of the causal interpretation of natural selection, but, on the contrary, should be inserted in a comprehensive manner in the debate surrounding this issue.

This paper takes a step in this direction and its argumentation is structured in three sections. Section 2 offers a brief outline of the manner in which Sober conceives group

selection. Section 3 exposes the difficulties that we encounter when we try to distinguish the processes of group and individual selection. This is done by way of a comparison with another recently debated distinction, that between selection and random drift. Finally, Section 4 outlines a possible way out of these difficulties, but shows that Sober's endorsement of the Price approach to quantifying multi-level selection contributions prevents him from taking this route and, consequently, makes it impossible for him to claim, at the same time, a causal status for natural selection *and* a separability of natural selection processes taking place at different levels.

2. A brief account of Sober's view of group selection. Sober defends what we might call a 'Double Selection-for View' of group selection. According to this view, group selection is a selective process operating between groups, whereas individual selection operates between the individuals belonging to any single given group. This can be clearly seen in the trademark example that he uses, namely the trait-group model for the evolution of altruism, that was first put forth by D. S. Wilson (1975, 1989), and later defended by Sober and Wilson (1998) together. In this model, even though within each of two groups containing different proportions of altruistic and selfish types individual selection favors the selfish individuals, between-group selection will tend to favor groups with a higher proportion of altruistic types (possibly leading, within certain parameters, to the evolution of altruism in the global population).¹ Since individual selection within groups cannot account on its own for the overall result, a different process of selection acting on groups (i.e. the fact that one group outgrows the other) should be taken into account, and the overall result will be given by the 'resultant' stemming from these two separate 'forces'. This is what I mean by 'Double Selection-for View' of group selection.

3. Distinguishable processes, distinguishable effects. Sober's Double Selection-for View of group selection implies two different claims:

(A) Natural selection is a cause;

(B) The selective processes operating at different levels of biological organization are separate, i.e. constitute selective processes independent from one another.

These claims have received criticism from the statisticalist view, according to which natural selection is not a process over and above individual events (births, mating, deaths etc.) caused by variation with respect to a certain pertinent trait; natural selection is merely a statistical aggregate of the outcome of these individual processes, and not a separate cause or a '*tertium quid*' (Matthen and Ariew 2009, 206). So, if natural selection is not a cause, but only a statistical result, then we are not dealing with separate selective processes at different levels, but only with different ways of calculating these statistical results, as is explicitly stated by some proponents of the statisticalist view:

if you want to explain why the altruist trait is increasing in frequency in the popula-

¹ An altruist in this model is an individual that offers a certain fitness benefit to another (indiscriminate) member of its group, while bearing himself the cost of this offered benefice.

tion as a whole despite declining within each group, it is best not to calculate the withingroup fitness of altruism, but to use the fitness of the altruistic trait across the population as a whole. On the other hand, if you want to explain the tendency of altruism to decrease in each group, you had better calculate the within-group fitnesses (Walsh et al. 2002, 471).

Sober's reply to this would, of course, be that such an approach 'fails to identify the separate causal processes that contribute to the evolutionary outcome' (Sober and Wilson 1998, 32). Which of the two positions is the 'correct' one doesn't concern me directly here. What I want to show is that Sober's arguments for group selection fail to fulfill *at the same time* the (A) and (B) claims or conditions stated above. In order to do so, I will begin by analyzing claim (B) through a comparison with another case found in literature, namely that of distinguishing between selection and drift. The means of distinguishing between these two processes have given way to heavy criticism addressed to the statisticalist approach, and it can serve as a model for us to see how a general distinction between two processes can be made. The two main arguments provided by the literature are outlined below.

a) The Ontological Separability Argument

In order to distinguish two processes, a most immediate way is that of trying to see if they can act independently of one another. If we are able to identify cases in which each of the two processes acts in the absence of the other, than it is safe to say that the two processes are distinct.

In the selection-drift distinction debate, such an argument – that I call the Ontological Separability Argument – is provided in Stephens (2004). He argues that we can see both selection and drift at work independently, on one hand by identifying cases where it is reasonable to think that alternative phenotypes are selectively equivalent (so any change must be due to drift), and, on the other hand, by theoretically imagining an infinite population size (thus reducing drift to zero, and reducing all evolutionary change to selection). Since the two processes can be viewed as acting separately, we should have no problem stating that they are separate processes.

