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# BOOK REVIEW

# Endless forms most strange: a review of *The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies*, by Bert Hölldobler and Edward O. Wilson

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**The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies**, Bert Hölldobler and Edward O. Wilson with line drawings by Margaret C. Nelson, 2009, W. W. Norton & Company, New York. 544 pp. Hardcover, $55.00 ISBN-13 978-0393067040.

In *The origin of species* Darwin (1859) devoted much effort to the many arguments and observations that seemed to weaken, or contradict, the notion that evolution by means of natural selection could explain why organisms are the way they are. Chief among the difficult phenomena was altruistic behavior, especially in its most extreme form of eusociality in the social insects, where most individuals within the group give up the opportunity to reproduce and instead develop into sterile, highly modified worker castes that assist the reproduction of one or a few individuals. Darwin wrote (p. 201):

> If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.

Although he recognized the challenges posed by altruism in general and the eusocial Hymenoptera in particular, he also already had a possible explanation at hand. Darwin argued (p. 237–238):

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family as well as the individual, and may thus gain the desired end. [. . .] Thus I believe it has been with social insects: a slight modification of structure or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification. And I believe that this process has been repeated, until that prodigious amount of difference between the fertile and sterile female of the same species has been produced, which we see in many social insects.

In other words, kinship may permit the evolution of sterile helper castes, which even though they do not reproduce themselves, nevertheless are favored by selection because their action strongly benefits the reproductive efforts of close relatives. Fast forward 200 years. Social insects and eusociality have emerged, as so many phenomena, not as challenges to Darwinian evolution, but as opportunities to further refine it, and ultimately as testament to the general validity and applicability of its basic framework. Many milestones got us to this point but two are particularly relevant for this review. In 1964, William D. Hamilton published his genetic theory of social evolution, formalizing the role of relatedness in evolution in what since has become known as Hamilton's rule: the idea that altruistic behavior by a donor will be favored by selection if its benefits to the recipient exceed its costs to the donor, weighted by the degree of relatedness between donor and recipient. Hamilton (1964) himself referred to this as "inclusive fitness theory," though it is often known by the term "kin selection" coined later by Maynard-Smith (Bourke and Franks 1995).

In the same papers, Hamilton suggested that haplodiploid sex determination in the Hymenoptera creates a particular opportunity for the evolution of altruistic extremes: because sisters inherit the exact same set of chromosomes from their

haploid father, in addition to one of the two chromosome sets from their diploid mothers, they end up sharing 75% of their genetic identity, rather than just 50% as in the more common diplodiploid form of heredity. Haplodiploidy may thus predispose lineages toward the evolution of societies consisting mainly of altruistic sisters. This *haplodiploidy* hypothesis, as it has become known, has played an important role in the debate about the origin of eusociality in insect societies ever since, and the hypothesis and its application and interpretation are in many ways the foci of the introductory chapters of Hölldobler and Wilson's new book, *The superorganism: the beauty, elegance, and strangeness of insect societies*. In many ways this book is an offshoot of the authors' pioneering book *The Ants* (1990), which probably more than any other publication cemented the field of myrmecology as a discipline. But it is also more than that.

First there is the notion of the *superorganism*, a term originally coined by an earlier pioneer of the field, William Morton Wheeler (1928), which describes the emergence of complex colony-level behavior through the coordinated action and cooperation of individuals to the benefit of the colony. Think of hive and mound building by bees, wasps, and termites, think of the coordinated raids of army ants, or the cooperative weaving-together of leaf nests by *Oecophylla* ants. The superorganism concept raises the question as to the nature of the forces that mediated the evolution of such breathtaking behaviors. Departing from previous perspectives, Hölldobler and Wilson use their new book as a platform to argue against the explanatory power of kin selection and in favor of group selection arguments and the notion that relatedness is not necessary for, and can not explain, the evolution of cooperation and altruism in insect societies. They do so, for instance, by highlighting well-known limits of the haplodiploidy hypothesis (e.g., queens often mate multiply thus decreasing relatedness among sisters, or termites are all highly eusocial but none are haplodiploid). But kin selection theory and the haplodiploid hypothesis are not the same. Instead, the latter is a special case of the former, and even though the special circumstances envisions by the haplodiploidy hypothesis may only apply in rare circumstances this does not diminish the importance of kinship in the origin of eusocial superorganisms. Or does it?

Hölldobler and Wilson use their book to extend arguments brought forward in earlier publications (Wilson 2005; Wilson and Hölldobler 2005) where they argue that selection on the level of the group, or colony, rather than kin selection, drove the evolution of altruism in insect societies. But in an excellent review of the subject, Foster et al. (2006) highlight that this is only possible if one relaxes the definition of altruism. True altruism, which by definition is individually costly, requires relatedness to overcome the discrepancy between fitness costs and benefits accrued in the interaction of nonrelated partners. Moreover, Foster et al. (2006) argue convincingly that the group selection scenarios envisioned by Hölldobler and Wilson are kin selection arguments in disguise and reveal themselves as such when one expands relatedness to include not just immediate kin but conditions in which genes are simply correlated across individuals.

Even though this first part of the book is therefore not necessarily a representative, commonly accepted view of the evolutionary biology of altruism and eusociality, it introduces much of the terminology and background information necessary to enter the main bulk of the book, which is devoted to the biology of social insects in general, and the biology of two subfamilies in particular, the ponerine and leafcutter ants. It is the authors' fascination with the exuberance and splendor of social insects that is fully apparent here and that no doubt contributed to the subtitle of the book, *The beauty, elegance, and strangeness of insect societies*. Chapters 3–6 introduce the reader to the organization and dynamics of colonies, division of labor and the biology of castes and caste formation, and communication. These are easy to read chapters, which reiterate but also update corresponding chapters in *The Ants* (1990). Chapter 4 expands previous horizons and introduces the field of sociogenomics and the use of modern molecular genetic and genomic approaches to the study of social insect biology. This is a field experiencing dramatic growth and progress, and reader gets at least a glimpse of its powers and promise.

But the crown jewels are the later chapters of the book, which detail the biology of ponerine (Chapter 8) and leafcutter ants (Chapter 9), ending with a spectacular chapter on nest architecture. Again, chapters reiterate much of what was already presented in *The Ants*, but also add and synthesize much new information. All are richly and beautifully illustrated. Many images are familiar to the avid ant literature reader, but there are also many new ones. Standing out are the absolutely exquisite photographs of nest architecture in Chapters 9 and 10.

*The Superorganism* is thus yet another beautiful book that weaves together ecological and behavioral richness and complexity informed by much natural history in a complex and thought-provoking evolutionary framework. It is by no means the final word on social insect evolution, instead it is a status report as seen through the eyes of the two leading pioneers of the field. But most of all, *The Superorganism* illustrates how the biology of social insects, rather than challenging the foundations of evolutionary biology, extends their reach and solidifies their grasp. No doubt, Charles Darwin would have been pleased.

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