

# Biological Complexity and Integrative Pluralism

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## Constitutive Complexity

The complexities of organization or structure have implications for the scientific theories and models that we devise to represent them. Which arrangements of parts are stable through time? Which are capable of evolving over time? And which will be selected for in light of their consequences on the fitness of the parts and the wholes made up of those parts? One of the lessons of the history of life on this planet is that complexity, at least if defined as the number of cell types in an organism (Bonner 1988, 1998), has increased. Multicellular organisms evolved from single-celled organisms, more differentiated organisms evolved from those with fewer specialized cell types. Some changes of this type take place in the span of a life-cycle, for example, in the slime mold *Dictyostelium discoideum*, which begins as a collection of single amoeba and develops into a multicellular, differentiated individual with stalk and fruiting bodies.

A parallel might be drawn to the development of social groups, as in social insects. Here individual ants, bees, and wasps join together to form a colony where different individuals perform different functions, such as food acquisition and reproduction.

In this chapter I argue that the parallel between the evolution and development of multicellular organisms and that of social organization of insect colonies can be misleading if the diversity found in both types of organization is overlooked.<sup>1</sup>

<sup>1</sup> This chapter is the product of merging two previously published papers: S. D. Mitchell, "The Superorganism Metaphor: Then and Now," in S. Maasen, E. Mendelsohn, and P. Weingart, eds., *Biology as Society, Society as Biology: Metaphors. Yearbook in the Sociology of Science* (Dordrecht: Kluwer Academic Publishers, 1995), 231–248, and S. D. Mitchell and Robert E. Page, Jr., "Idiosyncratic Paradigms and the Revival of the Superorganism," report NR. 26/92 of the Research Group on Biological Foundations of Human Culture, Bielefeld, Germany, 1992.

## 2.1. COMPOSITIONAL COMPLEXITY AND THE SUPERORGANISM METAPHOR

Our choice of models, and to some extent our choice of words to describe them, is important because it affects how we think about the world. . . . [O]ur choice of model decides what phenomena we regard as readily explicable, and which need further investigation. (Maynard Smith 1987: 120)

### *Introduction*

The complex behavior of termite, wasp, ant, and bee societies, with their division of labor and coordinated activity, has long been a subject of wonder and awe. Yet the cooperation among individual workers and their functional sterility, combined with helping the queen to produce offspring, were seen even by Darwin (1859) as problematic for a theory built around the competitive struggle for existence between individual organisms. Darwin resolved the problem, to his own satisfaction at least, by invoking a higher level of selection, that of the colony. Recently, there has been an attempt to revive colony-level selection as a special form of group selection, by reviving an old metaphor, that of the superorganism (Wheeler 1911), and to sophisticate it as a “theory of superorganisms” for social insects (Lumsden 1982; Seeley 1989; Wilson 1985b; Wilson and Sober 1989). The original application of a superorganism theory to explain social insects was posed as an addition to Darwin’s theory in which “. . . the struggle for existence is not more than half the truth. . . . To us it is clear that an equally pervasive and fundamental innate peculiarity of organisms is their tendency to cooperation or ‘mutual aid’” (Wheeler 1923: 3). In this essay I examine the renewed advocacy for the superorganism theory and argue against its revival. Unlike the original model of Wheeler and E. O. Wilson’s extension of that model, the theory as reformulated by D. S. Wilson and Sober (1989) and applied by Seeley (1989) rests on what we believe is an idiosyncratic paradigm that does not adequately represent existing entities. We argue that it is deficient in two ways. First, the commitment to a particular form of functional organization (ideal Weismannism) obscures the variety of ways in which social insect societies are in fact organized. Second, the selectionist criteria for identifying functional organization at the colony level obscure the role of other potential sources of organization.

There are two contemporary approaches to the superorganism theory. While both approaches coopt the name “superorganism,” they make use of conflicting accounts of the defining characteristics of a superorganism. The conflation of these accounts as a result of the common terminology tends

to obscure very important differences. We argue that while there are merits in each, it is a mistake to reintroduce the superorganism concept to legitimate hierarchical selection theory or to emphasize the role developmental processes play in generating the observed features of social insects. Both the original and revived superorganism theories invoke a narrow definition of an organism that is based on the Weismannian organizational paradigm of complete separation of germ plasm and somatic cells. This Weismannian ideal has been challenged as unsuitable for describing individual organisms in most taxa (Buss 1987), and we suggest that its superorganismic counterpart is equally deficient in describing most social insects. We believe that a more general theory in terms of complex systems allows both goals to be met without invoking a concept that carries its own history, inappropriate to the task at hand, and that lends itself to misuse. Of course, whether one uses the term “superorganism” or not is not at issue. One can clearly retain the term, but only by decoupling it from its historical usage and its Weismannian connotation, that is, by redefining it. However, we believe that the development of a general biological model in terms of hierarchical complex systems is more promising, since such modeling allows easier connection to even more general theoretical frameworks of complexity and order that are finding application in physics and chemistry as well as biology (Kauffman 1984; Nicolis and Prigogine 1989). If we construct biological theory on the basis of anthropocentric prejudices using idiosyncratic paradigms, we may preclude investigation and explanation of features shared by all complex systems, biological or otherwise.

### *The Superorganism*

Superorganism metaphors and theories take the individual organism as a model of functional integration or cooperation of parts and extend that model to describe and explore social groups of individuals. So, just as individual cells in the body cooperate in the development, maintenance, and reproduction of the organism, so, too, it is suggested by the metaphor, do individuals cooperate in the development, maintenance, and reproduction of a colony or a society. Clearly, an organism such as a human being, with 46 chromosomes, approximately 210 different cell types, and more than 30,000 genes, strikes some resemblance to a social organization, like a honeybee colony with its four worker castes and tens of thousands of individual workers engaged in a variety of coordinated tasks. The ways in which complex biological organizations are structured is the proximate result of developmental processes and the historical result of evolution. Recently, there has been renewed interest in

drawing the analogy between organisms and social groups by appeal to the superorganism metaphor. In what follows we critically assess the benefits as well as the costs of employing this choice of words in describing social insect societies.