But can we apply this argument to group selection? While it is obvious that there are cases where individual selection is acting in the absence of group selection, it is much more difficult to imagine group selection acting in the absence of individual selection when we use Sober's view of group selection.² This could be attempted, for example, in the trait-group model for the evolution of altruism by completely separating altruistic from selfish types (the two groups of the global population would be composed entirely of altruistic and, respectively, selfish types). The group containing only altruists will certainly outgrow the other group, while within each of the two groups there will be no indi-

² It should be *strongly emphasized* that, following Damuth and Heissler's (1988) and Okasha's (2006) distinction, I'm talking here about cases of MLS1 and not MLS2, i.e. cases where group fitness is defined by the average fitness of their constituent members (I'm leaving aside here cases where group fitness is defined by the relative number of groups that it engenders as is the case in MLS2).

vidual selection. But could this still be called group selection? It cannot, because if we isolate the two types like this, what we obtain can just as easily be named individual selection for a different trait of altruism, i.e. for altruism defined in a new way, as a behavior that benefits other members of the group as long as they exhibit themselves altruistic behavior. 'Pure' group selection and individual selection for the newly defined trait of altruism thus become interchangeable, and render the Ontological Separability Argument ineffective for the trait-group model.

But, since altruism is just a special case of group selection, could we find a case of non-altruistic group selection that could fit our Separability Argument? Interestingly, Sober himself denies this possibility. He imagines (Sober 2011) two herds of zebras subject to predation by lions. One herd is composed only of fast zebras, whereas the other herd only contains slow ones. The fitness of individual zebras is only dependent on each individual's speed and unaffected by what other zebras in its herd are like. This would be an ideal case of 'group selection': since there is no within-group selection (fast zebras are all equally fast, slow zebras are equally slow and speed is the only pertinent selective trait), all evolution should be the result of fitness variation between groups, i.e. of group selection in Sober's sense. But, of course, this 'pure' case is not a case of group selection at all, since the fitness differences only depend on individual traits and are unaffected by group character. The two herds don't even constitute 'groups', because, as Sober says, groups can only be properly defined as groups if there are fitness-affecting interactions between their members. This is consonant with my view that isolating all altruists and all selfish types in two 'groups' would not constitute pure group selection, but only a form of individual selection (since the groups themselves become redundant or cannot, by definition, count as groups). Thus, Sober himself endorses my claim that the Ontological Separability Argument doesn't hold for any case of multi-level selection of the MLS1 type. In order for us to rightfully call a process 'group selection' in Sober's sense of the term it has to act in the presence of individual selection.

b) The Distinguishable-effects Argument

There is however a different argument that could be put forth in order to distinguish between two processes even though they act together. In the debate surrounding the distinction between selection and drift, versions of this argument have been given by Millstein (2002), Stephens (2004), Reisman and Forber (2005), Shapiro and Sober (2007). The argument goes like this: in any given case of selection within a finite population, it might not be possible to explicitly indicate how much of the outcome is due to selection and how much of it is due to drift (Sober 1984 endorses this line of thought). It is however possible to show in principle that *both* of them are at work, and this can be done by experimentally constructing or theoretically imagining cases where one of them is modified while the other is hold fixed. If we keep the selection coefficient stable, while magnifying the population size, we will show that the probability distribution of the outcomes will be different than the one that obtains in an equal number of cases with the initial population size (Reisman and Forber 2005, Dobzhansky and Pavolvsky 1957); on the

other hand, if we hold fixed the population size, but alter the selection coefficient, we will obtain a different distribution of results in the outcome tests than the ones obtained in tests with the initial selection coefficient. Therefore, different effects stem from wiggling one of the two factors and, consequently, one can infer that those distinguishable different effects will have been the effect of the different contributions of the two *types* of causal processes involved. This is the 'Distinguishable-effects Argument' that is opposed – by dynamists, individualists and propensionists together – to the statisticalist view. We can infer that the two processes are distinct because we can differentially instantiate their effects by magnifying the influence of one of them while holding the other fixed, and by showing that the outcome distribution will be changed in this manner.

But could we apply the Distinguishable-effects Argument to the distinction between individual and group selection? The answer has to be negative. This is based on the fact that modifying one of the two 'factors' – individual or group selection – will immediately alter the other (we cannot modify group characters – the proportion of altruists in the groups, for example – without modifying the within-group fitnesses of the two types). So if we modify one parameter, we won't be able to hold the other one fixed, as the Distinguishable-effects Argument demands.

