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COMMENTARY

EVOLUTIONARY BIOLOGY: STRUGGLING TO ESCAPE EXCLUSIVELY INDIVIDUAL SELECTION

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A commentary on
Levels of Selection in Evolution. *Monographs in Behavior and Ecology.*
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"*Many an ecologist, equipped with no more than a flimsy analogy, marched cheerfully from the familiar Darwinian territory of individual organisms into a world of populations and groups. Populations were treated as individuals that just happened to be a notch or two up in the hierarchy of life*" (Cronin 1991, p 278).

"*The major transitions in evolutionary units are from individual genes to networks of genes, from gene networks to bacterialike cells, from bacterialike cells to eukaryotic cells with organelles, from cells to multicellular organisms, and from solitary organisms to societies*" (Keller 1999, p 60).

The first passage quoted above is a description of the bad old days, before the theory of individual selection (or is it gene selection?) became the reigning paradigm in evolutionary biology. The second passage is from a chapter of a new edited volume, *Levels of Selection in Evolution.* Far from being a bunch of heretics, the contributors include some of the most distinguished names in current evolutionary biology. This volume joins a number of other books (Maynard Smith and Szathmáry 1995; Seeley 1995; Frank 1998; Sober and Wilson 1998; Boehm 1999; Michod 1999) and special issues of journals (*American Naturalist* 1997; *Human Nature* 1999) on evolution as a multilevel process. Clearly, something has happened to make the bad old days look like the wave of the future.

Unfortunately, like a butterfly struggling to emerge from its pupal skin, *Levels of Selection in Evolution* presents an awkward picture of multilevel selection. Some chapters are excellent, but others are highly ambivalent and, in some cases, downright confused about what multilevel selection is and how it relates to its own past. It will be helpful to summarize the theory before evaluating the strengths and weaknesses of this particular volume.

What is Multilevel Selection?

In principle, natural selection can operate simultaneously at more than one level of the biological hierarchy. The classic multilevel se-

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lection problem is the evolution of altruism in groups of socially interacting individuals. Selfish individuals are more fit than altruists within each group (within-group selection), but groups of altruists are more fit than groups of selfish individuals (among-group selection). What evolves in the total population depends on the relative strength of the opposing levels of selection.

The rejection of group selection in the 1960s, and its replacement by the theory of individual selection, was based on the consensus that among-group selection is almost invariably weak compared to within-group selection. Unlike earlier biologists, who often uncritically described social groups, species, and even whole ecosystems as single organisms writ large, the modern biologist must rigorously restrict the concept of adaptation and natural selection to the individual level of the biological hierarchy. That is the message of Cronin's passage, which surely will be familiar to most readers of the *QRB*.

At least two major developments have eroded the skepticism of the 1960s and led to a revival of multilevel selection theory. The first is a reassessment of the models and data that led to the earlier consensus. A lot has happened in 35 years and it is now both theoretically plausible and empirically confirmed that genes can evolve by increasing the fitness of whole groups, despite being selectively neutral or even disadvantageous within groups. As theoretical biologist Joel Peck commented in a recent article on multilevel selection, "[t]here is no doubt that we were way too hasty in trashing group selection . . . [t]he theoretical models of the 60s and 70s were very oversimplified and should be taken with a pinch of salt" (Dicks 2000, p 33). The second development is the discovery of a wider field of application for multilevel selection theory than the original problem of altruism and selfishness in social groups. The origin of life, fundamental genetic and developmental processes, health issues such as cancer and disease virulence, the structure of multispecies communities and ecosystems, and the nature of human social organizations such as religions are but a sample of the subjects that can be understood as multilevel selection processes. The fact that such an incredible variety of subjects can be unified under a single theoretical framework explains the growing interest in multilevel selection despite the earlier skepticism.

One of the most dramatic realizations has been that individual organisms are themselves higher-level units of the biological hierarchy; they are the social groups and multispecies communities of past ages, which have become so integrated that we see the whole more than the parts (Maynard Smith and Szathmáry 1995; Michod 1999). We are one rung in a series of major transitions, each of which represents a triumph of higher-level selection over lower-level selection. Social insect colonies represent another rung in which the colony really can be regarded as an organism writ large, as Wheeler (1928) suggested long ago. Group selection was probably a strong force in human evolution, making the organismic conception of human social groups more appropriate than either biologists or social scientists have imagined over the past five decades (Sober and Wilson 1998; Boehm 1999). For every one of these major transitions in which higher-level selection dominates lower-level selection, there are probably hundreds of other cases in which higher-level selection is a significant, if not the dominating force. The days of thinking that natural selection is restricted to lower levels of the biological hierarchy are gone forever.

