Running head: MULTI-LEVEL SELECTION CONTROVERSY AND PSYCHOLOGY

Selection of Evidence for the Selection of Groups:

The Multi-Level Selection Controversy and Its Implications for Psychology

Cameron Clark

Simon Fraser University

1. Introduction – The Controversy and the Case Against Group Selection

In his 1871 book, *The Descent of Man,* Charles Darwin had the following to say about the selection of groups in relation to altruism:

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well endowed men and and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. (pg. 178-179, as cited in Richerson & Boyd, 2005)

Darwin was perhaps the first to realize that group-beneficial behaviours such as altruism, that are disadvantageous at the level of the individual, require a process of selection *among* groups to spread through a population. The basic problem can be summarized by the biological truth that any heritable trait that benefits other individuals at the expense of the actor will decrease in frequency within a group over generations (Sober & Wilson, 1998). With this in mind, the problem becomes reconciling the obvious existence of group-beneficial traits and behaviours in humans and other organisms (such as the evolution of sex ratio, prudent use of resources, alarm calls, and cooperation in general) with a proper biological and psychological account of their origins. Selection among groups purports to solve this problem by providing a higher level of organisation for the process of selection to operate at. Thus, as Darwin alluded to in the above quote, although some traits can be locally disadvantageous, they may still evolve if a higher level of selection exists to counteract the disadvantage at the smaller scale (Wilson & Wilson, 2007). Simply stated: selfish individuals can outcompete altruistic individuals within a group, but groups of altruists can outcompete groups of selfish individuals.

As time passed after Darwin's original insight, the issue of group selection was overshadowed by more important theoretical evolutionary issues, such as the implications of Mendelian genetics (Sober & Wilson, 1998). Unfortunately, many evolutionary biologists began

to assume, rather uncritically, that adaptations could quite easily evolve "for the good of the group" without considering the substantial impact of within-group selection. This position has come to be known as "naïve group selectionism". One often cited example of such naivety is the work of V.C. Wynne-Edwards, who produced explanations of a large number of animal behaviours with group selection alone (Wilson & Wilson, 2007). Richard Dawkins (1976) gives a specific example from Wynne-Edwards 1962 book, *Animal Dispersion in Relation to Social Behavior*:

> [Wynne-Edwards] proposes that when huge flocks of starlings mass at evening, or crowds of midges dance over a gatepost, they are performing a census of their population. Since he is supposing that individuals restrain their birthrates in the interest of the group as a whole, and have fewer babies when population density is high, it is reasonable that they should have some way of measuring population density. (pg. 115)

The human equivalent of Wynne-Edwards' theory of selection between large groups of unrelated individuals would amount to something like selection between the peoples of North America and the peoples of Europe! Needless to say, many researchers were beginning to become restless of this retrospectively naïve group selectionism.

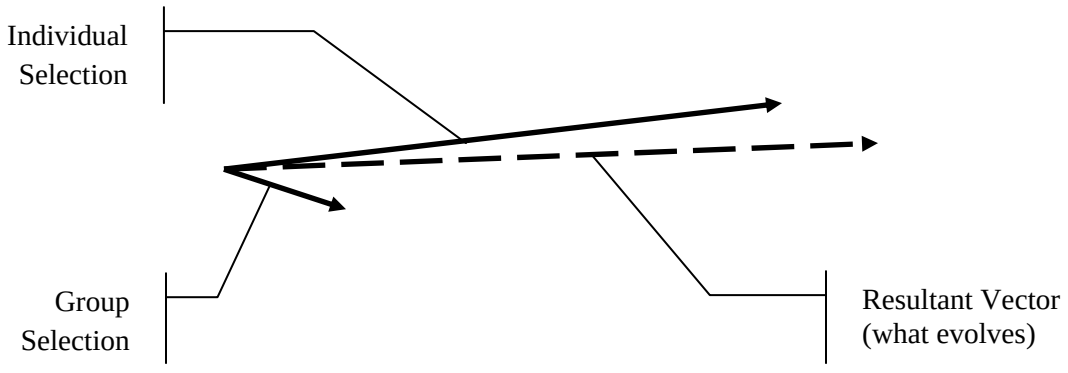
By the mid 1960s the issue of "multi-level" selection became a hot topic of debate for theoretical biologists, and resistance to the idea of began to grow. In 1964, W.D. Hamilton produced a theory of inclusive fitness which eventually became known as kin selection, which he interpreted as an alternative to group selection theory (Wilson & Wilson, 2007). In 1966, George C. Williams set out to expand on the work of Hamilton and correct, among other things, naïve group selectionism's sloppy application of the concept of adaptation in his book *Adaptation and Natural Selection*. He affirmed Darwin's original suspicion that group beneficial adaptations certainly require a higher-level of selection to evolve in a population. However, he made an

