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Groups on Groups: Some Dynamics and Possible Resolution of the Units of Selection Debates in Evolutionary Biology[1]

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Abstract. David Hull's analysis of conceptual change in science, as presented in his book, *Science as a Process* (1988), provides a useful framework for understanding one of the scientific controversies in which he actively and constructively intervened, the units of selection debates in evolutionary biology. What follows is a brief overview of those debates and some reflections on them.

1. Hull's framework

According to Hull's view, conceptual change in science is best seen as a selection process among conceptual systems (1988). There must be variation among conceptual systems, and change in conceptual systems "is a function of the differential perpetuation of the elements that make up these systems" (p. 513). While it may be tempting to envision this selection process in terms of individual scientists, Hull claims that the regularities in the scientific process are best understood through social division of researchers into demes. That is, the structure of the scientific community participating in this selection process is one of nesting and overlapping informal groups (p. 366). Hull emphasizes the local effects of group alliances, especially the animosities between groups. Thus, although the demic structure of scientific groups helps advance science, one price of this structure is "intergroup warfare", which can lead to a "stall" in the scientific process. As Hull says, "the price of small research groups is intergroup polemics. Views are not evaluated solely on their own merits but also because of the allegiances of their authors" (p. 395).

I review here a case which seems to fit nicely with several of Hull's claims about the process of scientific change, namely, the past debates and emerging consensus about units of selection, especially higher-level or group selection. The bonus is that Hull himself actually aided in reaching this consensus. But let us start nearer the beginning, reviewing some of the major research camps and their moves and countermoves.[2]

2. Overview of the debates and players

The recent discussions about higher-level selection, especially group selection, got their original impetus from Vero Wynne-Edwards' (1962) claim that evolution by natural selection produces benefits and adaptations at the group level, i.e., adaptations that should be understood as "for the good of the species." But, in 1964, William D. Hamilton changed the landscape by describing selection processes applied to kin and kin-groups through his inclusive fitness genetics models (Hamilton 1964). Soon after, John Maynard Smith (1964) distinguished group selection from kin selection, in order to focus attention on the defects of Wynne-Edwards' views. Hamilton's kin selection models were cast as versions of organismic selection, which was contrasted with Wynne-Edwards' selection "for the benefit of the group".

In 1966, George C. Williams articulated a strict set of standards for what it takes for something to be an adaptation; he was committed to very strong requirements, i.e., that an adaptation must be a complex trait providing a solution for a particular environmental challenge, and that an adaptation at a particular level requires a process of selection at that level. Williams emphasized the role of genes in evolutionary processes, as an antidote for the then-prevalent sloppy thinking that saw selection as being driven by benefits for the group. Under this strong, engineering view of adaptation, not every selection process will result in adaptations. Specifically, not every selection process involving groups will result in group-level adaptations, interpreted in this strong engineering sense. Thus, Williams set up opposition to group selection, and set the evidential standards for the debate for the majority of the following two decades.

Meanwhile, there was a tradition, especially in the United States, and especially among population geneticists influenced by Sewall Wright, of examining the consequences of the structure of populations on evolutionary dynamics. Out of this tradition came the next major step in the debates: Richard Lewontin's 1970 paper on the "units of selection" problem, in which he proposed a generalization of the natural selection process. Lewontin distinguished three aspects of a system necessary for evolution by selection: phenotypic variation; differential fitness; and inheritance of fitness differences. He argued that, empirically, there are several biological organizational levels which can fulfill these requirements. Moreover, supported by his and Dunn's analysis of the t allele in the house mouse, he claimed that several levels of selection can be operating simultaneously.