Metaphorical transfers between organisms, social insects, and human societies has had a long history. Yet each historical and scientific context has stamped its own character on the use of such language. In particular, we discuss the recent arguments for the "revival" of the superorganism metaphor for the study of social insects. After decades when mention of superorganism was anathema in social insect studies (see Wilson 1968, 1971), in the 1980s there were multiple pleas to "revive" the superorganism. These include E. O. Wilson (1985a, 1985b), who claimed that although no one used superorganism language through the reductionistic and empirical trends in entomology from the '50s until the '80s, even then it had a significant, albeit "semi-conscious," role. In addition, articles supporting the revival include Charles Lumsden (1982), Thomas Seeley (1989), and David Sloan Wilson and Elliott Sober (1989).

The new interest in using the superorganism metaphor raises a number of questions. How does this choice of models and choice of words affect the way one studies social insects? In effect, what does a superorganismic revival for theories of social insects amount to? The answer to this analytic question is further complicated by two factors: One is that the words chosen are explicitly metaphorical and hence require the explication of the transfer of conceptual content between the primary and secondary contexts of application. One might call this the horizontal dimension of transfer. The second factor is that the plea is to revive a framework that had originally been voiced in a very different historical and scientific context. To see what the theoretical and empirical content of the so-called revived superorganism model is now, one must also investigate the vertical transfer of content from the antecedent application of the metaphor to its contemporary instantiation. The story of the revival of the superorganism metaphor thus concerns the transfer of language and content both from one scientific context (theories of the organism) to a second scientific context (theories of social groups) and from one historical period (early twentieth century) to another (late twentieth century).

#### *Critical Theory of Metaphors*

Earlier in the twentieth century, philosophers of science had tended to view metaphors and models as merely heuristic, nonessential, and hence dispensable for science. While perhaps relevant to the context of discovery, like

hallucinations and other bogeymen of the peculiarly human psyche, it was thought that metaphorical language did nothing for explanation, justification, or the rational development of scientific theories. According to Bono, the "standard" view, developed in the scientific revolution in the seventeenth century, is that metaphors "introduce inappropriate, not literal meanings into science, contaminating . . . precise and stable meanings." That metaphorical language "compromises scientific inquiry and is to be avoided" (Bono 1990: 62). But this picture of science is being replaced by one in which metaphors are seen as ubiquitous, important, and powerful in scientific practice and hence demand critical analysis. "We need a critical theory of metaphor in science in order to expose the metaphors by which we learn to view the world scientifically, not because these metaphors are necessarily 'wrong'; but because they are so powerful" (Stepan 1986: 277). Philosophers have been engaged in the development of such a critical theory. The literature on this subject is vast, but we describe one trend within it that motivates the discussion of the organism metaphor that follows.

Metaphors were once understood to make explicit, definite claims of similarity or analogy between the primary reference or context and the secondary one. On this, the "comparison" view, communication with metaphorical language was possible only when all parties agreed with the specific similarity claims. With an admission of the less than precise and explicit nature of meaning necessary for communication, even for scientific discourse, this picture of metaphors has been replaced. Now, many philosophers defend a view of metaphor as more "open-ended" and "interactive" (Black 1979; Boyd 1979; Kuhn 1979).

Even with the loosening up of the criteria for metaphorical understanding, there are differences within this modern camp. Black, for example, claims that metaphors are useful only in pretheoretical stages of science, in pedagogical interactions, or in nontechnical popularizations. Boyd and Kuhn, however, find a place for metaphors in the construction and development of theory in mature science. Boyd refers to these as "theory constitutive" metaphors. Rather than require explicit similarity before a metaphor can be properly applied, Boyd claims that inductive open-endedness actually invites scientists to explore possible similarities. Metaphors are attempts to accommodate our language to not yet discovered causal features of the world. Kuhn, though differing from Boyd on the realistic or constructivist interpretation of such endeavors, agrees with this basic approach. Both endorse the view that, in Kuhn's words, "metaphor plays an essential role in establishing links between scientific language and the world . . ." (1979: 415-16). It follows that metaphors should not be left unjustified or "semi-conscious."

Rather, they, like any other theoretical postulate, should be accepted critically. Boyd says:

One should employ a metaphor in science only when there is good evidence that an important similarity or analogy exists between its primary and secondary subjects. One should seek to discover more about the relevant similarities or analogies, always considering the possibility that there are no important similarities or analogies, or alternatively, that there are quite distinct similarities for which distinct terminology should be introduced. One should try to discover what the “essential” features of the similarities or analogies are, and one should try to assimilate one’s account of them to other theoretical work in the same subject area – that is, one should *attempt* to explicate the metaphor. (1979: 406)

In addition to the horizontal comparisons between the two domains of application of a metaphor, a critical analysis of a specific metaphor requires the comprehension of the sources and implications of the use of the metaphor both within and outside the confines of scientific discourse. Metaphors, it is clear, are both enabling and constraining. While they structure our perceptions, allowing us to “see” causal structures in new domains, via the similarity to such structures in known domains, they at the same time proscribe certain observations, blind us to certain descriptions and awareness. While they serve as a program for research, they also run the danger of being confused for reality. And finally, while performing all these onerous tasks in scientific theorizing and practice, metaphors at the same time reflect the social structure, scientific organization, and cultural milieu in which they are invoked (see Mitman 1995). A critical analysis, ideally, should expose all of these aspects of a scientific metaphor. In this study, we undertake only part of this larger task.

In general, scientific theories make two sorts of ontological commitments in explaining phenomenological experience: one concerning which entities exist, and the other concerning which forces act upon those entities. The revival of the superorganism metaphor attempts to expand the ontology of Darwinian theory to include superorganisms as real, explanatory entities. We believe there are two different sources for the appeal to the reality of this ontological level, each resting on a different set of biological processes (see Table 2.1). E. O. Wilson (1971, 1985a, 1985b) and Lumsden (1982) describe superorganisms as entities subject to sociogenesis, the analog of morphogenesis, while Seeley (1989) and Wilson and Sober (1989) invoke superorganisms as entities subject to the forces of natural selection operating at a group level. Individual organisms are paradigmatic examples of both development and selection. They display ontogenetic processes of meiosis, mitosis, and cell differentiation and specialization – and hence a collection

Table 2.1. *Horizontal Transfer*

	Organism	Superorganism
<b>Entities</b>	Cells Organism	Individuals Superorganisms
<b>Organization</b>	Weismann’s preformationist development	Complete convergence of individual interests
<b>Processes</b>	Ontogenesis Selection on individual only	Sociogenesis Selection on colony only

of individuals may be seen as a superorganism if it is subject to a similar ontogeny. As E. O. Wilson (1985a: 1492) says, “[t]he workers of advanced insect societies are not unlike cells that emigrate to new positions, transform into new types, and aggregate to form tissues and organs.”