In conclusion, not only do we have two processes that always act together³, but we cannot even distinguish them as processes by differentially instantiating their effects. This is where the comparison with the debate regarding the selection-drift distinction seems to be reaching the limit of its usefulness for us.

4. Quantifying group and individual selection. There might however be a way out of this difficulty. If the Distinguishable-effects Argument works for the drift-selection distinction, it is because we can wiggle one of the two factors, while holding the other one fixed. But we were only forced to resort to this argument because, presumably, it is impossible to isolate the 'contributions' of drift and selection in any given concrete situation. However, this needn't be so in the case of individual and group selections. If we could find a way to accurately quantify their respective contributions to the total evolutionary outcome in every given situation, then we would have sufficient grounds for asserting the distinction between the two processes. All the more so since we can see one of the two factors at work by itself, i.e. we can identify cases where only individual selection is at work. Quantifying the effects of group and individual selection, respectively, and measuring these results against what would have happened had only one of the two factors been at work would therefore give us a way out of our difficulty.

This solution has to face several issues of its own, however. First of all, whether we can accurately measure the respective effects of group and individual selection is far from being an undisputed fact (see Glymour 2008, for example). But this issue is well beyond the scope of this paper, and I will not tackle it here.

³ More precisely: one of the two processes (group selection in MLS1 cases) never acts in the absence of the other (individual selection).

My concern in this paper is merely that of showing that Sober's arguments and choices concerning the means of quantifying the contributions of group and individual selection tend to take away or to eliminate the very thing that he tries to support by them, i.e. the *causal* nature of the two *separate* processes in play. To put it bluntly, between two ways of measuring the effects of individual and group selection that we now have at our disposal, Sober chooses the one that directly contradicts his initial intentions. The two concurrent ways of causal apportioning present in the literature are the Price approach (based on Price's 1972 equations) and the contextual approach, stemming from statistical linear regression analysis (Heissler and Damuth 1987, Goodnight et al. 1992, Okasha 2004, 2006). The two approaches partition the respective contributions of group and individual selection to the total evolutionary change in the following manners:

The Price approach: $\overline{w} \Delta \overline{z} = \overbrace{Cov(W_k, Z_k)}^{group} + \overbrace{E(Cov(w_{jk}, z_{jk}))}^{individual}$

(where \overline{w} is the mean individual fitness and $\Delta \overline{z}$ is the mean change in individual character z, W_k is the mean fitness of the kth group, Z_k is the group character value of the kth group – obtained by averaging individual character value z within the group –, w_{jk} is the fitness of the jth individual within the kth group, and z_{jk} is the character value of the jth individual within the kth group);

The contextual approach:
$$\overline{w\Delta z} = \overbrace{\beta_2 Var(Z_k)}^{group} + \overbrace{\beta_1 Var(Z_{jk})}^{individual}$$

(where β_1 is the partial regression of individual fitness on individual character, controlling for group character, β_2 is the partial regression of individual fitness on group character, controlling for individual character).⁴

Sober openly endorses the Price approach (Sober 2011) in a discussion around Okasha's 2006 book, while Okasha (2011) remains faithful to the contextual approach. Applying the two approaches to the trait-group model values (as they are given in Sober and Wilson 1998) yields, in fact, similar results. Both the individual and group selection values are greater according to the contextual approach, but since the two selection factors go against each other (i.e. we need to deduct the value of individual selection from that of group selection), the two approaches yield the same total evolutionary change, with a

⁴ Both in the Price and the contextual analysis equations given above I've eliminated, for simplicity, the transmission bias, as well as any other residuals.

slight difference in the proportions of the contributing factors (the Price approach accords 68% of the total selection to group selection, whereas according to the contextual approach group selection accounts for 63%). The results in this case are comparable, and, as Sober stresses, even if we have two different approaches,

The sums computed by the two approaches must be equal, which means that *the two* approaches agree on whether individual selection is stronger than group selection. However, they may disagree about the numbers. For example one approach might say that altruism will increase by 7% because group selection predicts a 10% increase and individual selection predicts a 3% decline, while the other says that the 7% increase will occur because group selection predicts a 15% increase while individual selection predicts an 8% decline (Sober 2011, 228-229).