additional claim that revolutionized the field of evolutionary biology (and subsequently evolutionary psychology) for decades thereafter. He claimed that between group selection (i.e. group selection) was nearly invariably weak compared to within-group selection. Although the selection of groups remains a theoretical possibility for Williams, he argued that it need not be considered in practice due to its inevitable weakness compared to the stronger force of within-group (i.e. individual-level) selection. It was this theoretical claim that led him to conclude that "…group-related adaptations do not in fact exist" (1966, pg. 93). To appreciate this claim in full, it is helpful to consider evolution by natural selection as a resultant vector composed of various levels of selection (see figure 1). Consider D.S. Wilson's (2007a) explanation:

> Multi-level selection theory is a stepwise procedure for calculating evolutionary change in a population that is subdivided into groups…The final outcome of evolution depends on the relative strength of within- and between-group selection, similar to a final vector made up of two component vectors. (pg. 215)

One can imagine that for a trait such as altruism, the component vectors of individual and group selection would actually be pointing in approximately opposite directions, as selection within groups favours selfishness, while selection between groups favours altruism.

Figure 1.



The fact that group selection is part of this diagram is not in question, nor has it ever been. Rather, the point that Williams made – a point of controversy ever since – is that the group selection vector is so small compared to the individual selection vector that it can be ignored completely when explaining how the products of evolution came to be (Wilson, 2007a). Wilson and Wilson (2007) note:

> Acknowledging the theoretical plausibility of group selection as a significant evolutionary force is not a return to the bad old days of naïve group selectionism. It has always been the goal of population genetics theory to provide a complete accounting system for evolutionary change, including selection, mutation, drift, and linkage disequilibrium. The question is whether group selection can be categorically ignored when natural selection has been separated into within- and between-group components. (pg. 332)

Williams' (1966) theoretical clarification had an enormous impact on subsequent theories of evolutionary biology. In fact, many of the influential theories produced during the 1970s were an effort to re-explain evolutionary concepts without invoking the concept of group selection, including most notably Richard Dawkins' (1976) theory of the selfish gene. Directly following his explanation of Wynne-Edwards' hypothesis quoted above, Dawkins had the following to say:

> …unfortunately the evidence [for Wynne-Edwards' theory] is not good. It consists of a large number of examples that could be interpreted in his [group selectionist] way, but which could equally well be interpreted on more orthodox 'selfish gene' lines. (pg. 115)

Resistance to the idea of group selection is still strong within much of academia. Wilson and Wilson (2007) cite John Alcock's influential (2005) textbook, *Animal Behaviour: An Evolutionary Approach*, in which "group selection is described as non-Darwinain and a near impossibility because of the near insuperable problem of selection within groups." (pg. 344). Before the veracity of such claims can be fairly judged, a full hearing of the arguments for group selection must be considered. The remainder of this paper will review the case for and against

group selection, with particular attention given to the implications of multi-level selection theory on the field of evolutionary psychology.

