

Ciprian JELER<sup>1</sup>

## **The critical role of time in the interpretation of multi-level natural selection**

Abstract. This paper attempts to show that considerations of time can play an important critical role in the way we interpret multi-level selection scenarios, i.e. scenarios involving evolutionary change in biological populations that is caused by selection processes operating at different levels of biological organization. The interpretation of multi-level selection scenarios that will be criticized here using considerations of time as a critical instrument is the one I will call ‘the double selection-for’ view of group selection, defended by Elliott Sober and David Sloan Wilson. The types of multi-level selection cases that are discussed here are known as cases of group selection with aggregate group characters, i.e. cases where the group character is defined as average individual character within the group (while the fitnesses of groups are defined as the average individual fitness of their members). The ‘double selection-for interpretation’ will be briefly contrasted with a different interpretation of this type of multi-level scenarios – namely, the contextual approach – through an analysis of the trait-group model for the evolution of altruism.

Keywords: group selection, causality, Sober, sorting, temporality.

This paper attempts to show that considerations of time can play an important role in the way we interpret multi-level selection scenarios, i.e. scenarios involving evolutionary change in biological populations that is caused by selection processes operating at different levels of biological organization. In particular, I will show that considerations of time can become critical instruments with respect to one way of interpreting multi-level selection scenarios that I will call here the ‘double selection-for interpretation’. The proponents of this interpretation that I will engage with here are David Sloan Wilson and Elliott Sober, and the type of evolutionary scenarios analyzed here is constituted by group selection in cases where the group character is aggregate, i.e. is defined as the average individual character of the individuals in the group. And, since probably the most famous case of this type is the trait-group model for the evolution of altruism, this critical examination of the role of time in assessing the validity

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<sup>1</sup> Interdisciplinary Research Department – Human and Social Sciences “Alexandru Ioan Cuza” University of Iași, ciprianjeler@yahoo.com

of the ‘double selection-for interpretation’ of multi-level selection should most suitably begin with a brief outline of this particular case.

*A brief outline of the trait-group model for the evolution of altruism*

D. S. Wilson (1975, 1989/2006) and, later, Sober and Wilson (1998) use the notion of evolutionary altruism in their description of the trait-group model. A behavior is evolutionarily altruistic if it benefits other conspecific members of the group and decreases the fitness of the behavior. This description doesn’t take into account the motives for such a behavior, but only the behavior itself (taking the motive into account would force us into a different theoretical domain that is governed by the notion of psychological altruism).

The trait-group model for the evolution of altruism supposes a population of selfish and altruistic types. The selfish individuals are neutral with respect to the others (their behavior doesn’t influence the absolute fitness of others), whereas the altruistic individuals offer benefits to the others’ fitness while bearing themselves the costs of this offered benefice. Since selfish individuals only benefit from the presence of altruists, in any given undivided or well-mixed population the selfish types will be more fit than the altruistic ones. At the number of offspring they would have in a neutral situation (i.e. in a case without altruistic behaviors) we must add the number of offspring that result from the benefit received from the coexisting altruist members in their group. While, conversely, even though altruistic behaviors can benefit other altruistic individuals, the altruistic individuals will also bear the costs of their behavior, and therefore will be less fit than their selfish counterparts. Even more so if we assume, as Wilson and Sober do, that while an altruist can benefit from another altruist’s behavior, he can’t however benefit directly from his own behavior. Therefore, the altruist can only benefit from the behavior of all the other altruists (except himself), while the selfish can benefit from the behavior of all altruists in the group.

So, selfishness will certainly evolve in any given group. However, and this is the crucial point, altruism can evolve if we assume that the population is divided into more than one group, as long as we assume that there is a significant difference in the proportions of altruistic and selfish types within these sub-groups. So, to follow Wilson and Sober’s example, let’s take a global population of 200 individuals, containing an equal proportion (0.5) of selfish and individual types. If we divide the global population in two equal groups (of 100 individuals) containing different proportions of altruist and selfish individuals (e.g. 80% selfish individuals in