STRENGTHS AND WEAKNESSES OF *LEVELS OF SELECTION IN EVOLUTION*

Levels of Selection in Evolution can be commended for representing the full diversity of subjects covered by multilevel selection theory. Two general chapters on multilevel selection (H K Reeve and L Keller; E G Leigh, Jr) are followed by chapters on the origin of life (E Szathmáry), the evolution of individual organisms as higher-level units (R E Michod), sexual conflict in animals (C M Lessells), parent-offspring conflict (H C J Godfray), intragenomic conflict (A Pomiankowski), conflicts within insect societies (L Keller and H K Reeve), nonhuman vertebrate societies (D M Kitchen and C Packer), human societies (J Maynard Smith), multispecies communities with a focus on figs and their associates (E A Herre), and a final chapter on selection at the level of lineages rather than groups (L Nunney). Many of the chapters are excellent, as might be expected from their distinguished authors. I especially appreciated the depth of some of the chapters, which went beyond broad generalizations to include the detail required for serious evaluation. These virtues make the book well worth reading and owning as a reference.

Nevertheless, the book fails to maintain consistency among chapters, and ultimately presents a confusing picture of multilevel selection theory. I will give a single example before analyzing the general problem. Once a trait and the appropriate population structure are identified, it is relatively easy to evaluate the direction of natural selection at each level of the biological hierarchy. Meiotic drive genes are favored by within-individual selection because they are more fit than alternative genes within the same individual. The same gene is often opposed by among-individual selection because individuals with more copies of the gene are less fit than individuals with fewer copies. A gene in a honey bee that increases its foraging efficiency does not increase at the expense of other genes within the same colony, but by causing the colony to survive and reproduce better than other colonies. It evolves by among-colony selection. A gene for female-biased sex ratio is less fit than a gene for an even sex ratio within a single group, but groups with more female-biasing genes will grow faster and contribute more to the total gene pool than groups with fewer female-biasing genes (under certain conditions). Female-biased sex ratios therefore evolve by among-group selection and are opposed by within-group selection. Virulent disease strains are often favored by within-group selection because they outcompete milder strains within single hosts, but opposed by among-group selection because they cause their entire group to go extinct, compared to less virulent groups. Many of the authors of *Levels of Selection in Evolution* employ this simple algorithm correctly, enabling them to speak precisely and unabashedly about higher-level selection. For example, Herre discusses the role of group selection in the evolution of female-biased sex ratios as if it is uncontroversial, as indeed it should be: "the key to understanding how much greater or lesser degrees of female bias are favored lies in understanding how among- and within-group selection are balanced" (p 217).

In contrast, consider the example of brave and cowardly lions as discussed by Kitchen and Packer (pp 190–191). This is not an imaginary example, but the result of painstaking research showing that lions vary in their degree of bravery; brave lions help their pride to survive in competition against other prides, while cowardly lions profit from the bravery of others without sharing the risk. Packer and Heinsohn (1996) summarize the results of their research as follows: "Female lions share a common resource, the territory; but only a proportion of females pay the full costs of territorial defense. If too few females accept the responsibilities of leadership, the territory will be lost. If enough females cooperate to defend the range, their territory is maintained, but their collective effort is vulnerable to abuse by their companions. Leaders do not gain 'additional benefits' from leading, but they do provide an opportunity for laggards to gain a free ride" (p 1216). It would be difficult to imagine a more classic example of altruism and selfishness that the theory of group selection was invented to explain. In fact, it is identical to the example of bravery and cowardice in humans that led Darwin (1871) to propose the first theory of group selection. Yet, Kitchen and Packer do not interpret bravery and cowardice as a balance between levels of selection, similar to female-biased sex ratios and reduced virulence in diseases. They state that "[n]o theoretical model currently exists that can account for such a diversity of individual strategies during intergroup encounters" (p 190). A close reading of their chapter reveals that what they mean by group selection is based on completely different criteria than the simple algorithm of comparing fitness differences within and among groups employed by other authors in the same volume.

