FEATURE ARTICLE

Teaching Evolution & the Nature of Science via the History of Debates about the Levels at Which Natural Selection Operates

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Abstract

Students should not graduate from high school without understanding that scientific debates are essential components of scientific methodology. This article presents a brief history of ongoing debates regarding the hypothesis that group selection is an evolutionary mechanism, and it serves as an example of the role that debates play in correcting faulty ideas and stimulating new research in the pursuit of extending scientific knowledge.

Key words: *Altruism; confirmation bias; cooperative behavior; Darwinism; inclusive fitness; kin selection; multilevel selection; reciprocity.*

Does natural selection occur only between individuals within a species or might it also occur between groups of individuals within a species (e.g., Mendelian populations) "for the good of the group," between species, between higher taxonomic groups (e.g., genera), or even between more complex biological systems (e.g., ecological communities)? Teachers who pose this question to their classes should not be surprised to find that most students have never considered the existence of "multilevel (group) selection," nor have they heard that the subject has been widely debated for about 50 years. This teaching technique has implications for students learning about debate as an essential component of scientific methodology. Don't look in your biology textbook for any help in this regard. If the teacher does not discuss it in the classroom, students will likely never fully understand how scientific knowledge grows. Creationists often use these kinds of debates as evidence that evolution theory is "in crisis." In the present article, I present a brief outline of the history of this debate, arguing against the notion that scientific debates indicate that a "crisis" exists, and illustrating the positive functions that debates perform. For information online about controversies in the public arena relating to evolution, go to http://evolution.berkeley.edu/evolibrary/controversy_faq.php.

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Teachers can present each of the following questions to their students for their consideration before presenting any relevant lectures. If students respond with ideas that are controversial and worthy of class time in further debate, that would be ideal. In any case, the posed questions are designed to stimulate student interest in finding the answers via class discussions, lectures, or reading assignments. The responses given here are only suggestions that may benefit from embellishments by the instructor. A response to each of these questions can be summarized in one or a few sentences for use in an assessment test of student understanding. The italicized text in this article indicates the kind of information that should be included in correct student responses.

Q1: What function(s) might scientific debates perform?

Science is a self-correcting process. Open public debates following publication of a scientific research paper might detect deficiencies or flaws in the project design, in the quality and/or quantity of the empirical data (sense-derived, with or without the aid of instruments), in the statistical methods employed in the analysis of the data, in the interpretation of the data, or in other factors. These criticisms and debates may stimulate other independent researchers to replicate the project and publish their results as either confirming or falsifying (refuting) the findings of the paper in question. Debate may also *stimulate new research* that corrects flaws in other publications. Because of these debates, the eventual fate of most scientific models (hypotheses, theories) is either modification or rejection in favor of better models, thereby *improving scientific knowledge*. Hypotheses do not become well-tested theories without the benefit of thorough debate.

Q2: What are some of the pre-Darwinian debates that had implications for later evolution theories? For assessment, ask students to give one example.

- Creationists believe that *evolution does not occur*. All organisms (including humans) were supernaturally created (by an

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"intelligent designer") about 10,000 years ago and have not changed since then; however, some kinds of organisms have become extinct. This debate is a philosophical one because it involves supernatural forces that are outside the scope of scientific investigation.

- The *age of the Earth* can be studied by scientific methods and is thus within the purview of scientific debates. The relative *ages of rocks containing fossil organisms* can be determined by stratigraphic methods; a fossil found in a higher rock layer (stratum) than one in a lower stratum is deemed to be a younger fossil. After Darwin's time, the age of rocks and their embedded fossils could be dated more precisely by determining the relative amounts of radioactive isotopes therein. Some fossil evidence of life has been dated at 2–3 billion years.
- *Catastrophism* is a geological theory proposing that the earth has been shaped by violent events of great magnitude (e.g., worldwide floods, collision with asteroids, etc.). *Uniformitarianism* is a geological theory that "the present is the key to the past." In other words, the phenomena of volcanism, erosion, glaciation, etc., that can be seen today have been operating through billions of years of earth history, and they are the primary forces that have made the earth what it is today.
- Is the *hereditary substance* of an organism easily modified by the effects of its environment (plastic heredity), leading to the inheritance of acquired characters (Lamarckism), or does it consist of solid particles (hard heredity) that are passed intact (unchanged) from one generation to the next?

Q3: What was the greatest flaw in Charles Darwin's theory of evolution (1859) by natural selection?

Darwin did not know how heredity works. The inheritance of acquired characters was really the only scientific theory of heredity available. G. Mendel (1822–1884) published his genetic hypothesis in 1866 while Darwin was alive, but it was not widely known or appreciated until 1900. Darwin died before the knowledge of chromosomes, mitosis, meiosis, haploid gametes, and diploid somatic cells became available. To fill this void, Darwin suggested his "pangenesis" theory. The problems with this theory were discussed in *ABT* by McComas (2012).

Q4: What is Darwinian fitness?

Fitness (or adaptive value) is the relative *ability of an organism to survive and transmit its hereditary material to the next generation compared with other individuals of the same species, population, or other defined group living in the same environmental conditions*. Competition for food and other limited resources of the environment tends to increase the numbers of the fitter individuals and decrease the numbers of the less fit organisms. This process is called natural selection.

Q5: At what level(s) did Darwin propose natural selection may operate?

Before Charles Darwin (1809–1882) published his *On the Origin of Species* in 1859, many people believed that all levels of life were created by God to be adaptive to their natural environments, from the individual organism to the species and to the highest levels of taxonomic grouping. This idea accounted nicely for the harmony and balance of nature assumed to exist in the biological world. Realizing that individual organisms were not living in harmony, but were almost always competing with one another for limited resources of their environment, Darwin proposed that biological evolution mainly occurs by natural selection operating on the heritable phenotypic variation (anatomical, physiological, biochemical, and behavioral traits) among individual organisms within a species. What is not always recognized is Darwin's allowance that *natural selection*, by competition or cooperation, *might also act on fitness variation at multiple levels* – between intraspecific groups of individuals (such as herds, flocks, colonies, varieties), between groups of related species, or even between higher taxonomic groups "for the good of the group" rather than only for the selfish interests of the individuals within a group. For example, he asserts that certain mountain varieties of sheep "will starve out other mountain *varieties*, so they cannot be kept together … As *species* of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera" (Darwin, 1859, p. 76).

Q6: Why did honey bees present a challenge to Darwin's concept of natural selection?

Darwin worried about many things as he wrote *On the Origin of Species*: the incompleteness of the fossil record, the complexity of the human eye, the existence of non-reproductive (sterile) female worker honey bees, and many other contentious issues. If natural selection works at the level of improving the reproductive fitness of individuals, how could it account for the existence of *worker honey bees who work for the hive instead of producing offspring of their own*? Frederick R. Prete (1990) discusses the bee problem in detail. He informs us that by 1838 it was known that a fertilized egg could develop into a reproductive queen bee if the larva is fed royal jelly (Lamarckian implications?). Also, the discovery of parthenogenesis in bees had been known from 1857 (unfertilized eggs develop into male drones; sometimes workers may lay unfertilized eggs that develop into drones). According to Prete, Darwin suggested community selection as a solution to the evolution of the honey bee problem.

Q7: According to biologist J. B. S. Haldane (1932), what was the reason many biologists had given up on Darwinism?

The ability of natural selection to account for the evolution of adaptive, specific (at the species level) characters had been questioned by some critics ever since Darwin suggested that natural selection could be responsible for the evolution of new species and higher taxonomic groups. Haldane gave one reason why early-20th-century biologists doubted Darwin's notion of group selection at the species level: "[T]here is no doubt that *innumerable characters show no sign of possessing selective value, and, moreover, these are exactly the characters which enable a taxonomist to distinguish one species from another*. This has led many able zoologists and botanists to give up on Darwinism" (Haldane, 1932, pp. 113–114).

Q8: Two books were published in the 1960s that polarized the debates over individual vs. group selection theories. Explain the beliefs held by the two authors in this regard.

Early in the second half of the 20th century, most biologists continued to believe that, if group selection exists, it cannot predominate over individual selection. Then, in 1962, British biologist Vero Copner Wynne-Edwards (1906–1997) reinvigorated the group selection debate by publishing his 650-page book *Animal Dispersion in Relation to Social Behavior*, in which he proposed that many animal social behaviors are adaptations at the group level even though they may be disadvantageous within groups. He called his theory of genetic selection "group selection" (Newton, 1999). Group selection is "much more important than selection at the individual level. The latter is concerned with the physiology and attainments of the individual as such, the former with the viability and survival of the stock or race as a whole. Where the two conflict, as they do when the short-term advantage of the individual undermines the future safety of the race, group selection is bound to win, because the race will suffer and decline, and be supplanted by another in which antisocial advancement of the individual is more closely inhibited" (Wynne-Edwards, 1962, p. 20).

According to Wilson and Wilson (2008, p. 385), Wynne-Edwards assumed that evolution of group adaptations required the action of group-level selection; essentially, *between-group selection always prevails over within-group (individual) selection*. However, group selection and individual selection may sometimes work in the same direction. From his field observations on red grouse and other species, Wynne-Edwards concluded that if members of a group cooperated in controlling their population size so as not to overuse the environmental resources, that group would likely survive longer than groups that were not so prudent. These ideas ran counter to the prevailing orthodoxy that the tendency of natural populations to always increase in size is limited by the Malthusian parameters of food supply, predators, diseases, parasites, and climatic conditions, not by self-restraint mechanisms. Wynne-Edwards explained that individual animals do not conscientiously deprive themselves of reproducing maximally, but rather succumb to hormonal stress effects when crowded or overpopulated due to excessive competition for territories, nest sites, poor nutrition, parasites, diseases, etc., resulting in fewer matings, fewer eggs laid, fewer offspring fledged, decreased reproductive life span, etc. Most evolutionists felt that selection at the individual level and selfish behaviors should always dominate any self-restraint behaviors. Nonetheless, Wynne-Edwards' book was widely read by biologists and ignited a controversy that still prevails to some extent among biologists.

Four years after Wynne-Edward's book was published, George C. Williams published his book *Adaptations and Natural Selection* (1966), in which he allowed that adaptations might evolve "for the good of the group," but only if between-group selection is stronger than within-group selection. For him, however, group-level selection is almost always weak in relation to within-group selection; essentially, *group selection never prevails* (Wilson & Wilson, 2008, p. 385). Both Wynne-Edwards and Williams proposed that one level of selection routinely prevails over the other. However, most biologists sided with Williams's position and rejected group selection theories altogether. "Generations of students were taught that group-level adaptations can evolve in principle, but do not evolve in practice, making 'for the good of the group' thinking just plain wrong" (Wilson & Wilson, 2008, p. 382). Most biologists thought that prosocial adaptations could be explained by forms of self-interest without recourse to selection at the group level.

Q9: W. D. Hamilton (1964) proposed a theory that a social act of an individual by natural selection is favored if it increases the "inclusive fitness" of the performer. What is the meaning of "inclusive fitness"?

In 1964, W. D. Hamilton explained mathematically how an altruistic trait could be maintained by *kin selection* or *family selection*, which he initially considered an alternative to group selection. His theory proposed that a social act is favored by natural selection if it increases the *inclusive fitness* of the performer. *Inclusive fitness consists of the individual's own fitness as well as its effects on the fitness of any genetically related neighbors*. Sterile female members of a honey bee hive "care for their *reproductive siblings* who carry gene line copies of the caring genes. If they care for other workers, it is because those other workers are likely to work on behalf of the same reproductives (to whom they are also kin), *not* because the workers are kin to each other" (Dawkins, 1982, p. 85).

Q10: By what mechanisms can altruistic behaviors be maintained in a population?

Actions of an individual that tend to increase the fitness of a recipient but tend to decrease the fitness of the "actor" are termed "altruistic behaviors." It seems that if prosocial behaviors are generally disadvantageous within groups, the only way that altruism can evolve is *when between-group selection is stronger than any contrary process of within-group selection*. Later generations of biologists after Darwin would also recognize that natural selection might act on cooperative traits as well as competitive ones. For example, a bird may altruistically call out a warning if a predator is spotted, even though doing so may make him a target for the predator. His calls may be intended for just his mate and/or kin, but unrelated birds of the same or different species (perhaps even mammals or other animal taxa) also might benefit coincidentally from the warning. If others contribute in some way (even unintentionally) by the actions of a few, it can be a win–win situation. Dugatkin (1997) outlines numerous cases of cooperation between non-kin in animal societies.

If you pick parasites from my back today, I'll do it for you later; quid pro quo. This process, known as "*reciprocity*" or "*reciprocal altruism*," was given detailed examination early on by Trivers in 1971. Nowak and Highfield (2011) recently proposed that "cooperation can only evolve and overcome selfishness through one of five mechanisms: direct reciprocity (I'll scratch your back if you scratch mine); indirect reciprocity (I'll scratch your back, you scratch someone else's, and eventually someone will scratch mine); special structure (back-scratching tends to bring back-scratchers together); group selection (groups that back-scratch do better than groups that don't); and kin selection (if you're a relative, I'll scratch your back even if you won't scratch mine)" (Nonacs, 2011). As with all types of altruistic behaviors, reciprocity is potentially subject to exploitation by "cheaters" who take benefits but do not give back.