In the mid-seventies, group selection was given new life. Michael Wade published his selection experiments, arguing that the results show that group-level traits can be selected at the group level, and that group selection of this type can yield evolutionary change. Pursuing a Wrightian approach, Wade developed a taxonomy of structured population models (1985), as well as an extensive list of empirical results documenting the efficacy of group selection in the laboratory. Wade also published an analysis of the biases present in previous group selection models, emphasizing their unnecessary assumptions that reduced the potential efficacy of group selection (1978). Meanwhile, David Sloan Wilson developed evolutionary models in which the populations were broken down into trait groups which underwent selection (1980). Wilson demonstrated that group selection on group-level characters can yield evolutionary change in a variety of conditions. With Robert Colwell, he documented cases of bias in sex-ratio, in which group-level characters are group selected, and yield evolutionary change (1981). Also, in 1975, Steven Stanley offered an explanation of evolution of sex through selection on the species level, and by 1979, was investigating the general consequences for macroevolution of species-level selection.

Through the late 1970s and 1980s, there were continued battles over the terms and empirical significance of different selection regimes, especially those involving multi-generational population structure. The original impetus for this seems to have come from Maynard Smith, who had, in 1964, been concerned to distinguish group selection from kin selection. After the publication of Wade's experiments in 1977, and through 1987, Maynard Smith rejected the American geneticists' models as being "real" group selection. He insisted on treating his 1964 model of group selection as an exemplar, claiming that, whatever process Wade, Wilson, or others were discussing, it was not "group selection". He emphasized the lack of continuous population structure able to sustain engineering adaptive changes at the group level.

Richard Dawkins, writing from 1976 through 1994 against group selection, followed Maynard Smith's line, and rejected Wade's and Wilson's experiments and models as being genuine group selection. He also expanded upon Williams' view that focusing on the gene is the best way to approach evolutionary questions. Perhaps most helpfully, he generalized the evolution by selection process, analyzing it into two functional roles: the replicator and the vehicle.

David Hull entered the fray in 1980, modeling his paper on Lewontin's 1970 paper in the same series. Hull introduced his piece as follows:

> On his treatment of the subject, Lewontin (1970) begins with a brief characterization of the evolutionary process and then proceeds to review evidence for and against the operation of selection at various levels of organization. I propose to do just the opposite, to investigate the general characteristics of the evolutionary process at great length and then discuss only briefly the particular entities that may or may not possess the characteristics necessary to function in this process (p. 312).

Hull then took up and revised Dawkins' distinction between replicators and vehicles. His analysis was both simple and coherent, and was general enough also to be applied to conceptual change in science (p. 402). Hull, thinking that some disagreements about levels of selection were the result of conceptual ambiguity, proposed a new set of definitions; he offered a comprehensive functional analysis of the distinct roles necessary to a process of evolution by selection:

> *Replicator*: an entity that passes on its structure largely intact in successive replication.
>
> *Interactor*: an entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential.
>
> *Selection*: a process in which differential extinction and proliferation of interactors cause the differential perpetuation of the relevant replicators.
>
> *Lineage*: an entity that persists indefinitely through time whether in the same or altered state as a result of replication.

Note that Hull's distinctions are different from Dawkins'; Hull showed that Dawkins' replicator really served two distinct functions, one of which is properly included in a vehicle-like phenotypic concept, which Hull named the "interactor". Hull argued that his replicator/interactor distinction allows us to investigate two distinct questions: What are the units of replication? What are the units of interaction? (Hull 1980, p. 414).

Hull's 1980 paper was crucial, partly because it was accepted and taken up by *both sides*, unlike the other extremely influential analyses of Lewontin and Dawkins, which were clearly identified and aligned with larger agendas. The result was that Hull's relatively neutral paper spurred on interaction and communication. As he notes, one apparent disagreement immediately disappears once the replicator/interactor distinction is in place: that between gene selectionists and organism selectionists.