group A and 80% altruists in group B) and assign certain numerical values to the cost of altruistic behaviors ( $c = 1$ ) and to the benefit this same behavior brings to another individual ( $b = 5$ ), we will notice that, after one reproductive cycle, in the entire population (groups A and B put together) it is the altruists that increase in frequency and not the selfish types (the frequency of altruists grows from 0.5 to 0.516). And this is so even if, within each of the two groups, it is the selfish types' frequency that increases (from 0.8 to 0.816 in group A and from 0.2 to 0.213 in group B). This somewhat paradoxical result, consisting in the increase in frequency of altruism in the global population even if in each sub-group of the population the frequency of altruists decreases is, as Wilson and Sober note, an example of a statistical phenomenon known as Simpson's paradox. But, more importantly, for our two authors this indicates a more notable process than that of a simple statistical phenomenon, a process that has been hinted at, in various manners, styles and with more or less precision, ever since Darwin (1859) under the name of group selection. According to Sober and Wilson's interpretation of this scenario, it is because one group (group B in our above description, the group with a higher proportion of altruists) outgrows the other that the overall frequency of altruists increases, even though they decrease in frequency within each of the sub-groups of the population. As mentioned above, I will call Sober and Wilson's view of this scenario the 'double selection-for interpretation' of group selection. This is to say that there are two selection processes at work in this model: there is individual selection against altruists (and for selfishness) within each of the groups of the total population and, on the other side, there is group selection favoring the group with a higher proportion of altruists. There are two selective processes acting on biological 'individuals' at different levels: one acting on organisms within groups, while the other is acting on the groups themselves. Therefore, in the expression 'double selection-for', the term 'double' points towards the two levels that are subjected to selection, or on which selection is acting, rather than the levels at which it is acting. So, to get back to our example, if the latter of the two processes is stronger than the first, then the 'resultant' that combines the two 'forces' put together will end up favoring the altruistic type within the global population.

#### *A temporality issue*

With all its elegance, the double selection-for interpretation of group selection has several difficulties to face. Here, I will only discuss a general temporal difficulty, leaving aside some more technical issues that this model has to face and that have been treated elsewhere (see Nunney 1985, Heisler and Damuth 1987, Okasha 2006, and Jeler (forthcoming)).

In order to get to clarify this temporal difficulty, let's note that the individual selection process that takes place within each of the groups stems from direct interactions between the members of these groups (altruists offering benefits to the other members of the group, selfish individuals receiving, when the case may be, these benefits without themselves inducing any additional cost or any 'harm' to the altruists). The other selection process, the one that is taking place between groups is of a different type, since it is not the interaction between groups that causes or brings about the selection process: if one group outgrows the other, it is by virtue of its own constituent members, and not by virtue of a direct influence of one group on the other. This is a point that Sober has addressed elsewhere (Shapiro and Sober, 2007), where he draws a distinction between what we might call selection by direct competition and selection by indirect competition:

Our reply is that no biologist would treat two individuals as part of the same (token) selection process if they were at opposite ends of the universe (...). The fact that x and y differ in fitness does not entail that there is a selection process impinging on both. Sometimes x and y experience the same token selection process because they causally interact; at other times they participate in the same selection process because they are affected by a common token cause. (Shapiro and Sober 2007, 252)

Sober and Shapiro go on to exemplify by saying, following a passage from Darwin's *Origin*, that two dogs fighting for food are just as subject to selection as two plants that don't interact with each other, but are both experiencing – and having different degrees of success if there is to be selection – the effects of a common cause, e.g. drought. The distinction between selections by direct and by indirect competition places the environment as a crucial element: there is either competition for certain resources of the environment (as in the case of the two dogs) or competition within a common environmental frame (one plant fares better than the other in drought conditions). Obviously, since the two groups in the trait-group model don't interact, they could not be facing selection by direct competition as in the example of the two dogs. This leaves us with the only solution of trying to identify the environment in which the two groups with different altruistic and selfish type proportions compete. However, since, by definition, the two groups are isolated, they do not actually share such a common environment. If we are to say that they compete, we can only state this after the two groups have merged or have become reunited into the global population. In other words, for there to be group selection, we need to have the subsequent reunification of populations: if this were not the case, than we would not be dealing with selection, but only with what we might call sorting (Vrba and Gould 1986); or, in Sober's words cited above where he and Shapiro were criticizing

Walsh (2000), we would only have a situation where ‘x and y differ in fitness’ but without there being ‘a selection process impinging on both’.