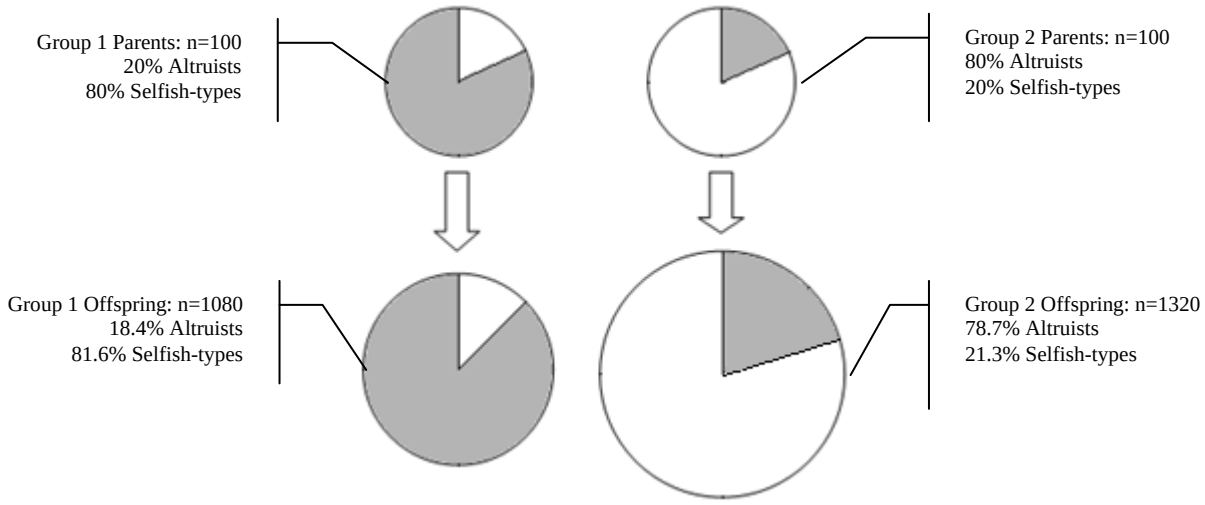
2. Arguments for Group Selection

In general, the resistance to multi-level selection can be parsed into three specific components. First, proponents of the orthodox individual selection paradigm argue that although group selection is possible in theory, it is not a significant evolutionary force in practice. Second, they argue that there is a lack of solid evidence in favour of group selection; and thirdly that there exist theories that can explain the observable phenomena without invoking group selection theory (Wilson & Wilson, 2007). Each of these arguments will be considered in turn, and respective counterarguments will be given.

2.1 Group Selection is a Significant Force in Natural Selection

Sober and Wilson (1998) argue that group beneficial traits such as altruism can only evolve via the force of group selection. Critics of this view point out that such a method is highly implausible because selfishness always trumps selflessness within a group, and that the frequency of altruistic individuals will therefore intuitively decrease every generation, until only selfish types remain. This criticism holds true, but the crucially important concept necessary for group selection to operate is often overlooked and misunderstood due to its counterintuitive nature: The presence of altruists within a group actually serves to help produce a higher global population of altruists (or carriers of another group beneficial trait) in the next generation, despite the reduction in frequency. Thus, although the relative frequency of altruists decreases, the number of altruists increase! (See figure 2, adapted from Sober & Wilson, 1998 pg. 24)

Figure 2.



The astute reader will realize however that this process of frequency reduction quickly meets with diminishing returns. So how can a group beneficial trait ever move through a population once it appears? Sober and Wilson (1998) explain:

> If the two groups are permanently isolated from each other, natural selection will eliminate the altruists within each group…The global [across both groups] increase in the frequency of altruists…will be a transient phenomenon of little interest. Suppose however, that the progeny of both groups disperse and then physically come together before forming new groups of their own. In this case…the increased frequency of the altruists…will become the average frequency for the next generation. If the process is repeated over many generations, altruists will gradually replace the selfish types, just as the selfish types replaced the altruists in the one-group example. (pg.25-26)

Thus, so long as groups are isolated but also subject to some migration, group selection can indeed be a powerful force in natural selection. Napoleon Chagnon (1981) provides evidence for just this sort of intergroup migration by documenting the patterns of village fissioning among the Yanomamo Indians of South America. He notes that population growth occurs fairly rapidly among the Yanomamo, and that the structure of their groups necessitates a fissioning, or splitting, process once a population of 100 to 150 is reached. Importantly, this fissioning process

serves to separate clusters of related individuals, such that the average relatedness between all group members is at its lowest point just after a fission occurs. If our ancestors were subject to the same fissioning and migratory behaviours as the Yanomamo, the conditions would have been right for the evolution of group-level adaptations such as altruism.