Individual organisms are also the paradigmatic subject of natural selection and the locus of adaptations – hence a collection of individuals may be seen as a superorganism if it is similarly subject to natural selection and its traits are adaptations at that level. Seeley thus claims,

It seems correct to classify a group of organisms as a superorganism when the organisms form a cooperative unit to propagate their genes, just as we classify a group of cells as an organism when the cells form a cooperative unit to propagate their genes. (Seeley 1989: 548)

While the first approach emphasizes the developmental processes affecting the organism, the latter is concerned exclusively with how natural selection operates on organism-like entities. In this chapter, we consider both of these types of superorganism metaphor and argue that in each case, adopting this framework does more to obscure the biological phenomenon than to illuminate it. Before exploring these horizontal transfers, we first consider the progenitor metaphor developed by William Morton Wheeler in the early part of this century.

*Vertical Transfer.* The historical dimension of the investigation of the superorganism metaphor is required by the explicit desire on the part of contemporary scientists to “revive” the superorganism of W. M. Wheeler of the 1910s and 1920s rather than to introduce a newly coined, or newly framed, metaphor born of the contemporary scene. We suggest that there are significant differences between these periods that, we believe, are sufficient to cast doubt on the desirability of reviving the metaphor.

One way to compare the two scientific contexts is to see what elements make up the respective contrast classes for the superorganism defenders in each. By so doing, we do not intend to thereby promote the drawing of

sharp dichotomies between naturalist and experimentalist, physiological and evolutionary questions (see Allen 1978) or vitalism and Darwinism (see Ghiselin 1974), but rather to also make apparent the range of views that allow for a middle ground. American biologists in particular tended to explicitly endorse the dissolution of dichotomies and the expansion of possibilities. For example, Charles Otis Whitman, a teacher and colleague of Wheeler's, asserted that the tendency to dichotomize into mechanism versus vitalism is destructive and confuses the important questions (1895; see Maienschein 1981).

When W. M. Wheeler invoked the organism as an appropriate metaphor for the study of social insects in 1911, what views was it designed to replace, and what choices were implicit for the 1911 reader that would situate Wheeler's theory? Similarly, when Wilson and Sober or Seeley defend, with some qualifications, the superorganism revival, what are the current distinct alternatives among which we are to prefer this approach? The metaphor appears to espouse the same transfer of structures from the primary domain of application of cellular organization of the body to the secondary domain of division of labor and specialization in the functional organization of societies. However, though the metaphorical word used may be the same, each may well be invoking a completely different meaning.

Let's look briefly at Wheeler (see Evans and Evans 1970). Wheeler began work in biology as a taxonomist and developmental biologist, publishing his first papers cataloging flora and fauna in his native Milwaukee in the late 1880s. He took his doctoral degree at Clark University in 1892, writing a thesis on insect embryology. He immediately took a position in the new University of Chicago, both under the influence of C. O. Whitman. He spent the next academic year in Europe, where he divided his time evenly between Theodor Boveri's lab in Wurtzburg and the zoological station in Naples. Wheeler was also a "regular" at the Woods Hole Marine Biology Laboratory in its earliest days. In 1899 Wheeler took a job and moved to University of Texas at Austin where he was to fall in love with the study of social insects, and with ants in particular. In Texas, Wheeler found himself virtually surrounded by numerous unidentified species of ant. He was to devote most of the rest of his career – academic positions at the American Museum of Natural History and a long-term association with Harvard University – to the investigation of social insects. Indeed, his observations are still now cited as primary resources, while his theoretical and conceptual frameworks have been less long-lived.

Wheeler's superorganism theory was proposed to explain what was characteristic of social insects. Wheeler saw this conceptual schema as a corrective

to Darwinism because "... the struggle for existence is not more than half the truth. . . . To us it is clear that an equally pervasive and fundamental innate peculiarity of organisms is their tendency to cooperation or 'mutual aid'" (1923: 3).

The appeal to "mutual aid" is of course to Kropotkin. It is worth investigating why it was that the mutual aid or cooperation metaphors employed by Kropotkin would have found resonating voice in the United States in the 1920s, in lieu of Darwin's "struggle for existence" metaphor. Daniel Todes suggests that Darwin's "struggle for existence" competitive individualist metaphor reflects the "unsurprising fact that he [Darwin] shared the ideological outlook of his class, his circle and family and that such language might identify the author as bourgeois Malthusian, or perhaps, typically British" (1989: 13). Todes goes on to argue that Russia, the context giving rise to Kropotkin's "mutual aid" metaphor, was a land suffering not from population pressure, but rather from the harsh elements against which people had to work collectively to survive. Perhaps the United States of the late nineteenth and early twentieth century, and especially the Texas landscape where Wheeler developed his devotion to the study of social insects, was more geographically and demographically like Kropotkin's Siberia than Darwin's London. However, ecological determinism is a strong thesis, and there is little evidence to suggest it played a major role for Wheeler's superorganic metaphor.

Wheeler defined the concept of an organism, which would form the backbone of his theory of superorganisms, to include three features: organization for nutrition, reproduction, and protection.

An organism is a complete, definitely coordinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other similar systems, known as offspring, and to protecting the system itself and usually also its offspring from disturbances emanating from the environment. The three fundamental activities enumerated in this definition, namely nutrition, reproduction, and protection, seem to have their inception in what we know, from exclusively subjective experience, as feelings of hunger, affection, and fear, respectively. (1911: 5)

Wheeler argued that an animal colony is properly identified as an organism and is not merely an analog of one because it displays the following three features: (1) individuality: it behaves as a unitary whole, has identity in space, resists both dissolution and fusion with other substances; (2) duality of composition: it displays the Weismannian division of germ plasm and soma; and (3) ontogenetic and phylogenetic development.

Wheeler's superorganism model provided him with a framework to describe and explain the observed cooperation of individual insects. One can begin to define the boundaries of Wheeler's superorganism metaphor by describing what it was meant to exclude. First, he seems to be rejecting a narrow reading of Darwin. It was narrow by emphasizing competition and struggle and ignoring cooperation and mutualism. Darwinian competition was between individuals, and most severe between individuals of the same species. In this sense Wheeler can be viewed as anti-individualistic when competition excludes cooperation. Of course, Darwin also was prompted by the phenomena of sterile insects to entertain ideas of individual sacrifice to group benefit. "If such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection" (1859: 236). Appeal to cooperation, at least in the case of social insects, was not an instance of anti-Darwinism, but rather opposed only to a narrow reading of Darwin.