In effect, we are able to see a growing emphasis being put by Wilson and Sober precisely on this element of group reunification. In an earlier description of the trait-group model (Wilson 1989/2006), only three conditions for group selection (and for the evolution of altruism) were named: a population of groups (the two groups in the case above), variation between these groups (in the proportions of altruistic and selfish types) and differential fitness of groups. Adding or reuniting the populations of the two groups in the end was a mere subsequent operation that didn’t need to be granted a condition status, but only a justification in an endnote (‘Adding the contents of both groups is justified biologically only if the occupants of the groups physically mix during a dispersal stage or compete for the colonization of new groups’ – Wilson 1989/2006, 73 n1). A few years later, in Sober and Wilson’s *Unto others*, the necessity of group reunification is given full condition status, along with the conditions of a population of individuals (or groups) that vary in heritable characteristics, with some variants more fit than the others. Here is the passage in question:

Fourth, although the groups are isolated from each other by definition (the S [selfish] types in group 1 do not benefit from the A [altruistic] types in group 2), there must also be a sense in which they are not isolated (the progeny of both groups must mix or otherwise compete in the formation of new groups). These are the necessary conditions for altruism to evolve in the multigroup model. (Sober and Wilson 1998, 26)

Furthermore, when the conditions for group selection are measured against the general (Darwinian) conditions for natural selection, the notion of competition is once again stressed: ‘The analogy extends to the fourth condition, since individuals are isolated units but nevertheless compete in the creation of new individuals. Thus, natural selection can operate at more than one level of the biological hierarchy’ (Sober and Wilson 1998, 26-27). The problem however is that this ‘competition’, invoked twice in the above citations, takes place only after the reunification of groups. This is a point that Sober and Wilson probably realize, given the slight awkwardness and imprecision of the expression ‘a sense in which they are not isolated’ that they use: as long as the groups are not reunited, even though one group outgrows the other, no actual group selection can be said to exist.

This shows us, in a distinct manner, how Sober and Wilson view their model, because it indicates that we need to distinguish here between:

a) an individual selection process that takes place within the isolated groups (selfish types are favored);

b) a process of differential growth of the two isolated groups (the group containing more altruists outgrows the other, i.e. produces more

offspring individuals than the other). But this process cannot yet be termed group selection.

c) Finally, group selection, that only comes about when the populations of the two groups are reunited.

It should be noted – and strongly emphasized – that group selection is not a different process than the differential growth of the two groups, but the two notions are not identical either. This is because the process of differential growth of the two groups only becomes a selective process after the reunification of their populations. In other words, the pre-existing process of differential growth of groups only receives a selective pertinence or a selective status after the reunification.

At first sight, this distinction between a process that is not yet a selective process and a properly selective process doesn't seem to be a problem per se, i.e. it doesn't seem to undermine Sober and Wilson's claim that natural selection should be viewed as a cause of evolutionary change. To see why, we should take a simple example. Imagine an organism that is subjected to a cold environment and, as a consequence, its immune system becomes weakened. This weakening of its immune system is a real process, and it affects the general physiology of the organism. But this process is not yet or not by itself a cause for sickness. It will become a cause for sickness only when other conditions will have been met (for example when and if the organism in question comes in contact with a certain virus). The weakening of the immune system process only becomes a cause for sickness in a subsequent context. The same thing seems to be happening with Sober and Wilson's group selection. The differential growth of the two groups is a real process, but it is not yet a selective process, i.e. it doesn't constitute a cause for the evolution of altruism yet. This process will only become selective – and will only act as a cause for the evolution of altruism – after the reunification of groups. So, at first glance, this distinction doesn't seem to directly undermine Sober's claim that natural selection is a cause.

The comparison made above might however not be entirely adequate to our purposes. There is an important difference between the trait-group model and the immune system's weakening scenario given above, and this difference might pose a significant problem for the double selection-for interpretation of the model. But before we get to that point, two remarks need to be made. First of all, we should note that some authors avoid the complication introduced by the distinction between a differential growth process and a properly selective group selection process. Samir Okasha, for example, offers a 'variation' of Wilson and Sober's model where this distinction is completely bypassed. Here's how he presents the case: 'Organisms assort in groups of size  $n$  for a period of their lives, during which fitness-affecting interactions take place; they then blend into the

