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REVIEW

Evolutionary Restraints: The Contentious History of Group Selection

by Mark E Borrello
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reviewed by EG Leigh Jr

Darwin argued that natural selection drives adaptive evolution. Individuals must eat to survive and reproduce. Those best at finding, or at using and digesting, suitable food, generally live longest and produce the most offspring. The environment thus selects successful reproducers, thereby adapting the population to its setting. Population growth creates shortage of resources such as food or nest sites individuals need to survive and multiply. Darwin concluded that such shortages led to "struggle" for needed resources. Life, however, is not all struggle: cooperation is also a necessity of life. How can cooperation arise from struggle? In *Evolutionary Constraints*, Mark Borrello discusses, in historical context, how VC Wynne-Edwards responded to this question, and the consequences of his response.

This book shows that

1. In his *Origin of Species*, Darwin sometimes invoked "community selection" to explain how sterile workers could evolve in colonies or "communities" of social insects. Knowing that most such colonies had a single reproductive, the "queen", Darwin also argued that selection favors queens that achieve the most effective division of reproduction between sterile workers and fertile offspring.

2. In his *Descent of Man and Selection in Relation to Sex*, Darwin proposed that morality evolved when human beings lived in small groups that often fought each other, because the groups whose members cooperated most effectively survived to produce new groups.

3. Because Darwin's *Origin* mentioned community selection so briefly, the Russian geographer Kropotkin, who liked the book, felt that Darwin underrated the importance of cooperation. Kropotkin also saw that, in the far north, ferocious climate and competition with members of other species were important selective factors. Despite diligent search, however, Kropotkin found no evidence of "struggle" among members of the same species.

4. Borrello's primary protagonist, Vero Copner Wynne-Edwards, another naturalist who found no evidence of competition within far northern species, thought that birds of some species produced fewer young than they could. In 1962, he wrote a famous book proposing that selection favored groups whose behavioral interactions limited their reproduction, thereby avoiding overuse of their food supply.

5. Wynne-Edwards's book briefly made group selection enormously popular among biologists. In 1966, however, George Williams annihilated its popularity with a book criticizing the evidence for group selection, arguing that only under very unusual conditions could selection among groups could override equally strong selection within groups. Although Williams's arguments were compelling, he never established what conditions would allow selection among groups to override within-group selection.

Unfortunately, neither Wynne-Edwards nor Borrello tried to learn why others doubted the effectiveness of selection among groups. In 1930, Ronald Fisher, who took the first and greatest step towards the "modern evolutionary synthesis" by reconciling evolution with Mendelian genetics, realized that reproductive competition among each group's members usually overpowers selection among groups. Fisher thought that social insect colonies suppressed such competition by allowing only one reproductive per colony. By 1963, many evolutionary biologists were wondering how group selection could override the within-group advantage of an animal that cheats by outreproducing its responsibly abstemious fellows. Wynne-Edwards and Borrello both ignore this instance of the central problem concerning any form of cooperation: how cheating is prevented.

Ignoring this problem makes it impossible for Borrello to understand the response of David Lack, Wynne-Edwards's first opponent, to the idea that birds lower their reproduction for the good of their group. In 1947, Lack had shown that in the Galápagos Islands, Darwin's finches had diverged adaptively in ways that allowed different species to coexist on the same island. This achievement helped incorporate ecology into the "modern evolutionary synthesis." In 1954, Lack wrote *The Natural Regulation of Animal Numbers*, showing without recourse to group selection how animal populations were limited by competition among individuals. In *Population Studies of Birds* (1966), Lack criticized Wynne-Edwards for thinking that group selection could eliminate unrestrainedly reproductive cheaters. Therefore, even though empirical evidence agreed equally with the presence or absence of group selection, Lack always decided against invoking group selection. Like Wynne-Edwards, Lack realized that hierarchical behavior, "pecking-orders" could limit bird populations. Lack, however, also realized that a bird would benefit by seeking food elsewhere rather than fighting a superior competitor for its food.

In 1983, I showed that group selection overrides equally intense within-group selection if groups exchange less than one successful migrant per two groups per group lifetime and if each group is founded by migrants from a single parent group (Leigh 1983). Despite these stringent conditions, selection among groups played a crucial role in several major evolutionary transitions, such as transforming certain parasitic bacteria into mitochondria. In *The Natural Selection of Populations and Communities* (1980), David Sloan Wilson showed that weak group selection can also exert major impacts on evolution.

Meanwhile, the group selection controversy has largely degenerated into exercises in non-communication. Borrello recounts how Wynne-Edwards's second book, *Evolution through Group Selection* (1986), declined to answer the reasons why his opponents thought that group selection was usually ineffective. In 1970 Richard Lewontin showed—in a classical paper which would normally be treated as appropriately refining Darwin's authoritative precedent in the use of words—that natural selection acts on any population of replicating entities, be they genes, individuals or groups, if entities differ in replication rate, these dif-

ferences are heritable, and replication is imperfect. Nonetheless, Borrello (p 8) notes that the philosopher Michael Ruse (1980) defined natural selection as (only) meaning selection among individuals. Nowadays, some, like West and others (2008) treat group selection as a form of kin selection, the process whereby, for example, sterile workers spread their genes by helping the queen, their mother, reproduce, a mathematical truth that is not always biologically insightful. On the other hand, Borrello himself (p 18), following Michael Wade (1984), treats kin selection as a form of group selection. This is erroneous: the concept of selection always applies to distinct, non-overlapping entities, as Maynard Smith clearly recognized, whereas kin groups overlap. Nowadays, most group selection controversialists agree on the facts, and the mathematics that explain them: the dispute centers on how to name these phenomena.

Those acquainted with the group selection controversy might benefit from this book. I learned much of interest from it about various aspects of the controversy. On the other hand, it makes a poor introduction to the controversy, because it communicates a very inadequate understanding of why opponents of group selection were so sure that it could rarely be effective. Borrello's presentation of Wynne-Edwards as the father of group selection is misguided: even group selectionists agree that Wynne-Edwards's application of the concept was inappropriate. Opponents of group selection might not like the noise, but Charles Darwin fathered that concept, as Borrello documents.

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