Despite the efforts of Sober, Wilson, and a few others over the last several decades to popularize this counterintuitive property of between group selection many modern researchers still hold on to the 1960s consensus that individual selection is the "right" way to analyse evolutionary hypotheses, without giving the alternative much thought. Examples of confusion regarding this multi-level selection process abound, but one example will have to suffice here. In his latest book, *Primates and Philosophers*, primatologist Frans de Waal (2006) elucidates his own theory of the evolution of human morality and had the following to say about the plausibility of group selection:

> Personally I am unconvinced that we need group selection to explain the origin of these [altruistic] tendencies – we seem to get quite far with the theories of kin selection and reciprocal altruism. Moreover, there is so much intergroup migration (hence gene flow) in nonhuman primates that the conditions for group selection do not seem fulfilled. In all of the primates, the younger generation of one sex or another…tends to leave the group to join neighbouring groups. This means that primate groups are far from genetically isolated, which makes group selection unlikely. (pg.16)

In light of the counterintuitive properties of group selection Sober and Wilson (1998) elucidate, de Waal's supposed evidence against group selection is actually evidence for it! As described above, migratory behaviour is, in fact, essential for group-beneficial behaviours to spread through populations. Acknowledgment of the theoretical plausibility of group selection and knowledge of its mechanisms would have allowed de Waal to identify migratory behaviour in primates as an ultimate mechanism of a group-level adaptation, rather than simply as an unsolved mystery. Wilson and Wilson (2007) note that this kind of misunderstanding is

inexcusable given the advancements of the past four decades since Williams' (1966) influential work. As if echoing across time, speaking to Williams himself, Wilson and Wilson (2007) make a final argument for the theoretical plausibility of group selection as a significant factor in natural selection:

> There is a form of naïve selectionism that needs to be corrected, as before the publication of *Adaptation and Natural Selection*, but today it is the naïve assumption that group selection can be consistently ignored. (pg. 332)

2.3 There Are No Empirically Valid Alternatives to Multi-Level Selection

Shortly after Williams (1966) imposed order on the scientific study of selection, George Price (1970) made an important theoretical contribution to the field of evolutionary biology. He produced a mathematical equation that parsed the total gene frequency change into its within- and between-group components (Frank, 1995). This equation (The Price Equation) became the quantitative cornerstone of multi-level selection theory. Upon reviewing Price's work W.D. Hamilton, the originator of kin selection theory adjusted his earlier work to account for the separate component vectors and re-published in 1975. Where he viewed kin-selection as an alternative to group selection before Price's work, he regarded it as a special type of group selection thereafter, and freely admits to the error (Wilson & Wilson, 2007).

Sober and Wilson (1998) argue that many of the individual level accounts of group beneficial behaviours actually subsume the logic of multi-level selection, and define group selection out of the equation. They call this the averaging fallacy. By averaging the fitness of individuals across groups, proponents of the individual selection mindset can easily point to the superior individual fitness of the successful organisms. The problem with this, Sober and Wilson (1998) claim, is that this average (represented in figure 1 by the resultant vector) already includes the contributions of both levels of selection. They state:

> The averaging approach makes "individual selection" a synonym for "natural selection." The existence of more than one group and fitness differences between groups have been folded into the definition of individual selection, defining group selection out of existence. Group selection is no longer a process that can occur in theory, so its existence in nature is settled *a priori*. Group selection simply has no place in this semantic framework. (pg. 32)

The main opponent of group selection theory to arise out of the aftermath of Williams' (1966) clarification, was Richard Dawkins' selfish gene theory. In the context of the averaging fallacy, the concept of genes as "replicators" and "the fundamental unit of selection" is exactly the same as averaging fitness over all environmental and social circumstances. Of course genes are selected on the basis of their fitness to the environment, but that environment contains selection pressures at the individual and group level. As we have seen, this average effect can be easily used to predict what evolves, represented by the resultant vector from figure 1. However, this is exactly the problem: entailed within a selfish gene view of evolution is a group-selection component that has been defined out of existence. In contrast, multi-level selection theory seeks to average the fitness of individuals in exactly the same way, but then to consider that average as a resultant vector of at least two components (Wilson & Wilson, 2007).

