NEW TITLES

Source: BioScience, 58(1) : 81-82

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2008)58[81:NT]2.0.CO;2

A Philosopher Looks at the Units of Selection

Evolution and the Levels of Selection. Samir Okasha. Oxford University Press, New York, 2006. 288 pp., illus. $55.00 (ISBN 9780199267972 cloth).

Do traits evolve because they are good for the group in which they occur? Darwin thought so, arguing that this was the right way to think about the barbed stinger of the honeybee and human morality. The idea that selection can favor traits that are good for the group as well as traits that are good for the individual was also part of the biologist's toolkit during the modern synthesis. Then, in the 1960s, everything changed. In the space of a few years, George C. Williams published *Adaptation and Natural Selection* and W. D. Hamilton developed his ideas on kin selection and inclusive fitness. A few years later, John Maynard Smith and George Price laid the foundations for evolutionary game theory. The idea of group selection was attacked not just as factually mistaken but as an example of fuzzy thinking. It was also attacked for being unnecessary—kin selection and game theory were said to deal adequately with apparently altruistic traits, and without using the tainted "g-word." This anti–group selection consensus was summarized in Richard Dawkins's popularization, *The Selfish Gene.*

Though many biologists regarded the critique of group selection as a fundamental step forward, there were dissenters. In 1970, Richard Lewontin wrote a review article in which he described the abstract features of the process of evolution by natural selection. If a "collective" contains "particles" that differ in their abilities to survive and reproduce, and if traits of parent particles are correlated with traits of their offspring, the composition of the collective will change. The organisms in a breeding population are one example of particles in a collective. But there are others—the different genes that exist in a single organism and the different groups that exist in an ensemble of populations. From this perspective, group selection is not a confusion. It is part of the Darwinian framework; it is conceptually coherent, though, of course, arguments for its existence and importance must be developed case by case by examining empirical evidence. The idea that selection takes many forms—that intragenomic conflict and group selection need to be considered as well as individual selection—came to form part of what is now called multilevel selection (MLS) theory.

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The other early challenge to the dismissal of group selection came from George Price. One reason that group selection looked like a mushy concept to many biologists was that there wasn't much in the way of mathematical models that could be used to anchor one's thinking. Price changed all that by developing a formalism that partitions the change in frequency that a trait experiences into the change due to individual selection and the change due to group selection. Before Price's innovation, Hamilton wrote that the idea of group selection must be "treated with reserve" because it lacked a mathematical foundation. After Price, Hamilton retracted his earlier rejection of group selection and recognized that his own work on inclusive fitness in fact involved a commitment to group selection.

What has happened since those early days of impassioned rejection and isolated dissent? Different biologists give different answers. Some still think that group-selection theory is the work of the devil. Others are comfortable with MLS theory, thanks in part to David Sloan Wilson's work in the late 1970s in which group selection was represented in terms of his idea of trait groups. (Personal disclosure: I coauthored a book in 1998 with Wilson defending MLS theory.) Current friends of the MLS approach emphasize that mathematical models are needed, and these models need to be tested against competitors. Naïve group selectionism should be avoided, but the same applies to naïve individualism.

Samir Okasha's wonderful new book, *Evolution and the Levels of Selection,* is a philosophical examination of the conceptual framework that MLS theory deploys. Lewontin's early formalism may give the impression that the idea of selection occurring at different levels of organization is straightforward and that the difference between group and individual selection is transparent. The complexities that have become visible since the 1970s show otherwise. One complication arises in connection with the Price equation. Consider this simple example: There are two groups of zebras, one composed entirely of fast zebras, the other entirely of slow ones. Suppose the fast group is less likely to go extinct. According to the Price equation, in this situation there is group selection and no individual selection, because all the variance in fitness is between groups. But surely it is possible that the groups differ in fitness just because there is individual selection for running fast. Selection at the individual level can create a fortuitous benefit for the group (as George Williams put it). The Price equation is unable to recognize this. Biologists have coped with this problem in different ways—for example, by invoking the statistical techniques of

contextual analysis and by employing a methodology called neighborhood analysis. Okasha skillfully analyzes the Price equation's strengths and limitations and these more recent attempts to do better.