Several other philosophers became involved in the units of selection controversies in the early 1980s. Robert Brandon applied and defended Hull's interactor/replicator distinction in 1982 and 1984. William Wimsatt joined the argument in 1980 and 1981, attacking reductionism in Dawkins, Williams, and Maynard Smith. Wimsatt applied and generalized Lewontin's three principles, in order to sort out which entities are doing which functions in a selection process. He took up the work of Wade, arguing that Maynard Smith, Williams, Dawkins, and others were mistaken about their conclusions regarding group selection. Elliott Sober, writing in 1981 and 1984, also took up Lewontin's approach, and criticized gene-level views for ignoring the importance of a phenotype's causal interactions with the environment. Sober also criticized Wimsatt's view, for not looking for real causal selection processes. In 1982, Lewontin and Sober published a full attack on the genic selection view, arguing that the natural selection process itself is a causal one, and genes (as replicators) cannot tell the whole causal story.[3]

Meanwhile, paleontologists were also involved, since 1977, through debates about the role of higher level selection in macroevolution. Niles Eldredge, Stephen Jay Gould, Joel Cracraft, Montgomery Slatkin, and Elisabeth Vrba argued that species level selection can have a role in evolution, but most required (until 1989) that a species-level selection process must involve species-level design adaptations, not just any old species-level trait. On this basis, Vrba and Gould argued that species-level emergent properties, which are species adaptations, are necessary for species selection processes.[4]

By the early 1980s, careful general analyses of hierarchical selection were starting to be available. Steve Arnold and Kurt Fristrup published the first, based on Price's covariance formulae, in 1982. John Damuth and Lorraine Heisler expanded the analysis in 1985–1988, arguing that population-level selection plays a role in evolution, and that emergent properties – design adaptations – are *not* required at the higher level in order for a trait to be playing a direct causal role in a higher-level selection process.

3. Progress toward consensus

Finally, it seemed that the foes of group selection began to relent. Williams acknowledged, in 1985, that evolution *can* occur with group-level properties playing a causal role, especially in macroevolution, and distinguished this type of process from adaptations developing at the higher level. Still, he declared his continued interest in group-level adaptations. His acceptance of the efficacy of higher levels of selection became completely explicit in his 1992 book, *Natural Selection: Domains, Levels and Challenges*.[5]

Similarly, Maynard Smith acknowledged in 1987 that evolution *can* occur as a result of a group selection process on traits that are not design-type adaptations. He seemed to acknowledge that American group-selectionists are justified in believing in the efficacy of the process they are modeling, but declared his continued interest in group-level adaptations. Maynard Smith's passage is worth quoting, as it is not widely acknowledged by his allies:[6]

> There has been some semantic confusion about the phrase "group selection," for which I may be partly responsible. For me, the debate about levels of selection was initiated by Wynne-Edwards' book. He argued that there are group-level adaptations . . . which inform individuals of the size of the population so that they can adjust their breeding for the good of the population. He saw clearly that such adaptations could evolve *only* if populations were units of evolution . . . Perhaps unfortunately, he referred to the process as "group selection." As a consequence, for me and for many others who engaged in this debate, the phrase came to imply that groups were sufficiently isolated from one another reproductively to act as units of evolution, and not merely that selection acted on groups.
>
> The importance of this debate lay in the fact that group-adaptationist thinking was at that time widespread among biologists. It was therefore important to establish that there is no reason to expect groups to evolve traits ensuring their own survival unless they are sufficiently isolated for like to beget like. . . .
>
> When Wilson (1975) introduced his trait-group model, I was for a long time bewildered by his wish to treat it as a case of group selection, and doubly so by the fact that his original model . . . had interesting results only when the members of the groups were genetically related, a process I had been calling kin selection for ten years. I think that these semantic difficulties are now largely over . . . with the use of the terms "intrademic group selection" and "trait-group selection" for the process envisaged by Wilson, and "interdemic selection" and "species selection" for that envisaged by Wynne-Edwards (Maynard Smith 1987, p. 123).

Despite this apparent concession of Maynard Smith's, when Dawkins published his second edition of *The Selfish Gene* in 1989, he stuck by the old Maynard Smith/Williams line that group selection requires group adaptations, and that what Wade and Wilson are discussing is not group selection.[7]

Meanwhile, since 1981, many philosophers of science, including Richard Burian, James Griesemer, Sandra Mitchell, Todd Grantham, myself, and others, have attempted to develop and apply the basic distinctions and frameworks provided by Lewontin in 1970, and Hull in 1980. I will not review those refinements and revisions here.