The deeper problem, of which the lion example is just a symptom, is revealed on the back cover of the paperback edition: "Ever since the groundbreaking work of George Williams, W. D. Hamilton, and Richard Dawkins, evolutionary biologists have recognized that natural selection generally does not operate for the good of the group, but rather for the good of lower-level units such as the individual, the cell, even the gene." According to this passage, there is still something terribly wrong about the concept of multilevel selection as it was understood in the 1960s. There was no error in the thinking of Williams, Hamilton, and Dawkins. The suggestion is that modern multilevel selection theory is derived, not from the original theory of multilevel selection, but from the theory of individual selection (or is it gene selection?) that replaced it. In short, as extraordinary as it may seem for a book entitled *Levels of Selection in Evolution*, the editor and some of the authors continue to think that natural selection somehow does not operate for the good of the group, even though it does operate for the good of lower-level units. Other authors are more consistently hierarchical, regarding groups as just like lower-level units as a potential unit of selection. A new book on multilevel selection should resolve this kind of confusion, not perpetuate it. For the rest of this review I will attempt to help distinguish the emerging theory of multilevel selection from the residue of its premature rejection that still characterizes some of the chapters.

GETTING HISTORY RIGHT

Nothing is more irritating than having a long conversation with someone, only to discover that the two of you were using the same words in completely different ways. What a colossal waste of time! The same problem exists when the history of a subject is misrepresented, making it critically important to understand what people said and meant when they used a word such as "group selection" in the past. The study of evolution is blessed with an army of historians and scholars who help us remember what was said and meant by our predecessors. Multilevel selection is only beginning to receive this kind of scholarly attention. When it does, the field will realize that it has been under the sway of a myth inhabited by cardboard heroes and villains rather than flesh-and-blood scientists struggling to sort out ideas. The historical sketch provided in Chapter 1 is typical of antigroup selection mythology. A single person—V C Wynne-Edwards—is made the exemplar of something called the "old" group selection, which is said to be decisively refuted by Williams et al., as if in a single stroke. The "new" group selection is completely different and "simply partition[s] ordinary individual fitness into within- and between-group components—often using the clever covariance approach of Price (1972)" (p 6).

This sketch is as distorted as the communist version of Russian history. Group selection theory begins with Darwin and has always focused on relative fitness comparisons within and among groups. The particular population structure that provides the stage for the conflict between levels of selection has always been flexible. For Darwin, the groups were human tribes competing by direct warfare. For Haldane (1932), they were tribes that compete reproductively by fissioning at different rates. For Wright (1945), they were isolated demes connected by a trickle of dispersers. For Williams and Williams (1957), writing five years before Wynne-Edwards (1962), they were sibling groups that last a fraction of a generation. The case of Hamilton and Price is especially instructive and has been recounted by Hamilton himself (1996), by Sober and Wilson (1998), and most recently by Schwartz (2000), who worked with private correspondence in addition to published material. Hamilton originally developed inclusive fitness theory as an alternative to group selection but he was profoundly influenced by Price's covariance equation, which partitions global gene frequency change into within- and among-group components. Both Price and Hamilton interpreted the among-group component of the equation as group selection, as the concept was understood in the 1960s. In Hamilton's (1975) development of the Price equation, he began with Haldane's tribe-splitting scenario but then adopted a transient group model, identical to my trait-group model (Wilson 1975), because it was more mathematically tractable. For Hamilton, this was just a modeling detail. An ounce of scholarship reveals that calling the Price equation "ordinary individual fitness" is a distortion of history. If Price had the independence of thought to accept group selection in the early 1970s, and Hamilton had the integrity to change his mind, why does the rest of the field rewrite history rather than follow suit?

REPLICATORS AND VEHICLES

Selfish gene theory is founded on the concept of genes as replicators, also termed "the fundamental unit of selection." In Chapter 1, Reeve and Keller express impatience with the fact that the replicator concept is so often confused with multilevel selection theory, which concerns the nature of vehicles rather than replicators. They seem befuddled about the source of the confusion and simply declare it ended, as if by decree. To appreciate the extent of the confusion, consider the following two examples. The *New York Times*, whose science reporters are very smart and work hard to get things right, recently described Williams's main contribution to evolutionary biology in this way: "In 1966, he refuted the idea that adaptations arise for the good of the species or group. Rather, he said, adaptations are the result of successful genes spreading themselves through the population" (Goode 2000, p F1). A recent article on Richard Dawkins described his main contribution to evolutionary biology this way: "[*The Selfish Gene*] was designed to banish an infuriatingly widespread popular misconception about evolution. The misconception was that Darwinian selection worked at the level of the group or the species" (Parker 1996, p 42).