In the trait-group model, the numbers are not the ones indicated by Sober above, but the point is the same. To sum it up, Sober's reasoning seems to be the following: since the interactionist definition of groups – briefly outlined at point a) in Section 3 – saves the Price approach from its greatest pitfall (that of identifying group selection even in cases where all selection takes place at the individual level), and since the two approaches agree upon the 'comparative' strength of the two selections at work, the Price approach can continue to be used. Sober therefore keeps endorsing it because, he claims, the contextual approach has even larger difficulties to face (ones that I will not detail here).

However, Sober's claim that the two approaches agree on the comparative strength of the two selective processes is wrong. To understand this, let's take an example given in Sober (2011) and modify it slightly. Imagine two groups of zebras of size 100 each. One group contains a majority of fast zebras (90% fast zebras, 10% slow ones), and the other contains a majority of slow zebras (90% slow zebras, 10% fast ones). The fitnesses of the two types of zebras are given by:

$$w_f = 0.9 + \frac{n \cdot p_f}{1000}$$
$$w_s = 0.2 + \frac{n \cdot p_f}{1000}$$

where w_f is the fitness of fast zebras, w_s is the fitness of the slow ones, *n* is the size of the group (= 100 for our two groups) and p_f is the proportion of fast zebras in the group. In this example, the fitness of any individual zebra doesn't depend only on its own phenotype, but also on the size of its group and on the phenotypes of the other members of its group. Therefore, this example passes the interactionist test for the definition of groups that Sober, following Okasha (2006), puts forth. But in this case the Price approach and the contextual approach give severely contrasting results. They both give the same overall result of the total evolutionary change ($w\Delta z = 0,191$), but they partition it in a manner that is much more puzzling that their slight divergence in the trait-group model for the evolution of altruism.

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When we do the calculations, we find out that according to the Price approach, individual selection accounts for only 33% of the evolutionary change, whereas group selection accounts for the other 67%. Conversely, according to the contextual approach, individual selection accounts for 91,6% of the total evolutionary change, while group selection only contributes by a mere 8,4%. The difference is enormous, but this time it is not just quantitative; it is also qualitative, since according to the Price approach the main 'engine' of evolution here is by far group selection (accounting for 67% of the change), whereas the contextual approach identifies individual selection as the main engine of evolution, only according group selection a minor role (8,4%). It is obvious that Sober's claim that the Price and the contextual approach give similar comparative results (i.e. 'agree on whether individual selection is stronger than group selection') is simply wrong. One of his reasons for continuing to endorse the Price approach is clearly unfounded.

But there is more to say about this, and it is from this point on that Sober's double claim about the causal nature of selection and about its separable 'actions' at different levels begins to lose its footing. Let's begin by noting that, in our case, both the component of individual selection and that of group selection have positive values. In other words, unlike the case of the trait-group model, here the two selection processes work in the same direction, both favoring increased running speed. The difference is that the two approaches partition the contributions of the two processes differently.⁵ However, when we try to compare the two results with what would have happened had only individual selection been at work, things begin to look complicated for Sober's position, particularly when we take into account his Double Selection-for View of group selection. According to this view, we should be able to see the effects of group selection by comparing the results of cases where both group and individual selections are present with cases where only individual selection is at work. There should be no difficulty in doing such a comparison since, as we've seen, it is on the basis of precisely such a comparison that Sober's inference of the presence of group selection in the trait-group model was made.

To set up a comparison of this sort, let's alter the zebra example given above and imagine that both groups contain equal shares of slow and fast zebras (group sizes are still n = 100 and $p_f = p_s = 0.5$ for each group). Some simple algebra in the formulas given above would show that here:

 $w_f = 0,95$

 $w_s = 0,25$

⁵ To offer some substance to the percentages indicated above, it might be helpful to give here the numbers that the two approaches assign to individual and group selection. According to the Price approach $\overline{w}\Delta \overline{z} = 0,063 + 0,128$ (where the first value on the RHS corresponds to individual selection, and the second to group selection). According to the contextual approach $\overline{w}\Delta \overline{z} = 0,175 + 0,016$ (where,

again, the first value on the RHS stands for individual selection and the second for group selection). The discrepancy, as we can see, is enormous.