One thread of development that I pursued, following Arnold, Fristrup, Damuth, and Heisler, was that many of the confusions in the debates rested on an ambiguity about *adaptation*: is an adaptation just another name for a result of a selection process? Or, as on Williams' 1966 definition, must an adaptation be a design feature benefiting the owner? On my analysis, this stronger design definition of adaptation was clearly what Maynard Smith, Dawkins, Alexander, etc., were interested in, because their main opponent was still Wynne-Edwards and his designed-benefit-for-the-group idea of selection processes. In fact, once this ambiguity about adaptation is clarified, it is easier to see that there is much convergence of general opinion, now, about the efficacy of certain types of group selection processes in evolution. While Wade, Wilson, Marcus Feldman, Robert Colwell, and Marcy Uyenoyama argued first for the non-adaptation models, there is now explicit acknowledgment, even by Maynard Smith and Williams, that these group selection models are legitimate, and that their evolutionary effects are not necessarily minor.

Some earlier advocates of a strong design requirement for higher-level selection, Gould and Williams, have been overt about withdrawing their previous positions, and about recognizing the importance of the distinction between evolution by selection at a level, and adaptation at that level (Lloyd and Gould 1993; Williams 1992).

On the other hand, some have accommodated this distinction without remarking on the change. Dawkins, in a rarely cited passage from 1989, admits that species selection is likely a major influence on evolution, although it is unlikely to lead to adaptations at the species level.[8] (He failed to recognize, however, the identity in structure between the species level models he supports and the group selection models he opposes.) Vrba also changed her views. Since 1984, she had focused on emergent properties as design-type adaptations. In her 1989 Oxford Surveys paper on species selection, however, she rejects her former requirement for strong adaptations, without notice. As Hull says, “the only way that advocates of a particular research program can maintain that their views are both immutable and correct over any period of time is to change them surreptitiously” (1988, p. 374).

Hence, it’s become clearer, since 1980, to all participants in the debates that there are a number of different questions one can ask about levels of selection and the entities involved. In fact, a wide consensus is emerging about what the issues are, what empirical evidence is relevant, and what the appropriate terminology is for various processes. There is now enough perceived consensus about the structure of hierarchical selection processes to urge the spreading of the new consensus to other fields.

One such attempt was made in a 1994 paper in *Behavioral and Brain Sciences*, by Wilson and Sober. Most recently, they present an expanded and refined version of their views in their 1998 book, *Unto Others*. However, I see problems with their particular dissemination, primarily because their discussion seems to lack the clarity and precision which has been developed over the past two decades. In fact, they seem to be taking a step backwards by switching between selection processes that produce design-type adaptations and selection processes defined purely in terms of interactors. These are not the same thing. Based on Sober's previous writings, it is reasonable to think that Sober and Wilson are adopting a weak definition of adaptation, one in which adaptations are simply any product of a selection process. Under that definition, group selection always produces group adaptations. But the terms they sometimes use, e.g., "complex adaptations" or "functional integration", suggest that they are drawing conclusion about engineering adaptations. Hence, some of the empirical evidence of group selection Sober and Wilson cite does not necessarily support the claim that they want to make, i.e., that natural selection has operated on human groups, and that strong adaptations have accumulated at the group level as a result (Lloyd 1999b).

In this case, Wilson and Sober are emphasizing the broad agreement about group selection in structured populations, while disagreeing with the fairly widespread recognition of the importance of distinguishing engineering adaptations from mere products of selection.

4. Groups on groups

With this quick review of some aspects of the recent history of the debates about higher-level selection in hand, let me point out how well this case fits Hull's general model of the process of scientific inquiry (1988, p. 367). According to Hull, the evolution of conceptual systems is driven by a combination of intergroup hostility and intragroup loyalty. On his view, the demic structure of science highlights that certain dynamics are to be expected in a scientific controversy:

Unity within views/demes
Markedly decreased communication across groups
Competition for privilege of naming

We see all of these clearly in these three decades of debate.

