

EVOLUTION

All for One and One for All

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Few scientists win a Pulitzer Prize. In 1991, Bert Hölldobler and Edward O. Wilson did for their magisterial *The Ants (I)*. Now these distinguished collaborators offer *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. In this ambitious book, they seemingly have three goals. Hölldobler and Wilson reprise and update themes from *The Ants* while broadening their survey to include other social insects (most notably honeybees). In a thread woven throughout the narrative, they argue that colonies of social insects should be seen and studied as superorganisms, a naturally selected level of organization a step above individual organisms. And they present the work in a format apparently intended to attract the broadest possible readership of both specialists and nonspecialists. This suggests the authors' probable primary motivation—they are advocating a conceptual framework for understanding insect sociality that has been out of favor for four decades.

Hölldobler and Wilson begin by updating the superorganism concept. They hold that “[t]he principal target of natural selection in the social evolution of insects is the colony, while the unit of selection is the gene.” They then treat this claim in detail through a historical and theoretical dissection of gene-centered, altruistic worker-centered, and colony-centered perspectives along with the controversies, sometimes heated, that have accompanied them. They seek synthesis under the umbrella of multilevel selection, which Wilson and David Sloan Wilson have recently advocated in general and specialist articles (2, 3). Ensuing chapters address the “sociogenesis” of colonies and two main organizing principles for social insect colonies, division of labor and communication. Several chapters on ants, the forte of both authors, round out the book. Each chapter after the introduction is a stand-alone review of its topic, rich in content and sometimes daunting in detail. The chapter on ponerine ants, in

particular, exemplifies the quantity, quality, and diversity of research on ants during the past two decades.

Numerous color photographs and original drawings illustrate interesting behaviors and traits, making the book enjoyable to page through and inviting to general readers. Literature citations appear as footnotes, which may be reader-friendly but results in the repetition of individual references (sometimes even more than once on a page). A glossary covers much, but not all, of the technical jargon. Even so, one wonders whether many general readers will make it through the long chapter on communication, much less through the book as a whole.

Ultimately, the book will be judged by its success in advancing the perspective that natural selection acts on social insects more strongly at the colony level than at the levels of individual organisms or genes. Most readers will be convinced of the clarity that the superorganism concept brings to an understanding of honeybees and behaviorally advanced ants. Some readers will remain skeptical, however, that the superorganism concept sheds much light on the origin, rather than elaboration, of sociality.

An intriguing aspect of the book is hinted at in the introduction, made apparent in the discussion of genetic social evolution, and finally explicitly acknowledged in the penultimate chapter: the co-authors disagree on which social insect colonies should be called superorganisms. Wilson favors broad application of the concept, beginning with the origin of sociality, whereas Hölldobler holds an individual-centered view of the origin of sociality and reserves the superorganism concept for species that have passed the “point of no return” marked by obligately sterile workers (4). Perhaps this disagreement would have been resolved if the authors had given greater



Without blueprint or supervision. Social insects, such as these Brazilian wasps (*Polybia emaciata*), construct complex nests by following behavior algorithms that reflect natural selection at the colony level.

attention to social insects such as termites, sweat bees, and wasps—all of which offer more promising pathways to enlighten the origins of social behavior than do ants or honeybees. Indeed, in several of the few places where research on wasps is sketchily described, that research is mischaracterized or incorrectly cited. Thus, the book is not a comprehensive review of social insects, and it falls short of being a gateway to understanding the origins of insect sociality.

But, let praise be given where it is due. For the focal topics, and especially when ants are featured, the technical reviews are comprehensive and up to date and will be of lasting value. Moreover, it is timely and appropriate that the authors have undertaken to restore the superorganism to

the conceptual framework and working lexicon for envisioning and discussing insect sociality. The book doesn't hard-sell the superorganism concept; there is no ringing conclusion at its end, for example. Instead, each case study or discussion topic concludes with a soft-sell assertion that the preceding passage clearly shows natural selection to be acting more strongly at the colony level than on individuals. The detailed contents will entice researchers to repeatedly return to the book. On every visit, they will re-encounter the superorganism message and, in doing so, grow accustomed to and comfortable with it. Our future discourses on insect sociality will thus be improved. *Superorganism* offers a clear and compelling picture showing that, in already-social insects, natural selection acts more strongly on colonies than on individuals to shape the genotypes and phenotypes of a colony's members—thereby giving rise to the sophisticated nest architectures, amazing (and amazingly complex) behaviors, and substantial ecological impacts that are the hallmarks of social insects.

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The Superorganism

The Beauty, Elegance, and Strangeness of Insect Societies

by Bert Hölldobler and Edward O. Wilson

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