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The Superorganism Revisited

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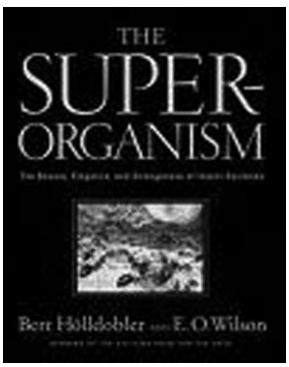
Some ideas in science appear to come and go like fads. Take the superorganism concept. Nearly 100 years ago, the American entomologist William Morton Wheeler first described social insect colonies as "superorganisms" because of the degree to which society members appear to operate as a unit (Wheeler 1911). Then, during the 1970s and 1980s, the superorganism concept largely fell into disrepute following the discovery that the workers in insect societies frequently manipulate reproduction in their own favor, often to the detriment of the colony as a whole (Bourke and Franks 1995). In an article that appeared in *Science* in 1989, Ross Crozier concluded: "Time was that social insect colonies were regarded as 'superorganisms,' analogous to the bodies of single animals in the devotion of their constituent members to the common good. No more. The colony, once seen as an optimized entity, dissolves into a welter of conflicting cooperative and competitive activities" (p. 313).



But now the superorganism is all the rage again, and two new books—one on ants and one on bees—are making a worthwhile attempt to bring the concept back into the working lexicon of the insect sociobiologist.

In the first book, *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies* (2009), the famous duo Bert Hölldobler and Edward O. Wilson reprise and update some of the themes set out in their magnus opus, *The Ants,* which in 1991 won them a Pulitzer prize (Hölldobler and Wilson 1990). Unlike *The Ants,* however, this new book is presented in a format that is friendly to a lay audience yet retains a lot of technical notes and scientific references in footnotes, which will be much valued by specialists. This beautifully produced book was eagerly awaited—in interviews preceding its publication, it was announced that it would "rewrite the subject of insect sociobiology." To add a touch of controversy, Wilson published a series of papers just before *The Superorganism* came out, some of them coauthored with the evolutionist David Sloan Wilson, in which he denounced kin selection and attempted to reinstate group selection as the explanation of insect altruism (Wilson EO 2005, 2008, Wilson EO and Hölldobler 2005, Wilson DS and Wilson EO 2007a, 2007b, 2008). This move baffled evolutionary biologists worldwide, and resulted in a fair amount of criticism by fellow scientists (Foster et al. 2006a, 2006b, Thompson 2006, Helanterä and Bargum 2007, West et al. 2007, 2008, Hughes et al. 2008, Gardner A and Grafen 2009, Wenseleers et al. 2009). At one stage, even Richard Dawkins (2008) felt obliged to reply (reciting his usual points about gene-level selection). And remarkably enough, Bert Hölldobler—Wilson's coauthor and long-time friend—did not agree with some of Wilson's new ideas either, resulting in delays in the completion of their joint new book.

Against this backdrop, I was curious to take a look at the final product. Luckily, and to my own relief, the large bulk of the book covers topics that are unrelated to this recent controversy on kin and group selection, and offers excellent accounts of such themes as division of labor, chemical communication, self-organization, and adaptive nest architecture. Also briefly mentioned is the burgeoning field of sociogenomics—the study of which genes are involved in social behavior—for which insect societies are an excellent model, thanks to the recent publication of the complete honeybee genome sequence. Here, the thesis is put forward that social behavior is nearly always prescribed by genes conserved from solitary ancestors—in other words, there are no true social genes. This conclusion might be premature, because many honeybee genes have as yet no function ascribed to them, and most of those that do have a tentative function were identified by matching them up to equivalent genes in the nonsocial fruit fly. But it will nevertheless be interesting to follow up on the idea.

One of my favorite chapters, "Earth's Ultimate Superorganism," discusses leafcutter ants. In addition to using one of the most complex communication systems known in animals, these ants have the most elaborate caste systems, build air-conditioned nests, and "invented" agriculture long before humans did, by growing a fungus inside their nests for food. Throughout, the book is lavishly illustrated, featuring countless line drawings and color photographs, including some truly stunning ones of the excavation of a mature *Atta* leafcutter ant nest by a team of Brazilian scientists, who poured 6 metric tons of cement and 8000 liters of water into the nest entrance to preserve its structure. Overall, the book is also quite an enjoyable read, although the level of detail might sometimes be a little daunting for nonspecialists.

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Those who expect a state-of-the-art review on insect sociobiology will be slightly disappointed, though. Unlike what is suggested by the subtitle, which refers to "insect societies," the book covers only ants—bees, wasps, and termites are hardly mentioned. This is a great shame because some of the best support for modern sociobiological theory comes from precisely these groups.

In addition, the book falls far short of the mark in its coverage of evolutionary theory and behavioral ecology. First and foremost, the book deals almost exclusively with the cooperative side of insect societies—the expression of reproductive conflict, and how such conflicts can be understood on the basis of kin selection theory, gets short shrift and a brief mention in only one chapter on Ponerine ants. The vast amount of work on sex-ratio conflict (Bourke and Franks 1995) gets one page; conflicts associated with queen-worker caste determination (Ratnieks et al. 2006, Ratnieks and Wenseleers 2008) are not mentioned at all. There is also no discussion on the suppression of within-colony conflicts, even though this is a key requirement for social insect colonies to acquire the properties of unitary superorganisms, in the same way that individuals can be considered units only if conflicts within the genome are effectively suppressed (Ratnieks et al. 2006, Gardner A and Grafen 2009). The fact that workers frequently force each other into sterility by eating or "policing" each other's eggs (Ratnieks and Wenseleers 2008)—a classic example of a conflict-resolution mechanism—is mentioned only in passing in the chapter on communication, where it seems somewhat lost. Also relating to the treatment of evolutionary issues, I felt it was a shame that the chapter on ant phylogeny merely gives a dry account of the relationships among various ant subfamilies. An analysis of some key social traits in a phylogenetic context would undoubtedly have been more useful, and several good, recent studies do exactly this (Fjerdingstad and Crozier 2006, Hughes et al. 2008).