global population, reproduce and die immediately' (Okasha 2005, 704). Since reproduction only takes place after the reunification of groups, a distinction between group selection and the differential growth of groups becomes completely unnecessary. But there is a deeper reason why the distinction between the differential growth of groups and the group selection process is bypassed here. To see it, we should start by noting that this sort of 'variation' of the trait-group model for the evolution of altruism stems from a completely different view of group selection. While Sober and Wilson's 'standard' view is based (see Sober 2011) on George Price's equations (Price 1972) that aim to offer a causal decomposition of evolutionary change in within-group and between-group selection, Okasha's way of putting things stems from a different statistical approach to quantifying group and individual selection, namely the contextual approach, which is an application of multiple regression analysis to multi-level selection scenarios (see Heisler and Damuth 1987, Goodnight et al. 1992, Okasha 2004, 2005, 2006 and 2011). The contextual approach partitions the individual fitnesses in two components, one that is determined by the individual character and another one that is determined by the group character (or the average individual character of the group to which the individual in question belongs, in this case). Without dwelling on the details of this issue here, let's just say that the contextual approach defines group selection as the differential effect that group membership has on the fitnesses of the individual types involved. Since the fitnesses of individual types are all that we should be concerned about according to the contextual approach, the notion of differential growth of groups becomes redundant. The reunification of the populations of the two groups will still be necessary for there to be group selection, but the differential effect of group membership on the fitnesses of individual types will be effective regardless of which part of the individuals' life-cycle had been affected by the fitness-affecting interactions that were brought about by group membership. This, then, motivates Okasha's 'version' of the trait-group model given as an example above, and this also explains why the contextual approach to group selection is not affected by the temporal problem that, as I will show below, tends to cast doubts over Sober and Wilson's double selection-for interpretation based on Price's equations.

The second remark that needs to be made here is that if Sober and Wilson hold on to their 'standard' version of the model, it is because they want to make a more clear-cut distinction between individual and group selection. Indeed, intuitively, their standard model offers a more direct view of two processes. Within each group, there is individual selection. In addition to this, there is a parallel differential growth of the two groups, but this process is not yet causally pertinent (i.e. while the groups remain

isolated, only individual selection is at work). Finally, group selection only comes into play when groups mix ‘or otherwise compete in the formation of new groups’, i.e. when the differential growth process receives a properly selective status. The main merit of this way of putting things – and the one that explains the fact that Sober and Wilson cling to this ‘standard’ version of their model – is therefore the fact that it places face to face, if I may say so, the two selective processes (individual and group selection) with regards to their outcomes: the outcome of the individual selection is there for anyone to see, it is already given within each group (selfish types are favored), but so is the total evolutionary outcome (the increase in frequency of altruists) that must come from an opposing process, which is that of group selection. In Sober and Wilson’s view, this way of putting things gives both a logical and a chronological ground for the distinction between individual and group selection, since we can clearly see what the outcome would have been had only individual selection been at work. To translate this way of presenting things in causal terms is pretty straightforward, according to Sober and Wilson: first, there is selection for selfishness within each of the two groups; secondly, there is selection of altruism in the global population; thirdly, if there is selection of altruism within the global population, this cannot be because of the individual selection within groups, but because there is a different process, i.e. selection for groups with higher proportions of altruistic types, that accounts for the divergence of the final outcome with respect to what would have happened had only the within-groups selection for selfishness been at work. And, since ‘selection-for is where the causal action is’ (Shapiro and Sober 2007, 254), we can, according to Sober, state that group selection is the causal process that accounts for the divergence of the outcome from what would have happened had only individual selection been in play. If Sober and Wilson keep using their ‘standard’ version of the trait-group model for the evolution of altruism, it is because this ‘standard’ version offers a clear-cut view of this double selection-for (i.e. selection for selfishness within groups, and selection for groups with higher proportion of altruists) that underlies, in their view, the causal dynamics of the trait-group model.

There might however, as I said before, be a more serious temporal problem that might undermine this double selection-for claim about the dynamics of the trait-group model. To see it, we need to return to the comparison between this ‘standard’ version of the model and the weakening of the immune system that acts as a condition for disease. In this latter example, as I said, the weakening of the immune system is a real process, but it only becomes a cause for disease when other conditions are met, for example when the organism in question comes into contact with a certain virus. In an apparently similar fashion, in the ‘standard’ version of the trait-



group model, the differential growth of the two separated groups is a real process, but it only becomes a selective one (i.e. a cause for the evolution of altruism) when another condition is met, i.e. when the populations of the two groups are reunited. There is however an important difference between the two cases. In the former, the weakened immune system has to be contemporary with the encountering of the hypothetical virus: the weakened state of the organism and the presence of the virus act together, at the same time, so to speak, and the result of this acting together is the disease. The simple fact that the organism comes into contact with the virus doesn't put an end to the weakened state of the organism in question, on the contrary, the two factors reinforce each other, and it is this reinforcement that the disease originates from.