The debates regarding the possibility of higher-level selection began with fierce dichotomization and developed quickly into dogma in the 1960s. This was followed by pioneering efforts from two groups of individuals, who were investigating rather different questions: one group trained with a particular approach to population genetics, and another group in paleontology. For about a decade, though, it seemed the only thing happening in the debates was name-calling, staking the rights to the term, "group selection", and obstinate and hostile rejections. (All the while, the new research into group selection continued.) This fits Hull's description of a stall in the scientific process through "intergroup warfare". As Hull says, "The price of small research groups is intergroup polemics. Views are not evaluated solely on their own merits but also because of the allegiances of their authors" (1988, p. 395).

I believe that much of the hostility in this case was amplified by a larger context of conflict; nearly all of the anti-group selectionists were also enthusiasts of sociobiology and of the general applicability of inclusive fitness theory as a method of doing genetics. Some of these authors form a fairly coherent group, recognizable by favorable cross-citation and commitments to the explanatory paradigms of inclusive fitness and game theory: John Maynard Smith, Richard Dawkins, Robert Trivers, John Krebs, Richard Alexander, Alan Grafen, as well as their philosophical supporters, Helena Cronin and Daniel Dennett most visibly.

Many of the researchers advocating the importance of group selection in evolution were, on the contrary, fiercely anti-sociobiology. Moreover, several were trained in Sewall Wright-style genetics, in which population structure was already understood as playing an important role in the outcome of evolutionary processes. Furthermore, they did not accept inclusive fitness theory as a full-fledged genetical theory, but rather saw it as shortcut, simplified genetics, good for modeling some systems, but not others. This is a less unified grouping than the opponents, primarily because its members can be broken into two subgroups, one concerned primarily with the ecology of population genetical models of selection in structured populations, and the other with selection and evolution above the species level. The members of the former group include Michael Wade, David Sloan Wilson, Richard Lewontin, Marcus Feldman, Montgomery Slatkin, and Marcy Uyenoyama, while those concerned primarily with selection at the species level and above include Stephen Jay Gould, Niles Eldredge, Elisabeth Vrba, Steven Arnold, Kurt Fristrup, Lorraine Heisler, and John Damuth.

Under Hull's analysis, science is characterized by research groups (1988, p. 367). In the units of selection case, the primary battles occurred between groups with different backgrounds, different training (especially in genetics), different projects, and most importantly, different opponents. Nevertheless, these groups found themselves opposing one another. Still, according to Hull, the opposition in the larger scientific context does not provide motivation for researchers; local rather than global credit is the driving force of science. In this case, the dogmatic views of the anti-group-selection deme were continually reinforced within that group, which, for about two decades, seemed basically impermeable to outside influence.

But the two groups couldn't remain impermeable forever. On Hull's view, "disseminators" are operative in the transmission process of conceptual change (1988, p. 377). It is not enough that discoveries are made locally; they need to be disseminated, and this is not always done by the discoverer. In fact, as Hull points out, often the disseminator actually promulgates his or her own view, rather than that of their named precursor. By clarifying – but also fundamentally altering – Dawkins' selfish gene view, Hull changed the conceptual terrain. The result was an increase in communication between the two camps, both of which found Hull's analysis to be accurate and congenial. The general acceptance of Hull's interactor/replicator distinction played an important role in the development of consensus among both philosophers and biologists. His analysis had the remarkable virtue of providing a relatively neutral common language in which the disagreements and discussions could be pursued.

But still, isn't a two-decade communications shut-down difficult to reconcile with Hull's optimistic picture of science as a process? While Hull accepts Merton's characterization of the scientific process as including "organized skepticism", he emphasizes that this skepticism is selective:

> Scientists, after some initial skepticism, become extremely attached to their own views and argue for them with a certainty that dismays the unconverted. Not infrequently they continue to hold onto them long after others think that they have been definitively refuted. Although this pigheadedness often damages the careers of individual scientists, it is beneficial for the manifest goal of science (1988, p. 377).