This characterization of Wheeler is further supported by his defense of Darwinism in arguments with Father Erich Wasmann, a Jesuit living in Holland. Wasmann studied insect parasitism and guest species, one of Wheeler's favorite subjects, and was an outspoken anti-Darwinist who thought natural selection was inadequate for explaining the relationships he observed. His solution was to propose new instincts and new forces in its stead. Wheeler did not reject a role for natural selection; rather, he wished to expand Darwinism to include nonindividualistic perspectives as well.

Wheeler has been accused of another brand of anti-Darwinism, namely, of being a "crypto-vitalist" (Ghiselin 1974). He merits this label by his academic association with both the University of Chicago and Harvard University, which, according to Ghiselin, housed biologists, philosophers, and social theorists "who often explicitly denied that they were vitalists, but whose positions amounted to much the same thing" (1974: 30). This accusation is the result, we believe, of Ghiselin's strict dichotomization of views of the period. It seems that for him any view that is not individualistic, mechanistic, and neo-Darwinian in the sense of the impending synthesis falls into the category of vitalism. But this is unfair to Wheeler. Although he was attracted initially to Bergson, he later departed from vitalistic views, remarking that "the resort to such metaphysical agencies (as *elan vital* and others) has been shown to be worse than useless in our dealings with the inorganic world and it is difficult to see how they can be of any greater service in understanding the organic" (1926, quoted in Evans and Evans 1970: 224). In 1928 he referred to *elan vital* and *entelechy* as "little more than fetishes" (quoted in *ibid.*). Perhaps his

most colorful rejection of vitalism appeared in 1911 in reference to Driesch's *entelechy*:

His angel child . . . comes, to be sure, of most distinguished antecedents, having been mothered by the Platonic idea, fathered by the Kantian *Ding-an-sich*, suckled at the breast of the scholastic *forma substantialis* . . . but nevertheless, I believe that we ought not to let it play about in our laboratories, not because it would occupy any space or interfere with our apparatus, but because it might distract us from the serious work in hand. I am quite willing to see it spanked and sent back to the metaphysical household. (quoted in *ibid.*: 255)

Though eschewing association with the vitalists, Wheeler also rejected the genetic reductionism born of the synthesis of Weismann, Mendel, and population genetics that makes external selection the only relevant cause for explaining biological diversity, adaptation, and evolution. Internal organization and development were left out of the synthesis, and Wheeler's early work on embryology may have predisposed him to reject a Darwinism that ignored development. Writing in reference to the "exquisitely adapted" specializations in termites and ants, he says:

And it strains our credulity to be told that such forms arise either from peculiar genes popping out of nowhere into the germ plasm or develop gradually under the guidance of natural selection from forms which, so far as I can see, must have an equal or even greater survival value. When we encounter such impasses as the foregoing, instead of embracing the Aristotelian *Entelecheia* . . . or joining the apostles of the survival of the fittest and forever croaking "natural selection!", it is surely more commendable to sit down in the laboratory or in the field and say nothing but "*ignoramus*" till we have made a much more exhaustive behavioristic and physiological investigation of the phenomena. (1928; quoted in *ibid.*: 261-262)

Nevertheless, Wheeler did not reject Darwinism entirely. He supported a broader interpretation of Darwinian theory, one that could redress the lacunae of developmental, internal processes made invisible by the genetics of his time.

In summary, Wheeler invoked the organism metaphor for social insects in the form of his superorganism theory against a strictly external selectionist interpretation of Darwin. This put him in the company of many Darwinian critics of the time, those concerned with internal processes, such as embryogenesis and other developmental considerations, who found that individual competition in response to external environmental conditions was insufficient to ground the kind of phenomena they were describing. Wheeler was, after all, a taxonomist constantly reminded of the variations distinguishing the

thousands of species of ants, bees, wasps, and termites and an embryologist who saw complexity developing in the lifetime of the organism. While competition between genetic individuals may not have been sufficient, neither did it require embracing a vital force, such as Dreisch's entelechy, Maeterlinck's spirit of the hive, or Bergson's *elan vital*, an agency existing separately from matter that directs, selects, or arranges the structure of matter that constitutes "life." Wheeler seems to have occupied a position that corresponds to what Tim Lenoir (1989) has described as "vital materialism," or a midpoint in Jane Maienschein's suggested continuum between mechanistic materialism and vitalism (1981). Wheeler vehemently opposed vitalism, while at the same time rejecting the complete reduction of biology to a form of physics.

#### *The "Revived" Superorganism*

Wilson and Sober (1989) use the superorganism concept to promote a hierarchical theory of selection. Their interpretation of Darwinian natural selection logically entails the rejection of privileging the individual organism as the only level at which selection can operate. Again, one can locate their position in contrast to a narrow interpretation of Darwinism, the latter being what S. J. Gould has called the hardening of the synthesis (Gould 1983). For them, higher levels of organization – such as groups, species, or superorganisms – are reasonable candidates for selection. Furthermore, Wilson and Sober argue that not only is it theoretically possible to have such levels of selection, but in fact the conditions for their realization are not overly restrictive (contra the early objections to group selection; cf. Wade 1978) and, in fact, they do exist in nature. However, it is ironic that the strategy they use to reject the hegemony of a single individual level of selection has features that are similarly restrictive. Just as the individual organism prejudice tends to privilege a single level as the only one relevant for selection, blinding biologists to the other levels, Wilson and Sober's superorganism theory privileges a particular form of functional organization at the group level, blinding one to diversity in this realm. The individual single-level theory they reject by invoking the superorganism metaphor is merely replaced by a group single-level theory, thereby obscuring the multiple levels at which selection can and does operate in social insect societies.

