TOWARD A UNIFIED THEORY OF SOCIAL INSECT CASTE

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A Review of

Caste and Ecology in the Social Insects. *Monographs in Population Biology, Volume 12.*
By George F. Oster and Edward O. Wilson. Princeton University Press, Princeton (New Jersey). $20.00 (hardcover); $7.50 (paper). xv + 352 p. + 1 pl.; ill.; index. 1978.

All social insects — ants and termites, and the social wasps and bees — have "castes", classes of individuals devoted for prolonged periods to particular tasks. The sterile "worker" caste of the social insects has attracted much attention as an extreme manifestation of "altruism" in animals. Only in the social insects is there a genetically programmed class of individuals so highly specialized for aiding others.

In spite of great interest on the part of theoreticians, and a multitude of detailed studies of the physiology of caste determination, the diversity of caste structure among the social insects is still poorly understood. Species differ in the degree of structural specialization between queens and workers, structural specialization among workers performing different tasks, age specificity in the tasks performed by workers, and caste flexibility in response to variations in resource supply and demand. Moreover, different species have different average numbers of each caste. A unified evolutionary theory of caste must show the adaptive significance of all of these variants.

In *Caste and Ecology in the Social Insects*, George F. Oster, an important contributor to the mathematical formulation of ideas regarding insect sociality, and Edward O. Wilson, a long-time student of caste and social evolution in ants, have combined their considerable talents to attempt such a theory. They have devised models which consider virtually all of the important "decisions" handled by a colony during its growth and reproduction: the size and number of workers produced relative to the number of queens; the timing of the switch from worker to sexual brood production; the preferred ratio of investment in males and females from different points of view (queen, workers, and colony), with or without male production by workers; the relationship of caste number and specialization to the number of tasks performed; optimum caste ratios; and the reasons why certain sets of characters (e.g., large colony size, physical polymorphism, and slow colony growth) tend to be associated in a given species. All of this is preceded by a beautiful frontispiece by Turid Holldobler depicting a group of bronze, polymorphic weaver ants. It is difficult to imagine a more pleasing and informative arrangement of twelve ant bodies, seventy-two legs, and a pile of gleaming eggs and larvae.

Anyone who wants to understand the models well enough to use them effectively will wish to follow the mathematical derivations. However, all of the major conclusions are verbally outlined and discussed in the text, with technical details relegated to appendixes, making the main ideas easily comprehensible to any interested biologist.

This book has two profoundly influential cornerstones: ants and ergonomics (a term borrowed from economics, meaning the quantitative study of group efficiency). Although other social insects and other interpretative frameworks are mentioned, these two predominate. The authors originally intended to explain the evolution of highly polymorphic ant societies in terms of ergonomic principles — optimization of energetic efficiency in converting environmental resources into reproductive offspring (new queens and males). These two themes are well matched. Many of the most striking and well-studied ants have markedly polymorphic specialized workers and single queens which are highly specialized to laying eggs — in short, societies approaching the "superorganismic" level of group unity and cooperation. And ergonomic efficiency means *colony* efficiency, a reasonable basis for explaining such extreme worker specialization to celibate functions. But the attempt at a simple unitary explanation ended in "disillusionment," with the realization that "caste polymorphism represents but one evolutionary strategy to enhance ergonomic efficiency" (preface), another being behavioral flexibility (which, as they discuss later, may not always be based on ergonomic efficiency at all). The authors conclude (preface, pp. vii–viii) that "the ultimate reason why a species takes the evolutionary road to physical polymorphism may be imponderable"; that it might be historical accident; that the attempt at a unified theory was a "conceit"; and that, after all, "the function of science is to explain what can be explained, not what should be explained."