and that after one reproductive cycle we get the following frequencies of fast and slow zebras:

$$p_{f}' = 0,79$$

$$p_s' = 0,21$$

But in my initial case with groups containing 0,9 fast zebras and 0,1, respectively, the frequencies of the two types obtained in the total population were: $p_f' = 0.82$

and p_s ' = 0,18. In this case, as noted above, there was not only individual selection at work, but also group selection. In other words, individual selection acting alone would have increased the frequency of fast zebras from 0,5 to 0,79 and would have decreased the frequency of slow ones from 0,5 to 0,21. However, when both individual selection and group selection are at work, the actual frequency of fast zebras increases from 0,5 to 0,82 and the frequency of slow zebras decreases from 0,5 to 0,18. But if the difference made by the presence of group selection is so small (taking the frequencies from 0,79 to 0,82 for fast zebras and from 0,21 to 0,18 for the slow ones), can the Price approach – and Sober who endorses it – still maintain that group selection accounts for 67% of the total evolutionary change, whereas individual selection only accounts for 33% of that change? I find that extremely problematic.⁶

In my view, if Sober wants to maintain that group selection is not reducible to individual selection,⁷ the difficulty I've just presented would leave him with only four possibilities.

1. He could continue to support the Price approach and claim that the comparison I've just made between the results of the case where only individual selection is at work and the case where both individual and group selection are in play is unjustified. But he could claim this in only two ways. First of all, he could say that these results don't allow us to account for the interplay between the two factors in situations when both of them are at work.⁸ But – and this is the crucial point – I've already noted that both $Cov(W_k, Z_k)$

⁶ Let's note here that the contextual approach renders a much more palatable result. When it partitions the evolutionary change by assigning 91,6% of it to individual selection and only 8,4% to group selection, it comes very much closer to the values we see in the comparison between the case where only individual selection is present and the case where both group selection and individual selection are at work.

⁷ If that were the case, the difficulty presented above would be of no importance, since all the causal work would be at the individual level. If so, than both the Price and the contextual approach would offer statistical decompositions of the total evolutionary change, but neither could claim to offer a causal decomposition, because the causal work would not correspond to a multi-level frame, but to a single-level frame.

⁸ An interplay between the two factors would allegedly explain why, as if by magic, individual selection ceases to increase the frequency of fast types from 0,5 to 0,79 as it would do if group selection were not present and, by taking this sort of 'causal step back', would allow group selection to account for most of the phenotype change within our population (i.e. for 67% of it).

and $E(Cov(w_{jk}, z_{jk}))$ are positive in our case; in other words, the two processes don't go against each other here, and therefore the value of one of them doesn't get subtracted from the value of the other, as was the case for the trait-group model. What this crucial point tells us is that this 'interplay' between the factors that Sober might appeal to is not an interplay between the outcomes of the two processes, but it would have to be an interplay *between the processes themselves.*⁹ If Sober were to choose this way of reasoning, he would loose all possibility of claiming that the two processes of individual and group selection are separate processes. He would have to claim that group and individual selection are essentially interconnected or 'entwined' *as selective processes*, and not merely connected via their sharing of certain common supervenience-base non-selective processes (see R. A. Wilson 2005, where this position is spelled out in a comprehensive, though sometimes ambiguous manner due to his failure to distinguish between MLS1 and MLS2 scenarios).

2. Sober's second possibility would stem, again, from a continuation of his support for the Price approach and of the claim that the comparison I've set up is misguided. But this time, he would not resort to an interplay between the two factors, but would choose to invoke a common cause for the two factors. In this case, individual and group selection would both become by-products of a different, common cause. This again could allegedly explain why, as soon as group selection is also in play, individual selection would 'refrain' from producing its 'default' results and would allow for most of the results to be accounted for by group selection. But, in this case, the crucial point is that of noting that Sober wouldn't be casted in the group of 'gene's-eye view' theorists of natural selection, since the idea that individual and group selection are joint effects of a common cause could be shifted down to the level of the gene without qualitative change. (The individual level could, for example, be taken as the allele level, and the group-level could be taken as being a pair of alleles at one locus in a diploid organism model; however, even in this case, selection at both levels would still be joint effects of a common cause, a cause that would not belong to either of the two levels). Therefore, if he were to choose the 'common cause' way out of the difficulty, Sober wouldn't become a Dawkins follower, but an outright statisticalist. If a common cause were always at work behind individual and group selection – at any level of the biological hierarchy were we to place the two factors – then this would amount to saying that natural selection is nothing more than the statistical result of events taking place at a level where selection is not a causal force (or, as statisticalists say, of births, mating and deaths, that are caused events, but where the causal work is a complete stranger to selection). If the first way out of the difficulty made it impossible for Sober to claim that group and individual selection are separate processes, the second way out - the 'common cause' strategy - would strip selection of all its causal power and would turn it into a mere statistical result.