Both of these passages commit the fallacy of using the replicator concept to argue against group selection. They also point to the source of the confusion. In *Adaptation and Natural Selection*, Williams (1966) developed the replicator concept alongside his argument that genes are unlikely to evolve by increasing the fitness of whole groups. Both Williams and Dawkins (1976), who expanded upon the replicator concept in *The Selfish Gene*, regarded it as a decisive argument against group selection. Only in retrospect does the argument appear obviously fallacious. I have asked both men why it ever seemed reasonable, since even the most traditional group selection models attempt to show how genes can spread by virtue of their effect on whole groups. Both just shrugged their shoulders and said that the 1960s and 1970s were a long time ago. It therefore remains for historians to reconstruct through careful examination of the literature what the main proponents have already forgotten.

The purpose of identifying the source of the confusion about replicators and vehicles is not to lay blame but to put an end to the confusion. Errors such as this are not ended by decree. When Williams, Hamilton, and Dawkins are described on the back cover of *Levels of Selection in Evolution* as heroes that got everything right in the 1960s, when *Adaptation and Natural Selection* and *The Selfish Gene* are assigned to students as if their contents are as infallible as the Bible, confusion about replicators and vehicles will remain pervasive. Only by turning heroes back into scientists and Bibles back into books that get some things wrong in addition to getting other things right can the field progress as a scientific discipline.

GIVING MULTILEVEL SELECTION THEORY FULL REIGN

Wynne-Edwards and other "naive group selectionists" were guilty of invoking higher-level adaptations uncritically and without sufficient attention to mechanism. Williams and others were right to stress that higher-level adaptations evolve only by a process of higher-level selection and should never be invoked otherwise. Modern multilevel selection theory must abide by this principle, but in every other respect it should be free to explore traits and population structures that are associated with the so-called "old" group selection. For example, groups that last for many generations, such as the isolated demes envisioned by Wright (1945) or the haystacks envisioned by Maynard Smith (1964), might be effective units of selection after all, contrary to the arguments of the 1960s and 1970s. The evolution of reduced virulence in disease organisms provides empirical support for multigenerational groups as effective units of selection. Groups that are initiated by many individuals can be effective units of selection because the partitioning of genetic and phenotypic variation is influenced by more than sampling error (Wilson and Kniffin 1999; Swenson et al. 2000a,b). The ability to move between groups can have positive effects on group selection in addition to negative effects, depending upon the specific assumptions (Wilson and Dugatkin 1997). Despite all the scorn that has been heaped upon Wynne-Edwards (1962), his hypothesis that groups evolve to regulate their population size to avoid overexploiting their resources remains plausible, although not in the grandiose form in which it was proposed. Williams "annihilated" Wynne-Edwards, not with data, but with an imaginary example involving a park full of robins practicing voluntary birth control invaded by a mutant robin that breeds at full capacity. Today this argument appears facile because it ignores the possibility of social control mechanisms that cause groups to behave adaptively without being strongly self-sacrificial within groups. The evolution of reduced virulence in diseases and parasites provides empirical support for Wynne-Edward's thesis. Why should we be shy about saying so and looking for similar examples in nonparasitic organisms? These and other possibilities are still treated as heretical by the authors who cannot reconcile modern multilevel selection theory with its own past, but they emerge naturally when the theory is given full reign, unconstrained by its premature rejection 35 years ago.

WORTH IT FOR THE BUTTERFLY

I have been forced to spend the bulk of this review discussing the flaws of *Levels of Selection in Evolution*, which prevent it from being the state-of-the-art volume on multilevel selection that it aspires to be. Nevertheless, some of the chapters do provide excellent reviews of specific subjects from a multilevel perspective, which make the volume worth reading despite its flaws. I hope that this review will serve as a guide for distinguishing the emerging theory from its fading, but still constraining, past.

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