The reader will be either relieved or disappointed (depending on his or her sentiments regarding ergonomics and optimization theory) to find the modest pessimism of the preface shortlived. The rest of the book, with the exception of the last chapter, "A Critique of Optimization Theory in Evolutionary Biology," is full of optimistic optimization models, its authors largely undaunted by the conscientiously explicit reservations attached throughout. Evidently they decided to go ahead with ergonomics, in spite of its limitations, since to them it "appears to be the only theme that is both unifying and sufficiently explicit to offer some hope of empirical verification" (p. ix).

In reading the book I was less bothered by the failure to explain why so few species have polymorphic workers than I was by the failure of the models to encompass the hundreds of less than "superorganismic" species of social insects. Indeed, the discussion of caste flexibility as a superior strategy in certain ecological circumstances seemed a satisfactory explanation for the lack of ubiquity of physical castes among highly social species. And ergonomic models can predict the optimal mix whether flexible or fixed. On the other hand, the models presented do not explain why (in evolutionary terms) there is "queenlike" behavior (especially, oviposition) by "workers"; do not adequately relate individual and colony selection in the evolution of caste; and do not tie together with one truly unified set of concepts both the origin of the reproductive division of labor between queens and workers, and the evolution of subcastes (temporal and structural) among workers.

A truly synthetic evolutionary theory of caste must deal with both individually advantageous role-divergence and colony efficiency, and ergonomic models effectively treat only the latter. Although intragroup competition is repeatedly mentioned in the text, the models themselves view the colony as a superorganism, with different forms of social organization, task specialization, caste ratios, etc., the result of adaptation to different *environmental* (vs. internal, social) circumstances. Some students of multi-queen ants, wasps and bees, and of the (diploid) termites, will be bothered by the lack of generality of models presuming a single haplodiploid queen.

In this book individual selection is seen as "opposed" to the colony selection represented by the models, and is often invoked to explain deviations from the model predictions. This creates a mistaken impression of the relation between individual and group selection, which must often be synergistic, as I shall discuss below. In fact, individual selection must commonly act to screen the characters available for the action of higher levels of selection. If this is so, virtually all persistent characters must be advantageous (or at least not harmful) at *both* the individual and the colony level.

Viewing individual selection as "opposed" to group selection is one consequence of thinking in terms of colony optima and then trying to explain observed failures to attain them. Describing natural selection as an optimizing process is a slight, but important, distortion. The optimum is the best possible (of all *conceivable*) alternatives, whereas natural selection produces the best feasible (of all *available*) alternatives. It is like the difference between the best possible and the lesser of evils. It seems useful to invoke optimization theories (like ergonomics) to describe the extremes toward which selection might tend in specified circumstances. But it is a mistake to consider "optimization" synonymous with "adaptation," and declare (p. 292) that "biologists view natural selection as an optimizing process virtually by definition." In fact, the use of optimization theory is currently a matter of vigorous controversy among evolutionary biologists. Oster and Wilson recognize (p. 315) that "the concept of lone optima toward which many species can be said to be moving along certain trajectories appears to be an unsupportable metaphysical notion." And they devote the entire penultimate chapter to a critique of optimization theory. Coming at the end of a book so thoroughly committed to an optimization theory of caste, this frank critique is a bit unsettling, like an analysis of the health effects of cigarette addiction written by a pair of chain smokers. One is left wondering at what point serious reservations about a cherished procedure should lead to its abandonment.

Specialists will notice the tendency to sail past controversy in other matters. The haplodiploid hypothesis for the origin of hymenopteran sociality is accepted as established, even though students of both wasps and bees — the only groups in which this question can be attacked via comparative study — conclude that it was probably of minor import, since long-term monogyny probably often followed rather than preceded the advent of sterile workers. The statement (p. 98) that it is "the usual circumstance in the social Hymenoptera" that workers control the ratio of colony investment in males vs. females implies generalizing to all ants and social wasps and bees from a still controversial study of monogynous ants (R. Trivers and H. Hare, *Science,* 191: 249-263, 1976). The only study known to me in which adequate investment ratio data were painstakingly gathered for a single species shows the queen, not the workers, to be in control (K. Noonan, *Science,* 199: 1354-1356, 1978).