⁹ Note that there is no non-linearity in my example.

3. A third, more radical option for Sober would be that of giving up quantifying altogether. But this would lead us to one or the other of the two possibilities indicated above. Since neither the Ontological Separability Argument nor the Distinguishable-effects Argument work for the individual-group selection distinction (in Sober's sense of the latter), we would be left either with two processes whose causal contributions and interrelations we couldn't identify, or with two pseudo-processes that are both the effects of a common cause that is not selective by nature. Worse still, since we gave up quantifying altogether, we would have *absolutely no grounds* for distinguishing or for choosing between these two possibilities.

4. A fourth and final option would remain available for Sober or his followers. It would be that of pointing out a difficulty in the comparison I made in order to cast doubts over the Price approach. The objection would indicate that when I chose the case for when individual selection is the only factor in play, I chose a situation where the total population is already divided in two groups with equal frequencies of fast and slow zebras. Or, as indicated above, the individual fitnesses in each group don't depend only on the individual's base fitness and on the trait values of the other members of its group, but also on the size of the group it is in. But in this case, the objection follows, a fair assessment of what individual selection would have been in the absence of group selection would be given by a calculation of the frequencies change in the total population in the absence of any partitioning of the population in groups. At first sight, this objection seems fair. However, even so, the Price approach wouldn't gain much ground on the basis of numbers alone,¹⁰ but this is less important here. What is more important is that, by making this objection, Sober would admit that the dividing of the total population into groups is to be considered as a component of group selection and not as part of individual selection. In other words, this last attempt to save the Price approach actually makes us unwillingly give up the Price approach in favor of the contextual approach, since the latter defines group selection as 'direct selection on the component of individual fitness that is determined by group membership' (Okasha 2011, 242). And here the group membership affects individual fitness not only via the traits of the other members of the group, but via the size of the group as well, precisely as the final objection to my argument stated. The final attempt to save the Price approach therefore forces us to define group selection not only as differential fitness between groups, but also in the more general terms of the effects of group membership on individual fitness. By taking this last option Sober would therefore adopt the contextual approach and would have to face the specific problems that this definition of group selection imposes on the contextual approach.

¹⁰ To see why, we need to calculate the values of what would have happened had only individual selection been at work in the undivided population. The values would be the following: $w_f = 1$, $w_s = 0.3$ and $p_f' = 0.77$, $p_s' = 0.23$. In this case, the supporters of the Price approach would still have to explain why individual selection alone would take the frequency of fast types from 0.5 to 0.77 and group selection and individual selection together take it from 0.5 to 0.82, but still group selection is doing most of the causal work (67%) in the latter case.

Conclusion. Elliott Sober's endorsement of the Price approach, when combined with his 'Double Selection-for View' of group selection, seems to lead him in unpredicted directions. He is forced either to state that group and individual selection are non-separable causal processes, that an essential interconnectedness ties them together in their proper capacity of *selective processes*, and not simply inasmuch as these processes depend on other supervenience-base non-selective processes; or, on the other side of the alternative, he is forced to strip natural selection of all its causal powers. Neither of these positions was, of course, what Sober intended when he began his defense of the reality and efficacy of group selection. Moreover, either of these positions would certainly force us to reconsider the way we see not only multi-level selection, but natural selection in general.

The only other possible way out of this bind for Sober is an endorsement of the contextual approach to measuring the contributions of group and individual selection to evolutionary change. Whether the contextual approach avoids the 'interconnectedness' of group and individual selection *and* the non-causal status of natural selection in general is far from being an established fact. But this issue should be treated separately, and is beyond the scope of this paper.