For Wilson and Sober, a superorganism is "a collection of single creatures that together possess the functional organization implicit in the formal definition of organism" (1989: 339). They adopt the Random House dictionary definition of an organism to be "a form of life composed of mutually dependent

parts that maintain various vital processes" (Wilson and Sober 1989: 339). While this formal definition is consistent with Wheeler's articulation of three essential activities of nutrition, reproduction, and protection – that is, the various vital processes – Wilson and Sober's use of functional organization is further restricted to organization around reproduction. They summarize their superorganism model as follows:

- (i) A population is subdivided into a number of groups. . . .
- (ii) Groups vary in properties that affect the number of dispersing progeny (group fitness).
- (iii) Variation in group fitness is caused by underlying genetic variation that is heritable. . . .
- (iv) No differences exist in the fitness of individuals within groups. (1989: 339)

Wilson and Sober (1989: 340, 343) claim that functional organization is the key to identifying at which level natural selection is operating. Functional organization is that which allows individual organisms or superorganisms to successfully survive and reproduce. When the four conditions are met, they claim that natural selection will endow groups with the same properties of functional organization that we normally associate with individual organisms (1989: 342). Their argument is as follows. Since natural selection can act both within and between groups of individuals, be they organisms or superorganisms, there are three possibilities. First, within-group selection overwhelms between-group selection, and the result is a collection of individuals. Second, between-group selection overwhelms within-group selection, and the result is an organism in the formal sense. Third, when neither level wins, the result is part collection and part (super)organism.

Implicit in their development of a superorganism is a particular form of functional organization of the parts of the paradigmatic individual organisms, namely, a Weismannian preformationist developmental schema. On this view there is a sharp division of germ plasma from soma, and the germ line is sequestered so early in development that there is no opportunity for competition between somatic cells to have evolutionary consequences. The Weismannian legacy makes variation during the development or experience of the parts (soma or workers) irrelevant to evolution because it entails the complete, early separation of germ cells from somatic cells. Weismann's theory, requiring the rejection of Lamarckianism, was a cornerstone of the modern synthesis.

However, Buss (1987: 20) has convincingly argued that this very ideal image of the functional organization of cells in an organism fails to be

approximated by most taxa or throughout most of geological time. Buss's list of all the taxa displays how rarely the Weismannian ideal is met in the primary domain of the biology of individual organisms. So, too, is the idealized Weismannian superorganism rarely approximated by the range of organization found in social insects.

### *The Variety of Functional Organization in Social Insects*

There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy. (Shakespeare, *Hamlet*, first quarto, lines 607–608)

The Wilson-Sober model of superorganisms requires that there be no differential "fitness" between units at levels lower than the colony or between levels (their condition iv). Differential fitness is differential survival and reproduction for them, the conditions required for there to be evolutionary consequences of selection at a given level. However, competition at levels lower than the colony can occur among individual colony-mates, among males, or even among genes, for example, with meiotic drive or segregation distortion genes. Competition can even occur between workers and queens over determining the colony sex ratio. Any of these would make the colony something less than a superorganism. The superorganism ideal may be achieved by either eliminating all genetic variation among the subcolony units, and thereby removing a necessary condition for selection to operate at that level, or by suppressing all competition among genetically variant subcolony units at all levels by means of mechanisms, such as meiosis, for making such variation effect no change in the distribution of traits in offspring.

Rather than produce a complete table of social insects, listing those that do and those that do not qualify under the stringent condition of no variation in fitness at below colony levels, we instead point to some of the sources of within-colony competition that result in most, if not all, social insects failing the criterion.

Haplodiploidy leads automatically to differential fitness among male members of societies. Males arise from unfertilized eggs laid by diploid females, queens, and workers. Recombination in females leads to a vast array of potential genomes embodied in egg gametes. If left unfertilized, the egg undergoes development and maturation and produces a haploid male individual. Each male then replicates the genome that originated it thousands or millions of times (there is no recombination) and changes the sex of the cell embodying the genome from female (egg) to male (spermatozoon). These identical male gametes are packaged within haploid individual organisms (males) that then

compete for resources within the nest, such as food and care from workers, and for mates outside the nest. Their competitive abilities are at least to some extent dependent on the gamete that produced them and, therefore, represent a form of gametic/individual selection unique to haplodiploid organisms. (This is different from what we normally think of as sperm competition because the competitive abilities of spermatozoa are probably mostly determined by the genotype of the male that produced them.) Elimination of competition at this level would require that the reproductive success of males be independent of their genotype, an unlikely condition.

Termites, on the other hand, are diploid and monogamous and do not have these particular difficulties. However, termite societies often have supplementary reproductives and not a single king and queen, probably resulting in within-colony variability in reproductive success during at least some stages of colony development (Wilson 1971; see discussion of polygyny below).

Polyandry is characteristic of many species of ants, wasps, and bees in which the queen of a colony mates with multiple males. This reproductive strategy can give rise to many different sources of within-colony competition. First, males must surely compete for matings with the queen on her nuptial flight, as they compete for resources within the colony during their early development and outside it while they prepare for reproduction. The queen mates during a few days of her life, then forms a colony and dispenses the stored sperm over her lifetime, which for honeybees can be several years. Thus, competition between males may reflect fitness differences for the ability to mate at all, for quantity of sperm deposited, for longevity of sperm for use during the queen's lifetime, and for the ability of sperm to fertilize queen eggs rather than worker eggs. There is evidence that sperm use by the queen is not random. Given that males differ genetically, such fitness differences, which obtain below the level of the colony, are likely to have evolutionary consequences.

In addition, given that multiple males father the "body" of female workers, different subfamilies are formed in a colony. (All workers share the same mother, but some will share the same father and differ from others in that respect.) In the social Hymenoptera, females develop into queens or workers on the basis of what they are fed. If workers that feed larvae can recognize those that are more closely related to them, that is, members of their own subfamily, then competition may arise among individuals of different subfamilies over which larvae are raised as queens versus workers. Competition can be eliminated if workers are unable to distinguish among potential queen larvae. Empirical work with honeybees has demonstrated that workers have the ability to discriminate among larvae under some experimental conditions

(Noonan 1986; Page and Erickson 1984; Page et al. 1989a; Visscher 1986; cf. Oldroyd et al. 1990 and Page and Robinson 1990).

To eliminate competition due to polyandry at these levels, the following unlikely conditions must be met:

1. Mates of queens contribute equal numbers of sperm;
2. Sperm will have equal viability and longevity;
3. Sperm are used randomly to fertilize eggs; and
4. Workers are unable to discriminate among larvae with different subfamily relationships.

These are very unlikely conditions.