The authors make the useful innovation of considering the inclusive fitness of the colony as a whole, in order to evaluate colony-level effects of conflict of interest over male-female investment ratios. Likewise, including the success ratio (S) of males vs. females in the community (population) in expressions for inclusive fitness is important, especially for the social insects in which there is often a great disparity between the value (and cost) of large or swarm-endowed females and that of males. Hamilton's earlier formulation of a similar correcting factor (1972, *Ann. Rev.*

Syst. Ecol., 3: 193-232) has been largely neglected (it is also not cited by Oster and Wilson), as has his point that the ratio of success (or value) of offspring of the two sexes should be proportional to the equilibrium population sex ratio.

The chapter on "Optimum Caste Ratios" is the longest in the book, and because its models seem likely to be among those most amenable to empirical test it seems worth commenting on some of them in detail. Oster and Wilson propose two optimization models of caste polymorphism: the "one-task, one-caste" model, which predicts a linear relationship between the number of tasks in a species' behavioral repertoire and the number of castes performing them; and the "allometrics space" model, which predicts that the number of castes increases as the logarithm of the number of tasks. They suggest distinguishing between these two models with a comparative study of many species to test whether the task-caste correlation is in fact linear or logarithmic. Ignoring for the moment the difficult problem of making equivalent definitions of "task" for different species so as to yield truly comparable quantities, both models presume that there must be an increase in number of tasks to produce an increase in worker specialization to particular tasks. This seems unrealistic, since specialization to particular tasks can obviously occur with no change in the number of tasks at hand: three ants can either be generalists (each capable of guarding, foraging, and nurse duties) or specialists (a guard, a forager, and a nurse). Furthermore, even if there does prove to be an increased number of tasks in more polymorphic species, the causal relationship may be the reverse of that implied. Specialization may extend the behavioral repertoire of a species, increasing the number of "tasks," rather than the number of tasks dictating the number of specialties. (For example, a specialized guard caste might develop a new ability for entrance-blocking in a species previously lacking that behavior.) That is, task increase could *follow* the evolution of caste specialization rather than lead to it, and thus confound the meaning of any mathematical relation found.

The discussion of "risk-taking" ("tychophilic") and "risk avoiding" ("tychophobic") species is satisfying, despite the tinge of terminological teleology, because it summarizes and begins to explain sets of characters frequently associated in nature. Variable or flexible castes often characterize species with short-lived, rapidly growing colonies able to take advantage of a varying environment ("risk taking" species). And highly polymorphic species usually (if not always) have large, long-lived, "secure" colonies (are "risk avoiding" species). The authors introduce some confusion, however, by later noting that fast-tempo short-lived workers seem to characterize large colonies, which they term "r-selected," contrasting them with small, slow-tempo "K-selected" colonies. If one then makes the obvious comparison of dichotomies, using the common denominator, colony size, it is evident that something is wrong: the authors call small-colony species "risk-taking" (rapidly growing, taking advantage of changing environments) and "*K*-selected." But "risk-taking" characters include some supposedly characterizing *r*- (not K-) selection (e.g., rapid opportunistic colonization of new areas). The additive sloppiness of the two dichotomies makes their juxtaposition awkward.

In general, however, the book is clear and well written. There is a certain amount of new jargon, though less than in books written by Wilson alone (some may have been Osterized for ergonomic reasons). In addition to "tychophobia" and "tychophilia" there is a "Lebensraum strategy" (a tendency to expand). And activity rate is "tempo" — in keeping with the general theme of group harmony, orchestrated by colony selection and paced by the ecological metronome, ergonomic efficiency. I was disappointed when fast-tempo colonies were termed "hot," and slow ones "cold," rather than "allegro" and "adagio," or "velociphilic" and "velociphobic."