Another complication that arose as MLS theory developed was that there really are two types of MLS. In discussions of the evolution of altruism, a group's fitness is usually defined as the number of offspring *organisms* the group produces. But one can also conceive of group fitness in terms of the number of daughter *groups* (regardless of size) the group produces. This second type of MLS has been important in discussions of species selection and of major evolutionary transitions. Both concepts raise questions about what heritability at the group level means, and here again Okasha does much to clarify what is at stake.

Older discussions of group selection have usually presupposed the existence of biological hierarchy instead of explaining it. The standard question was framed as follows: Given that a species is made up of an ensemble of populations, how might traits that are good for the group evolve? But where does group structure—the existence of herds and hives—come from in the first place? The same question, one level down, is important as well. Rather than focusing on the question of how traits evolve that help multicellular organisms to survive and reproduce, given that such organisms already exist, one also might ask how multicellularity evolved in the first place. This is the subject of the major evolutionary transitions, an exciting area in recent evolutionary theorizing. The new question isn't one of understanding evolution *in* a preexisting hierarchy but the evolution *of* the hierarchy itself. Okasha ably discusses how older questions about group selection connect with this newer set of issues.

The units-of-selection problem is part of evolutionary biology, but it has attracted a great deal of discussion within the philosophy of science over the last 30 years. Some philosophers doubt whether the question has a factual answer at all, suggesting that it is a matter of convention whether we choose to view natural selection in terms of group or individual or genic selection. Others have seen MLS theory as a context in which questions about emergence and reductionism matter to the practice of science. And the suggestion has been floated that looking at evolution just from the point of view of genes misses the causes of evolution at higher levels of organization, which has led to reflection on the role of causal thinking in science generally. Okasha makes interesting and novel contributions under these headings. It is gratifying that his book engages the details of mathematical models and at the same time connects those details with broader philosophical questions. Okasha sees both the trees and the forest.

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doi:10.1641/B580113
Include this information when citing this material.

HUMANS, DISASTERS, AND HUMAN DISASTERS

Environmental Disasters, Natural Recovery, and Human Responses. Roger del Moral and Lawrence R. Walker. Cambridge University Press, New York, 2007. 220 pp., illus. $48.00 (ISBN 9780521677660 paper).

Roger del Moral and Lawrence R. Walker, authors of *Environmental Disasters, Natural Recovery, and Human Responses,* say their book demonstrates "the lessons natural systems have to teach us about coping with human-inflicted disasters, including how to most efficiently conduct restoration efforts" (p. ix). And according to the front material, the book will "appeal to ecologists and land managers, as well as anyone curious about the natural world and natural disasters." Nonetheless, the question that I kept asking myself as I read was, "Who is the audience?"

Environmental Disasters is an overview of the effects of disturbance on plant communities. After the introduction and a chapter on the various types of disturbances, del Moral and Walker get to the heart of the book: four chapters on disturbances and their effects that divide the world into a two-by-two matrix of site productivity (infertile versus fertile) and stability (unstable versus stable). The book concludes with a brief chapter on lessons learned from disturbances.

The topic of each of the four main chapters—for example, "Infertile and Unstable Habitats" (chapter 3)—is run through the same mill, consisting of an introduction, a description of the physical setting, a discussion of the topic in the lives of humans, ecological responses, human responses, and interactions with other disturbances. As the headings indicate, humans are a focus of this book.

The writing is sprightly and engaging. Sprinkled throughout the text are side boxes, many of which describe the authors' personal experiences—such as the time that Walker sat through Hurricane Hugo. These lend a welcome personal touch to the book. The numerous photographs, mostly black and white but with a few color plates, serve well to illustrate the topics.

A curious mix of topics are discussed in the four main chapters, with some disturbances defined by type (e.g., fire or hurricane), and others by the type of habitat in which they can occur (e.g., dune or salt marsh). The sections on glaciers, volcanoes, and lava are the most thorough, reflecting the research areas of the authors. Unfortunately, organization on the basis of site characteristics creates the false impression that disturbances are confined to certain habitat types; for example, fire can occur in any

type of habitat, not just in those that are fertile and stable.