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References

- BOUCHARD, F. and ROSENBERG, A. (2004): Fitness, Probability and the Principles of Natural Selection. *British Journal for the Philosophy of Science* 55, 693-712.
- BRANDON, R. (2005): The Difference between Selection and Drift: A Reply to Millstein. *Biology and Philosophy* 20, 153-170.
- DAMUTH, J., HEISSLER, L. (1988): Alternative Formulations of Multilevel Selection. *Biology and Philosophy* 3, 407-430.
- DOBZHANSKY, T., PAVLOVSKY, O. (1957): An Experimental Study of the Interaction between Genetic Drift and Natural Selection. *Evolution* 11, 311-319.
- GLENNAN, S. (2008): Productivity, Relevance and Natural Selection. *Biology and Philosophy* 24, 325-340.
- GLYMOUR, B. (2008): Stable Models and Causal Explanation in Evolutionary Biology. *Philosophy of Science* 75, 571-583.
- GOODNIGHT, C. J., SCHWARTZ, J. M., STEVENS, L. (1992): Contextual Analysis of Models of Group Selection, Soft Selection, Hard Selection and the Evolution of Altruism. *American Naturalist* 140, 743-761.
- HEISLER, L., DAMUTH, J. (1987): A Method for Analyzing Selection in Hierarchically Structured Populations. *American Naturalist* 130, 582-602.
- LEWENS, T. (2010): The Natures of Selection. British Journal for the Philosophy of Science 61, 313-333.

- MATTHEN, M., ARIEW, A. (2002): Two Ways of Thinking about Fitness and Natural Selection. Journal of Philosophy 99, 55-83.
- MATTHEN, M., ARIEW, A. (2005): How to Understand Causal Relations in Natural Selection: Reply to Rosenberg and Bouchard. *Biology and Philosophy* 20, 355-364.

MATTHEN, M., ARIEW, A. (2009): Selection and Causation. Philosophy of Science 76, 201-224.

- MILLSTEIN, R. (2002): Are Random Drift and Natural Selection Conceptually Distinct?. *Biology and Philosophy* 17, 33-53.
- MILLSTEIN, R. (2006): Natural Selection as a Population-Level Causal Process. British Journal for the Philosophy of Science 57, 627-653.
- OKASHA, S. (2004): Multi-Level Selection, Covariance and Contextual Analysis. British Journal for the Philosophy of Science 55, 481-504.

OKASHA, S. (2006): Evolution and the Levels of Selection. Oxford: Clarendon Press.

- OKASHA, S. (2011): Reply to Sober and Waters. *Philosophy and Phenomenological Research* 82, 241-248.
- PRICE, G. (1972): Extension of Covariance Selection Mathematics. *Annals of Human Genetics* 35, 697-701.
- REISMAN, K., FORBER, P. (2005): Manipulation and the Causes of Evolution. *Philosophy of Science* 72, 1113-1123.
- ROSENBERG, A., BOUCHARD F. (2005): Matthen and Ariew's Obituary for Fitness: Reports of Its Death Have Been Greatly Exaggerated. *Biology and Philosophy* 20, 343-353.
- SHAPIRO, L., SOBER, E. (2007): Epiphenomenalism: The Do's and the Don'ts. In: G. Wolters P. Machamer (eds.): *Thinking about Causes: From Greek Philosophy to Modern Physics*. Pittsburgh: University of Pittsburgh Press, 235-264.
- SOBER, E. (1984): The Nature of Selection: Evolutionary Theory in Philosophical Focus. Cambridge MA: MIT Press.
- SOBER, E. (2011): Realism, Conventionalism, and Causal Decomposition in Units of Selection: Reflections on Samir Okasha's Evolution and the Levels of Selection. Philosophy and Phenomenological Research 82, 221-231.
- SOBER, E., WILSON, D. S. (1998): Unto Others: The Evolution and Psychology of Unselfish Behavior. Cambridge MA: Harvard University Press.
- STEPHENS, C. (2004): Selection, Drift, and the "Forces" of Evolution. Philosophy of Science 71, 550-570.
- WALSH, D., LEWENS, T., ARIEW, A. (2002): The Trials of Life: Natural Selection and Random Drift. *Philosophy of Science* 69, 429-446.
- WILSON, D. S. (1975): A Theory of Group Selection. *Proceedings of the National Academy of Sciences* 72, 143-146.
- WILSON, D. S. (1989/2006): Levels of Selection: An Alternative to Individualism in Biology and the Human Sciences. Social Networks 11, 257-272.
- WILSON, R. A. (2005): Genes and the Agents of Life. The Individual in the Fragile Sciences: Biology. Cambridge University Press.

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