In addition, polygyny, or multiple queens, is widespread in the termites, wasps, and ants (Wilson 1971) but is rare in bees (Michener 1975). Some ant colonies have literally thousands of functional queens. Here competition within the colony can arise through differential egg laying by the different queens. Also, like polyandry, it could result in competition among workers in the different subfamilies generated by the multiple queens. Competition among queens can be eliminated only by a lack of heritable variation in the production of reproductive offspring by the queens. This seems also to be an unlikely condition to be met.

Genotypic variability among individual organisms and, therefore, variability in reproductive success within insect societies may arise through polyandry, polygyny, and recombination. Larvae with different genotypes, for any of the above reasons, may compete to become reproductives. Larval competition may explain why it takes 21 days for a worker honeybee to develop from egg to adult, while it takes a queen only 16 days, even though she is twice the size of a worker. Or why the fate of a larva, with regard to its development into a queen or worker, is not determined until more than halfway through larval development, the only phase of development where immature stages feed and can be fated to become a queen.

Several virgin honeybee queens are simultaneously reared by colonies and fight to inherit the maternal nest after the queen mother leaves with an entourage of workers. The first queens to mature, that is, that have the shortest development time, have an advantage over those that are still developing because they sting and kill immature queens before they complete their development into adults.

Sometimes a colony loses its queen to disease, old age, or accident and raises a replacement by selecting a few young worker larvae from among thousands to raise as queens. Only those immatures that are not already fated developmentally to become workers can become queens. Those that become

queens obviously have greater reproductive success than those that become workers, although one might argue that if as workers they raise only sisters related by three-quarters, then they have greater reproductive success than producing sons and daughters related by half. Even so, queens live a lot longer and produce far more reproductive offspring than workers care for in their short lives, so the reproductive success of being a queen, rather than a worker, may be quantitatively greater.

Egg-laying workers are common in societies of ants, wasps, and bees (Bourke 1988). They often occur simultaneously with one or more functional queens and even more often in colonies that are queenless. Studies of honeybees have shown unequal, but significant, reproductive success of laying workers in queen-right and queenless colonies (Page and Erickson 1988; Robinson et al. 1990; Visscher 1989; see below for more details). Some species of ants belonging to the genera *Monomorium*, *Pheidole*, *Pheidologeton*, and *Solenopsis* completely lack ovaries and therefore are exempt from any possible individual reproduction (Hölldobler and Wilson 1990). However, at least some member species of these genera are polygamous and/or polyandrous (Page 1986; Ross 1989).

Social insect colonies will fail to be superorganisms by failing to meet condition iv, the complete suppression of competition at levels internal to the organism, the extension of the Weismannian ideal model to social groups. There are good reasons to believe that there is reproductive competition among colony units at lower organizational levels. The most likely candidates to qualify as a Wilson and Sober superorganism would have a single queen that mates with a single male and workers that lack functional ovaries. Admittedly, some ant species fit this ideal; however, they represent only a small fraction of the different kinds of colony organization displayed by social insects. Insect societies are rich in diversity with respect to how they are functionally organized for reproduction, just as Buss has shown that individual organisms are similarly diverse in their internal functional organization. The social insect colonies, even when different in their reproductive organization, may be similar with respect to organization around defense or nutrition, two aspects of a superorganism that Wheeler emphasized and Wilson and Sober ignore. That these strong conditions are intended by Wilson and Sober is shown by their claims that "social insect colonies really do cease to be superorganisms, to the extent that natural selection operates within single colonies" (346), and "The essential criterion is absence of within-group selection, which may be accomplished either by creating genetically uniform groups, or by suppressing the differential reproduction of genetically diverse groups" (348).

Wilson and Sober promote the revival of the superorganism, but it is not Wheeler's metaphor that they invoke. The major differences are:

1. Wilson and Sober limit functional organization to organization around reproduction, ignoring the nutritional and protective organization that Wheeler included; and
2. While Wheeler found selective scenarios insufficient to explain super-organismic phenomena, Wilson and Sober make selection at the group level the defining characteristic.

The scientific context for Wilson and Sober, the contrast class in which to situate their superorganism, is the individualistic theories that "have dominated evolutionary biology for the last twenty years" (353). The superorganism is supposed to provide a "radical departure" from this narrow interpretation of Darwinism by acknowledging multiple levels of selection. They promote a hierarchical picture of natural selection, one not restricted to a single level, yet one logically consistent with the teachings of Darwin. In these regards, Wheeler and Wilson and Sober are similarly fighting their respective hegemonic, narrow interpretation of Darwinism, offering radical departures that nevertheless do not step outside the bounds of what is "truly" Darwinian. Wilson and Sober's superorganism, however, depends on the Weismannian ideal organism and not the contemporary picture of a plurality of organismic organization. The horizontal transfer of content with respect to the organization of the whole from its parts seems to be in their case oblique. The Weismannian organism when elevated to the Wilson and Sober superorganism contravenes their very goal of supporting a broad and hierarchical Darwinian theory. The Wilson and Sober superorganism makes invisible the diverse array of truly hierarchical organization found in social insects on which hierarchical selection can operate. Their agenda is to rid biology of the myopic picture of selection operating only at the individual organism level. Their explicit reasons for reviving the superorganism model concern the inconsistency of adopting a theoretical framework that focuses only at the individual level. And while in fact they admit within-organism selection (in the primary context of the metaphor) as well as within-colony selection (in the secondary context of the metaphor), their overly restrictive model of the superorganism obscures these admitted facts.

By exploring the transfer of content and contexts of the original superorganism metaphor for social insects developed by William Morton Wheeler and comparing it with the "revived" superorganism of Wilson and Sober, the complex ways in which metaphors acquire their meanings begin to be clarified. The appeal to ancestral authorities to inspire allegiance to a theoretical

construct may have rhetorical success, but only by virtue of ignoring the differences that made appeal to the metaphor salient in its own historical and scientific milieu. The Wilson and Sober superorganism's credentials as a "revived" form of Wheeler's original metaphor can be judged only by such a comparison. And as argued above, their model and that of Wheeler are substantially different.

Whether the superorganism metaphor and model proposed by Wilson and Sober should be accepted, regardless of its pedigree, depends on the content and promise of such a conceptual framework. The model's content is understood by means of the horizontal transfer of structure from the primary context of application, the organism, to its new domain, social insects. On that score we have argued that, ironically, the model obscures our vision of just the sort of variability Wilson and Sober wish to highlight, and it does this by transferring the Weismannian ideal structure of the organism to define the structure of the superorganism.