Things are very different for the double selection-for interpretation of the trait-group model though. The reason is that the reunification of the two groups is not only a co-condition for the evolution of altruism, but is also an event that puts an end to the differential growth of the two groups. If the differential growth of groups is in itself a real process – and this can hardly be disputed –, it is however a process that is halted or brought to an end by the reunification of groups. But if it is this reunification that turns the differential growth process into a properly selective process that acts as a cause for the evolution of altruism, than we are faced with a process that only becomes effective after it has ended, after it was chronologically terminated by that very reunification. We would therefore have a cause that only becomes effective or efficient after it has been halted as a process, after it has ended as a process.

One could however object that the effects of the differential growth of groups on the fitnesses of the two individual types are already there, already determined by the effects of the group characters on the growth of the two groups. The reunification of the global population would therefore only make these effects visible. But, precisely, this is not the case. The differential growth of groups determined by the group character doesn't have anything to do with the individual fitnesses of the two types while the groups are separated, and indeed it couldn't have anything to do with them since it only concerns the difference in average fitness between the two groups. Individual fitnesses cannot be regarded as connected to the differential growth process, since the latter denotes a fitness difference that is at a different level than the first, namely the simple difference in average fitness between the two groups. And the average fitness of the two groups doesn't have, by itself, anything to do with the fitnesses of the individual types involved. It is only after the reunification of groups that the variation in group characters will have had an effect on the fitnesses of the two individual types, but by that time the differential growth process will have

been terminated. In other words, group selection only becomes a cause for the evolution of altruism after it will have ended as a process, and this is a conclusion that must be drawn as long as one accepts the double selection-for view of the trait-group model.

The question that needs to be posed is whether this type of causation – where a process only becomes a cause after it will have been chronologically terminated – is even possible. Obviously, this question is tightly related to the metaphysical problem regarding the nature of the relationship between cause and effect, and regarding their ontological separability. In other words, what we would need to know is whether it is possible for a cause to only have effects after it has stopped acting as a process.

I would certainly not dare offer here even the slightest hints towards a possible answer to these profound and almost abyssal questions. However, what is more important is that I don't even need to, since the burden of proof has to be on the proponents of this double selection-for interpretation of the trait-group model. If, as they claim, the double selection-for view underlies the causal dynamics of the trait-group model, than it would also be their task to show how a cause can have an effect after it has stopped acting as a process.

#### Reference list

- Darwin, C. (1859) *On the Origin of Species*, Cambridge MA: Harvard University Press, 1964.
- Goodnight, C. J., Schwartz, J. M. and 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, I. L. and Damuth J. (1987) 'A Method for Analyzing Selection in Hierarchically Structured Populations', *American Naturalist* 130, 582–602.
- Kerr, B. and Godfrey-Smith, P. (2002) 'Individualist and Multi-level Perspectives on Selection in Structured Populations', *Biology and Philosophy* 17, 477–517.
- Nunney, L. (1985) 'Group Selection, Altruism, and Structured-Deme Models', *American Naturalist* 126, 212–230.
- Okasha, S. (2004) 'Multi-Level Selection, Covariance and Contextual Analysis', *British Journal for the Philosophy of Science* 55, 481–504.
- Okasha, S. (2005) 'Altruism, Group Selection and Correlated Interactions', *British Journal for the Philosophy of Science* 56, 703–725.
- 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.
- Shapiro, L. and Sober E. (2007), 'Epiphenomenalism: The Dos and the Don'ts', in *Thinking about Causes: From Greek Philosophy to Modern Physics*, eds. G. Wolters and P. Machamer, 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. and Wilson, D. S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Cambridge MA: Harvard University 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.
- Vrba, E. S. and Gould S. J. (1986) 'The hierarchical expansion of sorting and selection: sorting and selection cannot be equated', *Paleobiology* 12, 217–228.
- Walsh, D. (2000) 'Chasing Shadows: Natural Selection and Adaptation', *Studies in History and Philosophy of Biological and Biomedical Sciences* 31, 135–153.
- 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, 257–72. Quoted from its reprint in *Conceptual Issues in Evolutionary Biology*, ed. Elliott Sober, Cambridge MA: MIT Press, third edition, 63–75.