Almost everybody feels that they understand Darwin’s Theory of Evolution by natural selection. It is as simple as “survival of the fittest.” There is, though, an important subtlety that is often omitted by the biology textbooks, providing a radical shift in the way we view evolution and natural selection. In the early twentieth century, theorists uncritically assumed that Darwinian selection could apply and produce adaptations at many levels of the biological hierarchy, from individuals to populations to ecosystems. In the 1960s and 1970s, a scientific shift occurred and evolutionary biologists began viewing genes as the fundamental unit of selection. Noted evolutionary theorist Richard Dawkins wrote the revolutionary, and now classic, book *The Selfish Gene* in 1976, explaining the new genetic view and making it more accessible to lay-people and scientists alike. “Naive” group selectionism – such as the belief that any and all individuals would unconditionally sacrifice themselves for the survival of the species – was expelled from the accepted scientific understanding of natural selection, and held up as an example of how not to think. Only in recent years has a newer version of the group selection theory come back into the arena of debate, arguing that populations should be viewed as vehicles of selection in the same way that individual organisms are. This new perspective is mainly supported by the writings of E.O. Wilson and David Sloan Wilson, two respected American evolutionary biologists. The controversy between purist gene selectionism and the Multilevel Selection Theory (MST) may seem theoretical, but the reasoning behind the two perspectives profoundly changes the way scientists understand evolutionary changes, kin altruism, and group behavior. The claim now becomes a question: “survival of the fittest what? Gene? Organism? Or group?”

The gene selectionist perspective proposed by Dawkins and others in the 1960s is the predominant view among modern evolutionary biologists. The main premise relies on the concept of the “gene” as being the ultimate, fundamental unit of natural selection. By the basic principles of natural selection, genes that are more successful at replicating themselves will, by default, become more numerous in the population. Therefore, a gene that happens to increase the general fitness of the individual in which it is located will be more likely to be passed down to the next generation. This understanding leads us to the concept of the “selfish gene,” where natural selection applies at the level of individual genetic codes; genes which make the organism behave in ways that “selfishly” increase the chances of the immortal gene’s survival will become more frequent in any given population. The organisms which carry thousands of these genes can then be viewed as “vehicles” of selection, since they constitute a coordinated, fairly unified collection of genes. Genes must work together in organizing the survival and reproduction of the host vehicle, because they are all locked in the same “boat.” For example, a gene for powerful jaws and hunting skills would not help the organism survive if all the other genes were coded for the body of an herbivore; the organism would be less likely to survive and reproduce, thereby stopping the genetic line and reducing the frequency of that particular carnivorous gene in the population (Dawkins, 1976). Although natural selection actually operates at the level of selfish genes, the general fitness of individuals often corresponds with that of the genes. This makes it appear as though selection applies at the individual level, and for the sake of convenience, biologists often refer to fitness levels of organisms determining the selection process. It is always important, though, to be able to return to what Dawkins calls the “gene’s eye view” of evolutionary change - justifying organism’s behavior on the basis of gene preservation (Dawkins, 1976).

Groups or populations can also be viewed as vehicles of replicators, but far weaker, and less distinct, than individual physical colonies of genes or cells. In this sense, then, a sort of “group selection” could in theory be possible, but it seems unlikely that group-level adaptations between populations would occur. Lower-level selection likely overrides most of the influences from higher-level selection, so the relevance of any possible group adaptations is debatable. Genes are still central as the only units of
replicator selection (Cronin, 1991; Dawkins, 1976).

The controversy regarding group selection has its roots in the question of demonstrated animal altruism: why do individuals sacrifice themselves or their time and energy in order to help other organisms? In the early days of group selectionism, this sort of behavior was thought to have evolved “for the good of the species” or “for the good of the group.” The most common form of altruistic self-sacrifice is reproduction and the care of offspring. Altruistic behaviors are also common between close family members. This altruism results in the increased fitness, survival, and likelihood of reproduction of non-descendant relatives, also called kin selection. As Dawkins explains in his 1976 book The Selfish Gene and in a 2008 journal article entitled “The Evolution of Altruism: What Matters in Gene Selection,” kin selection is still indirectly driven by selfish gene behavior. Individuals are programmed by their genes to help close kin survive and reproduce because, by doing so, they help perpetuate copies of their genes – since offspring and relatives share up to 50% of the altruistic individual’s genetic material. This explanation of kin selection provides a very acceptable model of the evolution of cooperative behavior. Sociobiologist W. D. Hamilton delineated the mathematical model of kin selection, calculating the probability that two individuals, either directly descendent or with common ancestry, will share genetic material (Hamilton, 1964).