Thus, the mathematics of group selection can be translated directly into the mathematics of "individual selection", and will actually make the same predictions (Richerson & Boyd, 2005). However, the two paradigms differ in what they are willing to define as an adaptation, which can sometimes even have political consequences, as we shall see in the next section.

2.3 There is Solid Evidence for Multi-Level Selection

The rejection of group selection theory in the 1960s was not based on any specific evidence, but rather on Williams' assertion that individual-level selection is more parsimonious due to the theoretical implausibility of group selection as a major force in natural selection. (In

relation to figure 1, this argument amounts to considering only the individual level vector, because it is simpler than considering the supposedly weak group selection vector as well.) Wilson and Wilson (2007) note that parsimony alone can be an excellent criteria for deciding between competing hypotheses, but that it can never substitute for an actual evaluation of the available data. As Sober and Wilson (1998) note "Parsimony is a tool for interpreting observations, not for doing without them."(pg. 126). If group selection is an important force in natural selection, its specific effects need to be parsed out and considered in context, rather than ignored wholesale. Thus, the strength of the argument for parsimony is inversely proportional to the amount of evidence it ignores, and there have been enough developments since the 1960's to at least warrant a scientific look into the matter. It is not as if the theoretical issue of group selection could be solved once and for all, especially with only very little data to draw from.

Over the last 40 years, several empirical studies have affirmed the influence of group selective processes (Wilson & Wilson, 2007; Sober & Wilson, 1998). I will forego the details of these studies here as they are heavy in biological details, and carry only the weight of the above stated conclusion – that group selection is, in some fashion or other affirmed. However, one current area of considerable controversy involving group selection and psychological processes in general is the study of religion from an evolutionary perspective. A clear division can be made between the scientists that view religion as a by-product of other adaptations, and those who view religion as a group-level adaptation (Clark, 2007). Consider the following passages from Richard Dawkins' (2006) *The God Delusion*, and D.S. Wilson's (2007b) book *Evolution for Everyone* summarizing his 2002 book *Darwin's Cathedral*:

> As a scientist, I am hostile to fundamentalist religion because it actively debauches the scientific enterprise. It teaches us not to change our minds, and not to want to know exciting things that are available to be known. It subverts science and saps the in intellect. (Dawkins, 2006, pg. 284)

> My main hypothesis [is] that religious groups are products of group selection and are indeed like bodies and beehives. A given religion adapts members to their local environment, enabling them to achieve by collective action what they cannot achieve alone or even together in the absence of religion. The primary benefits of religion take place in this world, not the next. (Wilson, 2007b, pg. 237)

As might be guessed from earlier sections, Dawkins is no proponent of group selection, and therefore must find some way to explain the existence of religion in terms of individual selection (Clark, 2006). He advocates the by-product view of religion, proposing specifically that the impulse toward religion might be explicable as a by-product of always following the advice of one's parents while young, which would serve an adaptive function by keeping children out of harm's way. The upshot of Dawkins' view is that religions serve no purpose in themselves, but simply result from a misfiring of cognitive equipment that does serve a purpose. Wilson, in vivid contrast suggests that due to group selective processes, the impulse toward religion is actually a group-level adaptation, and therefore played a crucial role in the history of human evolution. From these passages, it is evident that the way one views religion from an evolutionary perspective can actually impact ones view of the entire subject.