We can see this in the levels of selection case. Williams succeeded in persuading biologists to be extremely skeptical about any group selection hypothesis; in fact, by 1968, the view that group selection could be operating in a given system became a mark of scientific incompetence. Anti-group adaptationism had become dogma. Worse yet, Williams' work was converted by others into a rejection of the very methods that were ultimately necessary to test whether, in fact, group selection was operating or not.[9]

In what way, exactly, can we understand this dogmatism to have *benefited* the goals of science? The reluctance of Maynard Smith, Dawkins, and others, to recognize structured population genetic models as group selection gave rise to a mystery – a puzzle – which in turn prompted increased concentration on the problem, by biologists, and later by philosophers. This ultimately has led to a convergence and agreement on some views, while it has also become clear that the researchers in question were interested primarily in different things: one group, in the evolutionary dynamics of selective systems *per se*; and the other group, in the existence and frequency of design-type adaptations at higher levels of biological organization.

In *Science as a Process*, Hull presents empirical studies of both the effects of group allegiance on the refereeing process, and of the role of personality type and individual behavior in gaining supporters for new research programs. In this paper, I can offer only a quick suggestion of the roles of these factors in the debates about higher level selection. For example, one noticeable effect of personality was that Maynard Smith (but not Hamilton), was aggressive in staking out the meaning of “group selection”, and effectively prevented the serious examination of Wade’s and Wilson’s and Colwell’s results, for more than a decade, and in some cases, even longer. Dawkins, for instance, when asked why he dismissed Wade’s and Wilson’s models as “real” group selection in his 1989 second edition of *The Selfish Gene*, replied that Maynard Smith said that it wasn’t group selection, and that was good enough for him.[10] We learn two things from this. First, Dawkins and others did not feel it necessary to actually examine the American group selectionist claims for themselves. According to Hull, appeals to authority were routine among the scientists he interviewed.[11] Moreover, Hull found scientists identifying with a group although they were unable to answer even the most rudimentary questions about the views of the leaders of these groups. (Such a description does not apply to Dawkins.) Second, we learn that Maynard Smith’s 1987 retraction of his opposition to the new group selection research, that I quoted before, was not widely disseminated by Maynard Smith (or anyone else), to his own research community.

I have no evidence to offer on the effects of group allegiance on the refereeing process. Still, I have witnessed attempts to publicly humiliate researchers who even entertained higher-level selection scenarios; they’re characterized (for example, by Trivers), as being hopelessly confused about the current *findings* of evolutionary thought.[12] This is just the sort of behavior that, I think, Hull would anticipate under his demic view of the scientific process.

In conclusion, I think that Hull’s demic selection model of the scientific process fits nicely, and helps us to understand, the scientific debates over group selection models themselves.

Notes

1 Originally given as a talk at the “Symposium in honor of David Hull,” California Academy of Sciences, March 1994.

2 This review is necessarily rough and incomplete. I examine some of these authors in more detail in other places, e.g. Lloyd (1999a) and Gould (1993).

3 See below for discussion of Sober’s later work with David Sloan Wilson in 1994 and 1998.

4 In late 1980s David Jablonski, following Steve Stanley’s lead, provided impirical evidence that group selection had impact on course of evolution through species or lineage selection (1987).

5 Cf. W.D. Hamilton 1975. Sober and Wilson give an excellent discussion of this piece and its historical significance (1998).

6 I am indebted to Maynard Smith for bringing this passage to my attention.

7 Dawkins presents the same view in his (1994) criticism of Wilson and Sober.
8 Dawkins 1989b. Thanks to R. Dawkins for brining this piece to my attention.
9 See Lloyd 1988, especially chapter 7.
10 Personal communication, December 1989.
11 Personal communication, October 1999.
12 See similar testimony in Sober and Wilson 1998.

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