It seems that as the authors assembled this book, they were guided by the adage coined by University of California–Berkeley political scientist Raymond Wolfinger: "The plural of anecdote is data." *Environmental Disasters* is composed almost entirely of either very specific anecdotes or broad generalizations—although, to their credit, the authors are also careful to provide the necessary caveats to the generalizations. What is missing are data. The closest the authors come to supplying data is in the section on glaciers, where they include some information on the current effects of global warming on glacial melt. There is not a single graph in the book, and there are only a couple of data tables. It is this lack of data that makes me doubt the claim that this book will appeal to ecologists: to the professional ecologist, the generalizations are very likely already well known, even if the many anecdotes are not.

This book is not a good teaching tool, because it also lacks citations beyond a very short list of readings at the end of each chapter. Although the lack of in-text citations facilitates reading, it is impossible for someone to track down the details behind the anecdotes, to find out the bases for the generalizations, or to discover the people responsible for the ideas and information. A graduate student would be better off with more specialized texts, and an undergraduate would find much of the same knowledge in a good textbook.

Similarly, land managers interested in restoration would be frustrated by this book. One cannot plan a restoration project on the basis of anecdotes and generalizations, and a land manager would need to delve into much more technical books. Would a manager even learn anything new from *Environmental Disasters*? I would hope that any such manager would have at least a master's degree in ecology or in an allied field and would be sufficiently trained to already know the generalizations. If not, we academics have served our students poorly. The final chapter on lessons learned is a nice summary of the current state of the world, but it could stand on its own—the rest of the book isn't necessary.

Finally, for all of these potential audiences—professional ecologists, students, and land managers—one critical element is missing: general theory. Except for a brief description of relay floristics versus initial floristic composition versus the competitive-inhibition model (discussed in the section on glaciers about a third of the way through the book), the text is nearly devoid of ecological theory. Moreover, the few theoretical concepts that are presented are at least 50 years old.

So that leaves the general public as a possible audience. This book might well appeal to the same people willing to sit through Al Gore's *An Inconvienent Truth,* as it uses much the same approach of bringing a human face to nature, and it's filled with plenty of engaging asides. And if they are the audience, what is the message that this book conveys?

I part company with the authors when it comes to tone and substance, especially considering how much the first affects the second. The tone of the introductory chapter is designed to galvanize the masses—a disturbance is described as a "devastation" or a "catastrophe." Although del Moral and Walker admit that "'disaster' and 'catastrophe' are emotionally laden terms" (p. 17), they excuse their use of the terminology when they want "to emphasize impacts...or when we simply want to focus your attention" (p. 18). The very notion of "disaster," however, is human centric, which is demonstrated in this statement: "Ecosystems cannot repair themselves with sufficient speed... to avoid large, negative impacts on humans" (p. 145).

Throughout the book, the authors impose human-defined normative values on natural phenomena, making it seem as though ecosystems and nature are mostly at equilibrium, except when those nasty disturbances wreak havoc. The text claims that disturbances can cause landscapes to "degenerate," that succession is a process by which "ecosystems repair themselves" (p. 9), and that "natural recovery may resurrect an ecosystem" (p. 9). Although all of these statements are ameliorated somewhat by the details and caveats in the rest of the book, the viewpoint is set early on.

Professional ecologists gave up this "balance of nature" approach some 30 years ago, but it still stands as probably the most common ecological misconception held by the general public. If the general public reads this book, that misconception can only be perpetuated. Thus, despite the virtues of this book, I am afraid that it may end up doing as much harm as good.

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doi:10.1641/B580114
Include this information when citing this material.

A FEAST FOR THE INITIATED

Astonishing Army Ants: The Most Important Predators in Neotropical Forests. Carl Rettenmeyer. 2007. 55 min. $20.00. DVD (*www.armyantbiology.com*).

Army ants typically conjure images of stinging hordes of insects swarming through exotic jungles while villagers flee in terror. Although the truth is less likely to make tabloid headlines, the biology of real army ants is at least as fascinating. Knowledge about these insects has been hard won, as the army ant is no biologist's candidate for a model organism. They are nomadic, unpredictable, largely subterranean, and nearly impossible to culture. That we know anything at all about them is due to the efforts of a small cadre of researchers who revel in difficult field conditions and have the patience to follow meandering trails of ants for months at a time.

Chief among these researchers is Carl Rettenmeyer, professor emeritus at the University of Connecticut, who has tracked army ants through Neotropical rainforests since 1952. Rettenmeyer is

known for his pioneering photography of rarely seen aspects of army ants' natural history, his meticulous field observations, and his descriptions of the scores of arthropods that accompany colonies. He was the first to observe, and to photograph, the elusive act of army ant coitus. He was also the first to estimate the longevity of an army ant queen: at least five years, according to a recaptured specimen.

Rettenmeyer has distilled his considerable knowledge into a self-produced film titled *Astonishing Army Ants.* Any nature film written by a leading, practicing scientist is itself an astonishing find, especially given that most documentaries seem to burst forth, facts-be-damned, from the flashy marketing departments of cable television channels. This film's unique providence renders it a must-see for ant enthusiasts, and I was eager to get my hands on a copy.

The good news: I learned a great deal about army ants. The bad news: the process was exhausting. A career's worth of "astonishing ant facts" cascade in tightly compressed waves for nearly an hour, as if racing against the ant swarms themselves. Narrator Mark Roy, who does an otherwise admirable job, is dragged back and forth by a stream-of-consciousness script with too much information and too little structure. As the film accelerates from scene to scene, viewers are sporadically treated to non sequiturs about iguanas, sloths, and peccaries. Some topics appear twice, and others that might have been expected to be in an army ant film appear not at all.

Curiously absent from an educational film about army ants, for example, is a concise definition of the film's subject. Army ants are a single evolutionary lineage with sibling radiations in the old- and new-world tropics, a lineage that combines the traits of nomadism, group foraging, and wingless queens. The more attentive viewers may be able to piece together some of this definition as the film progresses, but such an essential clarification should not be left to the viewer.

The dense script is not without a silver lining. *Astonishing Army Ants* does manage considerable depth and breadth of subject matter. Viewers learn about foraging strategies, prey defenses, colony emigration, the nomadic cycle, sensory organs, mating, worker castes, division of labor, and colony fission. The star of Rettenmeyer's DVD is the spectacular *Eciton burchellii,* the most conspicuous army ant in new-world rainforests, but the film also provides welcome counterpoints to *E. burchellii* by visiting a number of additional species that specialize on different prey using alternate foraging strategies. The film is sprinkled with interesting asides: ants ignore the feet of ant-birds, ants prefer centipedes over millipedes as food, wasps that nest with ferocious *Azteca* ants avoid army-ant predation.

The footage Rettenmeyer has compiled over the past 35 years is uniquely valuable.... [He] has an eye for capturing significant behaviors that would escape less knowledgeable documentarians.

The footage Rettenmeyer has compiled over the past 35 years is uniquely valuable, which for ant aficionados more than justifies the price. Viewers are treated to shots of prey ants and prey wasps absconding in the face of impending swarms and of male ants being carried in emigration columns, in addition to the first-ever live footage of grotesquely swollen queens laying eggs. The quality of the cinematography is modest by current standards—much of it appears to have been captured with handheld video cameras—but the charisma of the ants radiates through. Rettenmeyer has an eye for capturing significant behaviors that would escape less knowledgeable documentarians.

Astonishing Army Ants is most engaging when the myrmecologists them selves make an appearance, humanizing the process of discovery: graduate students are wrapped in protective plastic to keep the ants' stings at bay, field assistants lay down string as they track a colony through the dense undergrowth, and in one scene, Rettenmeyer himself delicately marks *Eciton* queens under a microscope to study their movements. In the film's most memorable moment, a series of furious soldier ants are placed along an unfortunate volunteer's finger, and their fish-hook jaws sink into the skin to demonstrate how indigenous cultures used these ants as living sutures.

However refreshing this documentary may be, Rettenmeyer's project would have benefited from the input of more seasoned filmmakers. The mere presentation of information does not guarantee that a viewer will retain it. A film must also have appropriate pacing and a consistent, logical flow to be an effective educational tool. *Astonishing Army Ants* is more an archive of accumulated knowledge set to video footage than an enlightening tour for the uninitiated. It will appeal to those who are already enamored of ants, but the narrative is too erratic and too dense for general classroom use.

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doi:10.1641/B580115
Include this information when citing this material.

NEW TITLES

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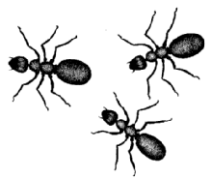

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