Given the book's title, this emphasis on the cooperative aspects of insect societies may well have been a deliberate choice. It is nevertheless unfortunate that reproductive conflict, which is such a central theme in insect sociobiology, gets so little attention. Most of the work in that area has been done since the publication of *The Ants,* and this new book would have presented a great opportunity to update the story, an opportunity that is, alas, largely missed.

Then, of course, there is also one chapter on the origin of social behavior. Here, some of Wilson's more controversial theories feature once more, although they are toned down compared with some of his recent papers. This probably reflects the moderating influence of Hölldobler, who wrote the bulk of the chapter's main text, although Wilson's more extreme and somewhat peculiar views still come through occasionally in some of the footnotes. Suffice it to say that this attempt at diplomacy results in a rather confusing read, with the authors criticizing kin selection theory in one place, supporting it in others, and at one stage admitting that kin and group selection are the same, while elsewhere maintaining that they are not.

Figure 1. Leafcutter ants: The ultimate superorganism. These* Atta colombica *workers incessantly carry leaves back to the nest to use as a substrate to grow a mutualistic fungus, which they farm as food for both queen and workers. Photographs: Courtesy of Christian R. Linder (top, queen with fungus) and Magnus Manske (bottom, worker ants).

The general claim is that multilevel group selection, whereby more cooperative groups outcompete less cooperative ones, would be a more suitable framework than kin selection for studying the evolution of insect sociality (cf. Wilson DS and Wilson 2007a). Nevertheless, this is clearly an overstatement. Although it is true that both kin selection and multilevel selection are mathematically valid approaches for the study of social evolution (Bourke and Franks 1995, Wenseleers et al. 2009), nearly all of the major insights on the evolution of cooperation and conflict in insect societies over the last 50 years have been gained from kin selection theory (Bourke and Franks 1995, Ratnieks et al. 2006). And at a theoretical level,

multilevel group selection is still plagued by various fundamental problems, including the inability to deal with anything but the simplest situations in which all socially interacting individuals in the population are equivalent and belong to a single sex (which may apply to microorganisms, but clearly not to insect societies) (West et al. 2008, Wenseleers et al. 2009). I feel it is highly ironic that Wilson, the prophet of sociobiology, now seems to want to let go of kin selection, one of the core theories of modern social evolution theory. But then again, as Dawkins (2008) remarked, Wilson's fascination with group selection is not new: In his otherwise great book *Sociobiology,* Wilson mistakenly discussed kin selection as a special case of group selection!

But let praise be given where it is due. For the topics that the book does cover, the technical reviews are comprehensive and up to date, and they will have lasting value. Moreover, it is timely and appropriate that the authors bring back the superorganism to the conceptual toolbox of insect sociobiology. The many fantastic photographs and illustrations alone make the book worth buying. For those interested in the more evolutionary side of insect sociality, though, I would recommend Andrew Bourke and Nigel Franks's excellent book *Social Evolution in Ants,* which, despite being more than 10 years old, is still surprisingly up to date (Bourke and Franks 1995).

For those who feel that honeybees are sorely overlooked in all this, there is Jürgen Tautz's new book, *The Buzz about Bees: Biology of a Superorganism* (2008), a translation of the original German edition, *Phänomen Honigbiene.* In contrast to *The Superorganism,* this book is aimed squarely at the general reader, and so falls in a different category altogether. Only a half dozen references are included at the back of the book, and the rest of the text is written in plain, accessible language. In addition, *The Buzz about Bees* is illustrated with countless, fantastic color photographs by Helga R. Heilmann, which beautifully capture all aspects of the life of the honeybee. Tautz has won several prizes for making research accessible to the public, and in this book he again succeeds very well. Like *The Superorganism, The Buzz about Bees* focuses mainly on the superorganismal aspects of the honeybee colony, discussing such topics as how bees obtain and communicate information about flowers, how they construct comb, how they keep the hive warm, and how colonies reproduce. Studies that have been done in these areas are for the most part accurately portrayed. One minor exception is that following Karl von Frisch's original theory, the round dance and the waggle dance are discussed as two distinct dances aimed at communicating the presence of food close to or far from the hive. More recent work, however, has shown that these dances are just the same, with both giving directional and distance information about the location of flower patches, but with the round dance having a very short waggle run (Gardner KE et al. 2008). Nevertheless, this study had probably not been released during the time *The Buzz about Bees* was written, so Tautz cannot be faulted for not mentioning it. Presumably for the same reason, the recent worldwide decline in honeybee

populations as a result of colony collapse disorder also is not mentioned (Oldroyd 2007).

One chapter discusses the unusual genetic relationships in honeybee colonies and how this leads to intracolonial conflicts over reproduction. Here I felt that Tautz, as a neurobiologist, could not do this topic full justice. There are basic mistakes in some of the relatedness coefficients given, and subtitles such as "Cooperation is always a good thing" seem to miss the point of decades of research that revealed just how hard it is for groups to evolve and stably maintain cooperation. In addition, the chapter gives undue credit to the idea that worker bees eat each others' eggs in order to remove inviable eggs, a theory that in fact has been convincingly disproven (Beekman and Oldroyd 2005).

But these are relatively minor quibbles. On the whole, *The Buzz about Bees* and its many stunning photographs will surely reward lay readers, apiarists, and professional scientists alike, even if for research purposes one might still prefer to go back to some of the more scholarly standard works (Winston 1987, Seeley 1995).

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