I raise the issue of religion here because it exacerbates the tension between the multi-level selectionists and the individual level selectionists. One of these highly respected scientists is wrong about group selection, and one of them is wrong about the evolutionary underpinnings of religion, most likely due to their opinion about group selection. Just as in the case for altruism, the evolution of a group-beneficial trait such as religion requires the strength of the between-group vector to be greater than that of the within-group vector. In brief, religion represents the strongest case for group selection. The between group component vector must be so massive that in many cases it overrides the selfish within-group component vector completely. If evolutionary

minds are to ever understand group selection, it must be through examples such as this. Selection at the level of the group allows us to invoke the concept of adaptation at that level, and thereby explain an entire range of behaviours that are otherwise inexplicable at worst, and cumbersome at best. However, as is often the case, misunderstanding can have almost dangerous political consequences:

> The problem with Dawkins' analysis…is that if he doesn't get the facts about religion right, his diagnosis of the problems and proffered solutions won't be right either. If the bump on the shark's nose is an organ [i.e. a group-level adaptation], you won't get very far by thinking of it as a wart [i.e. a by-product]. That is why Dawkins' diatribe against religion, however well-intentioned, is so deeply misinformed. (Wilson, 2007c)

4. Conclusion – The Light of Evolution

In 1973, Theodosius Dobzhansky famously stated that "Nothing in biology makes sense except in the light of evolution." Of course, what Dobzhansky is referring to is the ability of the mindless, algorithmic process of natural selection to account for the entire range of biological diversity apparent in the world today. Eyeballs and peacock's tails, and panda's thumbs and giraffes necks are all explicable by this process. However, there are a few concepts that still have not quite made it into the light that Dobzansky speaks of. Without acknowledging the theoretical plausibility of group selection as a major force in natural selection; without acknowledging that many of the alternative theories utilize group selection logic; and without acknowledging the recent biological and psychological evidence for group selection, group-beneficial adaptations such as altruism and religion (and who knows what else) may never be pulled into the light – they may never "make sense."

References

Alcock, J. (2005). *Animal behaviour: An evolutionary approach*. New York: Sinauer Associates.

Chagnon, N. (1981). Terminological kinship, genealogical relatedness and village fissioning among the Yanomamo Indians. In R.D. Alexander & D.W. Tinkle (Eds.) *Natural selection and social behaviour: Recent research and new theory*. New York: Chiron Press.

Clark, C.M. (2006). Natural explanations of supernatural thought. Unpublished manuscript, written for Charles Crawford, December, 2006.

Clark, C.M. (2007). Beyond belief: The modern denial of irrational thought. Unpublished manuscript, written for the SFU 'Institute for the Humanities', October, 2007.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dawkins, R. (2006). The God delusion. New York: Houghton Mifflin.

De Waal, F. (2006). Primates and philosophers: How morality evolved. Princeton, NJ: Princeton University Press.

Frank, S.A. (1995). George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology, 175*, 373-388.

Hamilton, W.D. (1964). The genetical evolution of social behaviour, I and II. *The Journal of Theoretical Biology 7(1)*, 1-52.

Hamilton, W.D. (1975). Innate social aptitudes in man: An approach from evolutionary genetics. In R. Fox (Eds.) Biosocial Anthropology. London: Malaby Press.

Price, G. (1970). Selection and covariance. *Nature, 227,* 520-521.

Richerson, P. & Boyd, R. (2005). Not by genes alone: How culture transformed human evolution.

Sober, E. & Wilson, D.S. (1998). Unto others: The evolution and psychology of unselfish behaviour.

Wilson, D.S. (2002). Darwin's cathedral: Evolution, religion and the nature of society. Chicago: University of Chicago Press

Wilson, D.S. (2007a). The role of group selection in human psychological evolution. In S. Gangestad & J. Simpson (Eds.) *The evolution of mind: Fundamental questions and controversies*. New York: Guilford Press.

Wilson, D.S. (2007b). *Evolution for everyone: How Darwin`s theory can change the way we think about our lives.* New York: Delacourt Press.

Wilson, D.S. (2007c, July, 4). Beyond demonic memes: Why Richard Dawkins is wrong about religion. Retrieved July 10, 2007 from Skeptic Website: http://www.skeptic.com/eskeptic/07-07-04.html#feature

Wilson, D. S. and E.O. Wilson (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology, 82(4),* 327-348

Wynne-Edwards, V.C. (1962). *Animal dispersion in relation to social behaviour*. Edinburgh: Oliver and Boyd.