Patterns of group behavior can be predicted within the selfish replicator theory by the use of John Maynard Smith’s concept of Evolutionarily Stable Strategies (ESS); Dawkins describes this important idea as “a strategy which, if most members of a population adopt it, cannot be bettered by an alternative strategy” (Dawkins, 1967). This means that the most effective survival plan for an individual, and the genes which inhabit it, depends upon what the majority of the population is doing. For example, if all the members of a group of animals are altruistic, the best reproductive strategy for one individual might be to act selfishly. Since these “selfish” individuals are more successful reproductively, the population will eventually become almost entirely “selfish,” at which point, there might be a reproductive payoff to acting altruistically. As the group dynamics oscillate back and forth between these two extremes, the most effective strategy for each individual will converge on some average, evolutionarily stable, strategy. Following any environmental change, there may be a period of evolutionary instability during which frequencies of survival strategies fluctuates until it reaches a relatively stable ESS. It is possible for humans to enter into conscious pacts which, in the long term, improve the survival and reproduction benefits of every member of the group, but in general terms of animal strategies, ESSs will evolve that give an average benefit to all members and that penalize any deviance from the norm.

The second and opposing point of view in this controversy is the new version of group selection, also known as Multilevel Selection Theory. Evolutionary theorists who support the view that selection can operate on higher biological levels include E. O. Wilson, V. C. Wynne-Edwards, David Sloan Wilson, and Elliott Sober. These renowned scientists do not renounce the gene as a basic unit of selection, but instead argue that since individuals can be regarded as populations of coordinated, cooperating genes, groups – as long as there is some degree of coordination and harmony in their parts – should also be viewed as distinct “organisms” that can act as vehicles of natural selection (Wilson & Wilson, 2007). Proponents of this perspective contend that these vehicles of selection are the important factors around which the entire view of selection must be restructured.

In the new perspective of Multilevel Selection theory, it is vital to differentiate between the environmental pressures and competitions within a group versus the competition between separate groups or populations. David Sloan Wilson accepts that within-group selection follows the basic principles of individual, selfish competition (McAndrew, 2002). In a 1997 journal article, Wilson argues that group-level adaptations do not evolve into adaptive units for all traits, but instead only for certain traits which increase the evolutionary “fitness” of each group in relation to other populations (McAndrew, 2002). He states that although the occurrence of individual altruism may appear to reduce the fitness of the organism, “it may sometimes become adaptive because groups of altruists will be more fit than groups of non-altruists under the right conditions” (McAndrew, 2002).

Some of the main evidence for group selectionism theories is based upon entomological studies. E. O. Wilson, in particular, has done a large amount of research in the field of Myrmecology, the study of ants, a branch of entomology. For ants, group selection theories appear very useful for explaining their behaviors and physiology. Ant colonies can be, and sometimes are, viewed as super-organisms, owing to the specialization of duties and extreme altruism of worker ants (Wilson and Elliott, 1994). Gene selectionists think that this may be due
in part to the fact that more than 50% of the kin ants’ genetic material is shared (Dawkins, 1976). Group selectionists maintain that eusocial insect relations, such as ants and honeybees, illustrate a classic example of group-level vehicles of gene survival.

Multilevel selectionists distance themselves from the naivety of the uninformed 19th century group selectionism theories. Instead, they focus on the importance of the group or population as an organism and as a vehicle of natural selection. Applying the theory of MLS to human social interaction, Wilson concludes that religious ideals and ethical norms may provide mechanisms which contribute to the coordination of group function. Culture, too, may represent a group-level adaptation that helps populations of humans adapt to environmental changes (O’Gorman, Sheldon, Wilson, 2008).

The controversy surrounding the gene selectionist and group selectionist perspectives is a complex and significant debate. There are important consequences of accepting either view, and criticisms of both theories that must be considered. For example, both David Wilson and E. O. Wilson criticize the selfish replicator theory for considering individual organisms, colonies of coordinated parts, as vehicles of natural selection which can be more or less “fit” in their environments and not following the definition to the same conclusion for groups. On the other hand, Dawkins proposes the question of how group selectionists are to decide which level is the important one for group adaptations. Following the multilevel selection perspective, since selection occurs between populations in a species and between species, who is to decide at what level the group adaptations become unimportant? “Should we not then expect lions to refrain from killing antelopes, ‘for the good of the mammals?’” Dawkins questions, partly tongue-in-cheek: “But then, what of the need to perpetuate the whole phylum of vertebrates?” (Dawkins, 1976).

Within the Darwin’s Theory of Evolution, specific perspectives such as these are still being debated, and as scientists collect more empirical research data about the actual behaviors of genes, organisms, kin groups, and populations, it will be possible to refine our understanding of the different processes of selection in nature. The comparison of purist gene selection and the new Multilevel Selection Theory is, to some extent, a debate of semantics. Whether we should view individuals and groups as vehicles of selection seems like an unimportant distinction, but it profoundly influences the context in which we view situations of group dynamics. Despite the propaganda put out by proponents of Intelligent Design and Creationism, the acceptance of the actual validity of the general theory of evolution is almost unanimous among scientists. Debates about specific perspectives within the Darwinian “survival of the fittest” model are actually useful and encouraged within science. The academic openness of the scientific method helps scientists in the continuing pursuit of a true understanding of the evolution of individuals and groups.

REFERENCES:


