

## The Evolution of Group Selection

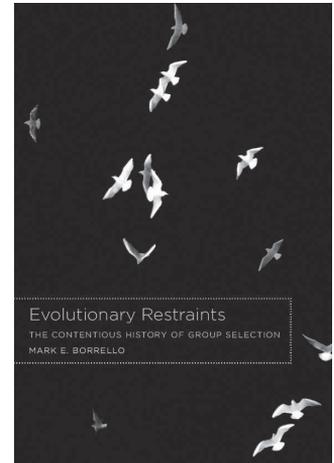
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The last few years has seen a resurgence of interest in group selection, or multilevel selection as it is often referred to now. While relegated to the backwaters of scientific discussion ever since the late 1960s, the idea never disappeared entirely. But in 2007 when Edward O. Wilson, previously a leading advocate for the gene-centered view of life, changed his position and endorsed the view of evolution operating at a higher level of selection, it offered permission for other biologists to take a second look (Wilson, Wilson, 2007). This has led to bitter debates between advocates of inclusive fitness and group selection in the scientific literature (Gardner, Grafen, 2009; Nowak et al., 2010; Okasha, 2010; Abbott, 2011; Boomsma et al., 2011; Strassmann et al., 2011; Ferriere, Michod, 2011; Herre, Weislo, 2011; Nowak et al., 2011). However, the latest analyses suggest that the mathematical models of both approaches are functionally equivalent (Traulsen, 2010; Marshall, 2011).

The publication of Mark Borrello's *Evolutionary Restraints: The Contentious History of Group Selection*<sup>13</sup> couldn't have been better timed to bring context to the history of this dispute. Borrello's highly readable book is primarily a history of the ornithologist Vero Copner Wynne-Edwards and his ill-fated formulation of group selection, a theory that resulted in Wynne-Edwards being discredited within the scientific community following the successful rise of neo-Darwinism in the 1960s. However, the traditional narrative of Wynne-Edwards' rise and fall is not as simple as the winning team has traditionally led us to believe. Borrello's detailed academic history of the dispute reveals that victory wasn't so much earned as asserted. A climate of intimidation followed in its wake, discouraging young researchers from pursuing the question themselves.

Ironically, Charles Darwin first introduced the concept of higher-level selection in *On the Origin of Species* as an explanation for neuter insects among the Hymenoptera. "[I]f such insects had been social and it had been *profitable to the community* that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection." (Darwin, 1859, p. 236). This line of thought was subsequently taken up by Russian naturalists such as Peter Kropotkin and Theodosius Dobzhansky, the latter of whom coined the term "group selection" and stated that animal "interactions obey rules *sui generis*, rules of the physiology of populations, not those of the physiology of individuals" (Dobzhansky, 1937, p. 120). Dobzhansky's influence on population genetics cannot be underestimated, and neither should the influence



<sup>13</sup> Borrello M.E. *Evolutionary Restraints: The Contentious History of Group Selection*. Chicago, London: University of Chicago Press, 2010. 240 p.

he had on Wynne-Edwards who would take up this concept and inspire a controversy that has yet to subside.

While Borrello's goal is clearly to rehabilitate Wynne-Edwards as the leading theorist of group selection, he accomplishes a great deal more. Like another work emphasizing a similar theme, Gregg Mitman's *The State of Nature* about the Chicago School community ecologists during the first half of the 20<sup>th</sup> century, Borrello's focus on group selection offers the opportunity to address larger questions of ideology and professional bias in the development of scientific theory. Borrello presents Wynne-Edwards as a highly stubborn man, single-minded in his devotion to his own theory, and dismissive of criticism from his colleagues. However, many of his critics don't fare much better. Wynne-Edwards' most persistent critic, David Lack, is shown repeatedly to reject the mechanism of group selection for want of evidence only to admit that, "there is equally no proof of my alternative view" (Lack, 1966, p. 275).

However, it was George Williams' *Adaptation and Natural Selection* that inaugurated the modern neo-Darwinist rejection of group selection. Williams set up his book as the culmination of a one hundred year struggle between those who emphasized natural selection as the primary creative force in evolution, opposed by those who minimized its role. He placed Wynne-Edwards in the latter category and insisted that group selection was fundamentally at odds with selection at the level of the gene, a view that Wynne-Edwards did not hold. The key for Williams was a distinction between "biotic adaptations," traits that promote the success of a biota, versus "organic adaptations," traits that promote reproductive success of individual organisms. "Any feature of the system that promotes group survival," Williams wrote, "and cannot be explained as an organic adaptation can be called a biotic adaptation." But he argued that biotic adaptations that promoted species survival were "merely an incidental effect" and "entirely explainable on the basis of adaptation for individual genetic survival."

Given the homage that is regularly paid to Williams for rejecting group selection, it is perhaps surprising that he intended no such thing. In the Preface to the 30<sup>th</sup> Anniversary edition of *Adaptation and Natural Selection* Williams wrote that, in the years after his book's publication in 1966, it "became fashionable to cite my work (sometimes, I suspect, by people who had not read it) as showing that effective selection above the group level can be ruled out".

My recollection, and my current interpretation of the text, especially Chapter 4, indicate that this is a misreading. I concluded merely that group selection was not strong enough to produce what I termed biotic adaptation. <...> Even without its producing biotic adaptation, group selection can still have an important role in the evolution of Earth's biota (Williams, 1966, p. xii).

In fact, both Williams as well as W.D. Hamilton would later accept a role for group selection; a fact rarely alluded to by those who lionize their work as Darwinian "purists" and champions of selection solely at the level of the individual (Williams, 1992, p. 49; Hamilton, 1975, p. 135–136; Hamilton, 1996, p. 173–174).

The "contentious history of group selection" is unlikely to end in the immediate future so long as ambiguity remains over which approach offers better predictions for a given aspect of social behavior. However, in line with Borrello's own conclusion on these debates, philosopher Samir Okasha wrote in *Nature* in 2010 that the argument over group selection had now descended into "tribalism" and, in so doing, biologists "risk causing serious damage to the field of social evolution, and potentially to evolutionary biology in general."

I contend that there is little to argue about. Much of the current antagonism stems from the fact that different researchers are focusing on different aspects of the same phenomenon, and are using different methods. <...> [K]in and multi-level selection are not alternative theories; they simply offer different takes on the question of how social behaviour evolved (Okasha, 2010).

With *Evolutionary Restraints*, Borrello has provided a useful and quite relevant contribution to the history of evolutionary biology, one that has the added benefit of providing context to the ongoing conflict happening before our eyes.

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