Wilson and Sober give us an idiosyncratic view of insect societies that may make invisible the diverse array of truly hierarchical organization on which hierarchical selection can operate. They are rightly concerned to rid biology of single-level theories in order to acknowledge multiple levels of selection and emphasize the fact that population structure matters to evolutionary processes, that is, that forming groups can affect the selection process and its consequences. Hence, a perspective that sees only a population of individuals will not be able to take such levels into account. We believe that a better route to encouraging this revision of evolutionary theory is in terms of a complex systems model that admits all the variations of functional organization. This would be more successful in addressing multiple levels of selection than the rigid, idiosyncratic superorganism model.

#### *Insect Colonies as Dynamical Complex Systems*

Even if we granted for the moment that social insects approximate the ideal, stringent criteria of the Wilson-Sober model of superorganisms, the dynamically changing status of such an organism is not represented in their theory. Not only are candidates for superorganisms extremely rare, but the superorganism status of a colony is not stable and may change dramatically with colony development. For instance, colonies of most monogynous species of social Hymenoptera change their reproductive structure when they lose their queen (see Bourke 1988). Workers undergo individual development where their ovaries become mature and they begin laying unfertilized eggs (or fertilized, if the workers are capable of mating). This can be demonstrated in the

honeybee, where there can be at least three identifiable colonies, depending on the reproductive status of workers.

*State 1: Queenright Colonies.* Queenright colonies have a functional queen. Nearly all reproductive individuals are progeny of the queen. This is the case emphasized by Seeley (1989) in his description of honeybee societies as superorganisms.

In at least some colonies, workers lay some unfertilized eggs that develop into males (Page and Erickson 1988; Visscher 1989). Page and Erickson (1988) reported one colony where all males produced were probably progeny of laying workers. Ratnieks and Visscher (1989) suggest that conflict occurs among workers within colonies, resulting in the cannibalism of most worker-laid eggs.

*State 2: Temporarily Queenless Colonies.* The first functional response to the removal of queens is the desuppression of queen rearing. Workers construct queen cells and raise a new replacement queen. If the colony successfully raises a queen and the queen successfully mates, then the colony returns to state 1. If the new queen fails to mate successfully, but survives, the colony returns to a degenerative state 1 colony where only drones are produced but they are the sons of the virgin queen. If the queen fails to survive or no queens are successfully raised, then the colony goes to state 3.

*State 3: Permanently Queenless Colonies.* Suppression of worker ovary development and egg laying is usually lifted after the loss of the queen, and all of the immature workers complete development and become adults (see Robinson et al. 1990 for review). After workers begin the transition from state 2 to state 3, they can be attracted to one of two alternative states:

*State 3a:* Here, one or more workers produce queen pheromone and suppress egg laying of other workers (see Robinson et al. 1990). These "false queens" then become the principal germ line for the workers. Colonies in this state appear to produce far fewer reproductives than the alternative state 3b.

There is an alternative trajectory for state 3a. Some races of bees produce females parthenogenetically at high frequency (all do it at some very low frequency). Those capable of high-frequency female production manage to maintain the integrity of the state 3a condition for several weeks or months and then raise a new reproductive queen and return to state 1 (Anderson 1963).

*State 3b:* This state is characterized by a progressive increase in egg laying by workers and appears to have some special functional properties, including: egg laying preferentially in drone-sized cells (this is important because drone larvae reared in worker brood cells develop into much smaller, and presumably less reproductively competitive, drones than those raised in special, larger-sized drone brood cells), egg and larval cannibalism, and a synchronous

onset of oviposition by laying workers (Page and Erickson 1988; Robinson et al. 1990). Egg-eating and egg-laying behavior are distributed nonrandomly among workers belonging to different subfamilies within colonies. The net result of differential egg laying and egg and larval cannibalism is differential reproductive success among colony members.

To summarize our argument so far, we have presented evidence for why the Weismannian superorganism model proposed by D. S. Wilson and Sober fails to describe most social insects. In addition, we have suggested that even if we relax their constraints on the defining functional organization of superorganisms so that existing social insect societies would more closely approximate it, the pure superorganism state remains an unstable one during the lifetime of the colony. We now argue that in addition to the organizational and dynamical variability that is hidden by a superorganism theory, there is the possibility of spontaneous origins of order at the colony level. That is, the Wilson-Sober model lends itself to a type of selectionism, albeit at the group level, which ignores the possibility of nonselectionist developmental explanations of colony organization.<sup>2</sup>

#### *Functional or Apparently Functional?*

A snapshot look at a complex system shows what appears to be the intricate, coordinated behavior of parts of the system in a seemingly goal-directed manner. Such coordination in living systems has led some to postulate an *elan vital* or *entelechy* as an invisible hand directing the coordination of the parts. For social insects, a spirit of the hive (Maeterlinck 1912) was postulated, which, like the soul of the body, was held responsible for an order that could not be the result of mere mechanical means.

These vitalistic interpretations long have been rejected by the biological community and replaced by mechanistic forces operating on living organisms. Natural selection, operating on heritable variation among individuals, can put into place features that seem consciously designed to solve the problems of existence that any organism faces: nutrition, reproduction, and protection. The primary role of natural selection as the only source of order or organization has been successfully challenged (Gould and Lewontin 1979; Kauffman 1984; Page and Mitchell 1991). Wilson and Sober's (1989) model of a superorganism theory and Seeley's (1989) use of it suffers from the same selectionist

<sup>2</sup> E. O. Wilson's superorganism theory does not suffer from the same sorts of restrictions. The major target of his theory is to account for colony development, that is, to provide a theory of sociogenesis.

bias that has characterized single-level organism theories of selection in the past. That is, they take the observation of apparent functional organization to be evidence of a history of group-level selection. This bias is the result of their account of functional organization.