Q11: When were debates about group selection terminated?

These debates continue today for a variety of reasons. The most important potential cognitive error in science, science education, and introspection is "confirmation bias," or the subconscious human proclivity to favor data and/or interpretations that support one's previous ideas while minimizing or trivializing counter evidence (Allchin, 2011). Assuming that they have kept up with recent research in the field, confirmation bias may at least partly explain why some advocates of evolution have steadfastly denied any evolutionary role for group selection in the evolution of prosocial behaviors and remain committed to competitive individual selection. Richard Dawkins (1982, p. 115) opines that group selection "has soaked up more theoretical ingenuity than its biological interest warrants." He and his fellow critics have remained steadfastly against group selection theories. Some recent studies have suggested that "individual selection might be adequate to explain many instances of social behavior" (Gadagkar, 2011, p. 834). For example, Leadbeater et al. (2011, p. 874) conclude that "[w]hile indirect fitness obtained through helping relatives has been the dominant paradigm for understanding eusociality in insects, direct fitness is vital to explain cooperation in [the wasp] *P. dominulus*." According to Krakauer (2011, p. 538), "All forms of cooperation can be understood in terms of individual-level selection operating in hierarchically structured populations." Beroukhim (1995) believes that group selection theories are waning, have become too problematic, and should be put to rest.

Other authors summarize the present status of group selection in more conciliatory ways. "Perhaps we can agree that the answer to the question of altruism and the levels of selection is a complicated one that will not be answered by the simple invocation of natural selection at any particular level, but will be understood as the result of selective forces at multiple levels combined with contingent forces of history and culture" (Borrello, 2005, p. 47). "The debate among biologists on the legitimacy of group selection theory continues unabated today…and the ongoing struggle to resolve interpretations of how selection acts at the 'organismal' or 'superorganismal' (or even cellular or molecular) level is certain to challenge the limits of human perspective for a long time to come. This struggle to find a resolution, to a seamlessly 'unified' selection theory that bridges the gap from the smallest nucleic acid to the largest populations, is essentially at the heart of smaller controversial issues like group selection, and is part of the reason why these heated topics have persisted since Darwin started it all" (Price, 2011).

Q12: How do creationists view scientific debates such as those over the levels at which natural selection operates?

Early-20th-century biologists were aware of the reproductive disadvantage of an individual (or species) using sexual reproduction rather than asexual reproduction. Why should an individual give up its ability to pass on all of its genes to offspring asexually in favor of a sexual mechanism that only allows a parent to pass on half of its genes to offspring? According to Dawkins (2010, p. 49), George Williams's *Sex and Evolution* (1975) "was the first book to wrestle with this paradoxical 'twofold cost of sex.'" He wrote this book "from a conviction that the prevalence of sexual reproduction in higher plants and animals is inconsistent with current evolutionary theory…[T]here is a kind of *crisis* at hand in evolutionary biology…" [emphasis added]. Thus, unfortunately, creationists are not the only ones that have referred to modern evolution theory as being in "crisis." More than 20 different hypotheses have been proposed to explain the failure of asexuality to predominate in the biological world.

Creationists like to use the term "Darwinism" in discussions of modern evolution theories, knowing full well that many of the things that puzzled Darwin have since been explained by natural processes rather than by supernatural intervention. *Whenever scientists disagree on some aspect of evolution theory, creationists claim that Darwinism is "in crisis."* About half of Americans believe that creationism should be taught along with evolution in public schools. Less than 30% of high school biology teachers are actively proevolution; 13% favor creationism. This problem is discussed in detail by Moore (2008). If there is a "crisis" it is in science education, not in the science of evolution. Good science education ensures that students know that some aspects of evolution science (such as the possibility of multilevel selection vs. individual selection) are still being debated and refined. It is far better that students learn this from their biology teachers than from reading creationist literature. Furthermore, students should also appreciate that these debates do not imply that the basic Darwinian principle of "descent with modification" (evolution) is in danger of being discarded ("in crisis"). Rather, these debates have historical and theoretical roots, dependent on the availability of empirical data at various times. They also serve to stimulate further research (heuristic function), and demonstrate that evolution science is still actively developing in the pursuit of new knowledge (epistemological function).

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