The strong emphasis on colony efficiency in *Caste and Ecology in the Social Insects* is a limitation in the search for a unified theory of caste. But it enables the book to fill an important place in the analysis of insect societies. Recent discussions of worker altruism have focused attention rather narrowly on individual selection (on queens and workers) as a determinant of colony organization. This book, on the other hand, sees the colony as a "factory fortress" (the authors' term) — a single unit of selection confronting certain environmental contingencies.

A unified theory of caste awaits a synthesis of both viewpoints. Caryl P. Haskins foreshadowed such a synthesis thirteen years ago in some remarks following a lecture by E. O. Wilson (see pp. 81-96 in *Insect Behavior,* Roy. Ent. Soc. London, 1966, P. T. Haskell, ed.). Because Haskins has so often concisely summarized important advances in this field decades before they occur, I cannot resist quoting excerpts from his comments here. Even his language anticipated that of Oster and Wilson's book:

> . . . These opposing evolutionary forces [individual and colony selection] which determine the optimum ratio of workers to queens . . . (a ratio which may be defined as the "optimal average" for a given community) will be complex, and the precise final values will inevitably vary from one situation to another. But it seems highly probable that no optimal equilibrium value in such a communal [multiqueen] structure could remotely attain that which would actually be most adaptive in colonies with single reproductives, where intra-communal reproductive competition among

reproductives with respect to the caste-plasticity of their daughters has been eliminated. . . .

In this respect the Formicidae [ants] could have been at a tremendous evolutionary advantage if, as seems probable, the pattern of initiation of new colonies by isolated single females is primitive in the group. For in this situation, intra-communal competition among females for genotypic representation in the following generation would have been eliminated at the very beginning of social evolution, permitting the early development of an extremely high worker:queen ratio, with its concomitant of a highly evolved division of labour and resultant colonial structure. By this device, the evolutionary pressures on the individual and on its community would have been brought into coincidence at the beginning of social development, rather than being kept permanently in a state of uneasy conflict, as they seem to be in the primarily polygynic (multiqueen) Hymenopteran community (op. cit., pp. 93-94).

That is, individual selection should play an important role in caste evolution, with ergonomically efficient "superorgansmic" colonies sometimes achieved via a coinciding of individual and colony interests (e.g, in single-queen colonies). It is in such colonies that elaborate specializations such as physical castes develop, and "optimal" caste features like those predicted by Oster and Wilson are most likely to occur.

Start by marking â€œCaste and Ecology in the Social Insects. (Mpb-12), Volume 12â€ as Want to Read: Want to Read savingâ€¦Â In this pathbreaking and far-reaching work George Oster and Edward Wilson provide the first fully developed theory of caste evolution among the social insects.Â The social insects play a key role in the subject of sociobiology because their social organization is so rigid and can be related to genetic evolution. Because of this important consideration, the authors' work has consequences not only for entomology but also for general evolutionary theory. ...more. Get A Copy. Amazon. The social insects play a key role in the subject of sociobiology because their social organization is so rigid and can be related to genetic evolution. Because of this important consideration, the authors' work has consequences not only for entomology but also for general evolutionary theory. eISBN: 978-0-691-20932-6.Â Caste and division of labor lie at the heart of colonial organization in the social insects. What makes an ant colony distinct from a cluster of butterflies, a swarm of midges, or for that matter a flock of birds, is its internal organizationâ€"the differentiation of its members into castes, the division of labor based on caste, and the coordination and integration of the activities that generate an overall pattern of behavior beyond the reach of a simple aggregation. of individuals. The social insects play a key role in the subject of sociobiology because their social organization is so rigid and can be related to genetic evolution. Because of this important consideration, the authors' work has consequences not only for entomology but also for general evolutionary theory. Read More. Information.Â 1.3. Concurrent Operations as the Key Advance. 1.4. The Eusociality Threshold. 1.5. Caste and Roles. 1.6. The Superorganism and Factory-Fortress. Summary. 2. Colony Life Cycles.