Functional ascription has played two roles in biological explanation. One has been as a purely descriptive account of the interrelatedness of parts of a system and their contribution to the system's capabilities (Boorse 1976; Cummins 1975; see Sec. 4.3 below). The other identifies functions with adaptations (Millikan 1984; Wright 1976). On the second view, identifying a feature as functional entails the claim that the feature had been selected in the past for its contribution to the system's survival and reproduction and has evolved as a result of that selection (Mitchell 1989). It is unclear which of these interpretations should be attributed to D. S. Wilson and Sober. On the one hand, they attempt to revive Wheeler's superorganism theory, which was clearly based on functional organization of the first type. Indeed, they say that functional organization is that which allows individuals to successfully survive and reproduce (1989: 340), a claim about the proximate contribution of parts to contemporary goals. Yet they also say that functional organization is the accumulation of properties that enhance relative survival and reproduction of individuals (343), a claim about evolutionary history. This blurring of the use of the concept of functional organization allows them to make the transition from an observation of the contemporary functional organization of a superorganism that appears to contribute to survival and reproduction to the conclusion that such functional organization must be the result of natural selection in the past. Their argument then uses the restrictive Weismannian ideal form of reproductive organization to further conclude that the selection must have been at the group level.

Antiadaptationist arguments have pointed to two ways in which evolutionary histories may diverge from the paradigmatic case of direct selection of a trait for its consequences on fitness. On the one hand, selection may be indirect, that is, operating on one trait and at the same time giving rise to evolutionary change of another trait by means of the developmental relationships between two traits. On the other hand, the evolutionary change in a trait may be the result not of selection, direct or indirect, but rather the spontaneous emergence of order.

#### *Direct versus Indirect Selection*

Evolutionary histories of given traits may not include direct selection or may be a mixture of episodes of selection operating at more than one level. The

Wilson-Sober superorganism model's identification of functional organization with group-level selection fails when the organized results are really emergent properties that result from individual level selection. West-Eberhard (1981) argues that many of the features of insect societies that appear cooperative in nature, and hence likely to arise through higher levels of selection, are easily explained as historical contingencies resulting from competition among alternative reproductive strategies of individuals. She argues that queen-worker division of reproductive labor and even worker age-polyethism, two of the presumably primary functional components of eusocial insect societies, may in fact have evolved through these competitive interactions. Thus, the group selectionist perspective may fail to see the truly hierarchical structure of selection operating.<sup>3</sup>

#### *Selection versus Spontaneous Order*

The Wilson-Sober assumption that all apparent functional organization is the result of a selection history can also be challenged. The three fundamental properties of insect societies that are regarded as the reason for their great ecological success – division of labor, mass action responses, and social homeostasis (Wilson 1985b) – may, in fact, be self-organized properties of groups and not the result of selection at any level. With simple computer simulation models, Page and Mitchell (1991, 1998) demonstrated that an ensemble of “computerized bees” exhibit a division of labor similar to that observed for social insects with only two requirements: First, they are tolerant and interact within a common environment, and second, the individual group members have different thresholds of response to sets of stimuli that elicit task-performing behavior. Individuals can have different response thresholds because of differences in individual experiences and learning; because they have different genotypes that set, or limit, thresholds of response; or because they are in different states of behavioral development. Age and experiential changes in behavior are characteristics that are not unique to social insects. In these cases, a selectionist perspective veils the intriguing potential for insect societies to display the spontaneous order that has been proposed for other biological systems (Kauffman 1984).

<sup>3</sup> This question about the actual level of selection (individual or group) is not equivalent to the debate concerning the unit of selection (replicator or interactor). The issue at hand concerns which causal interaction processes were involved in the evolution of a given trait, not whether any such interaction can be represented in genic terms. Wilson and Sober are well aware of this important distinction, but it is worth repeating to avoid unnecessary confusion.

*Toward a Dynamical Model for Hierarchically Organized Complex Systems*

Given the variety found in the empirical record of social insects and our arguments concerning the theoretical blinders that the superorganism theory entails, we wish to promote in its place a theory that avoids the pitfalls and adequately explains the phenomena. We suggest that such a theory have the following features.

1. Hierarchical selection (see Wade 1980): a theoretical model that embraces the multiplicity of levels at which selection can and does act and does not preclude simultaneous selection at more than one level (Wade 1980; see also Lewontin and Dunn 1960; Vrba 1989). Wheeler (1911, 1928) and E. O. Wilson (1985a) clearly allow for hierarchical selection to operate on their superorganisms, while D. S. Wilson and Sober (1989) allow selection only at the level of the group.

2. An ontological framework that corresponds to this hierarchy, namely, a focus on the properties of individual components of ensembles as well as the properties of the whole. Focusing on superorganism-level phenomena alone restricts our ability to understand the actual mechanisms involved in building higher-level phenotypes. Natural selection at the group level must change properties of component parts (individual organisms) in order to achieve higher-level functional properties. Gene frequency changes resulting from selection are a result of the substitution of alternative alleles at gene loci residing in the cells of individual organisms. The individual organisms define, in a sense, the parameter space on which higher levels of selection can operate and constrain the possible group-level phenotypes.

3. Multiplicity of explanatory strategies: a model that does not entail selectionism and hence allows for spontaneous order to emerge from interactions of component parts and explain group dynamical properties. The use of functional organization to simultaneously describe the current contribution of a part of a system to the system's survival and reproduction and to pick out an arrangement that is the result of a natural selection history makes nonselectionist explanations of functional order impossible. We need a descriptive language that does not bias the outcome of investigation into the developmental dynamics or selection histories of a given system.

4. This model should not be based on a restrictive Weismannian paradigm and instead should recognize multiple forms of functional reproductive organization and allow the conflict between levels of selection and among component parts and its incomplete resolution.

*Conclusion*

The superorganism metaphor and its more sophisticated relative, the theory of superorganisms, are used for a variety of purposes by their proponents. For Wheeler, the superorganism model provided a mechanistic framework to account for the observed cooperation of individual insects. He proposed it both as an alternative to the scientifically suspect invocation of metaphysical spirits and entelechies and as an alternative to a narrow reading of Darwinism that presumes a world filled with conflict among individual organisms. E. O. Wilson revived the superorganism as a developmental framework in order to model sociogenesis of social insects akin to the morphogenesis of individual organisms. D. S. Wilson and Sober and Seeley hope to make the superorganism theory do the bidding of a hierarchical theory of selection as an alternative to a single-level individual selectionistic framework.

In this chapter we have focused on the shortcomings of the Wilson-Sober model of the superorganism, not as an argument against the promotion of a hierarchical model of selection, but rather in its favor. We support a pluralism of explanatory strategies to apply to social insects, including cooperative, developmental, and hierarchical selection frameworks. However, because of the multiple purposes for which the superorganism concept has been used, and hence its equivocal reference in the contemporary revival, we believe such goals can best be achieved by developing an explanatory model in other terms.