Options for Wasps

The Social Biology of Wasps. KENNETH G. Ross and ROBERT W. MATTHEWS, Eds. Comstock (Cornell University Press), Ithaca, NY, 1991. xviii, 678 pp., illus. \$72.50; paper, \$34.95.

Anyone who has haplessly disturbed a large nest of yellowjackets can attest to the selfless and fierce devotion of worker wasps to their colony. Yet modern studies, reviewed in The Social Biology of Wasps, have revealed that the degree of altruistic commitment to the colony can vary from the nearly absolute to the decidedly half-hearted. For example, when a Dolichovespula queen is restrained to half of her nest, her workers abandon the queenless half and continue lavishing care on the queen and her progeny. In contrast, when a Polistes queen is tethered to one part of her nest, her nestmates seize the day, laying their own eggs outside the reach of the queen's punishing mandibles.

The two ends of the social spectrum are different enough to have fostered distinct research paradigms, both of which are represented in this book. The large, complex, integrated societies of yellowjackets (as well as ants, honeybees, and termites) are often viewed as superorganisms, with workers functioning like a metazoan soma, maintaining the integrity of the colony and promoting its reproduction through the germ line represented by the queen. The superorganism concept does not serve so well for the simpler societies like those of Polistes, where individuals often seek their own reproductive advantage, sometimes through dangerous fighting. If a Polistes colony is an organism, it is a very peculiar one, with the various body parts elbowing and kneeing each other aside, each vying to become a gonad. Individual advantage can in principle be reconciled with superorganismic colonies through Hamilton's inclusive-fitness logic; selection favors genetically successful individuals, but genetic success is sometimes best achieved by aiding kin other than offspring. Exactly how this comes about leads to the central questions of social insect evolution and to some of the great questions of biology. What circumstances lead to the evolution of altruistic behavior? Once it evolves, how can it become elaborated to the degree that a colony can profitably be

viewed as a superorganism, a new and higher level of organization and selection?

The range of social organization in wasps makes them ideal for addressing such questions. To find the answers, one must study individuals. The Social Biology of Wasps is the first book on the subject since the surge of individual-marking studies triggered by Hamilton's theory. No wasp personalities have yet joined Goodall's chimps in the popular consciousness, but maybe they should. Perhaps the chief lesson from recent studies is that social life is anything but simple in the wasps that lack morphological castes. A female is not simply a cog in the colony's machine; she has many reproductive options. If she stays on her natal nest, she can be a good citizen and help the colony, but she may do better by aiding only her closest relatives, by shirking risky duties in order to try to inherit the queenship, or by fighting for the queenship. Alternatively, she can leave to found a new nest, alone or with others, or she can try to usurp a foreign nest.

Eusociality, defined as the presence of overlapping adult generations, cooperative brood care, and a reproductive division of labor, is likely to have evolved only once in the Vespidae (Carpenter, chapter 1). This might have been a short book indeed if the solution to the puzzle of altruism involved only a single occurrence that has been retained in all of the hundreds of descendant species. Fortunately, individuals of species considered to have passed the eusociality threshold still have options, and we can study these to gain insight into the advantages of helping.

What factors favor helping when one has the option of unhampered reproduction on an independent nest? The abundance of social insect fauna suggests that sociality is a highly successful strategy and not just the last resort of females lacking either a nest site or adequate ovaries. It is possible that this success stems from efficiencies evolved in very advanced species, but it seems likely that eusociality itself contributes to ecological success. One important advantage is that grouping may be a way for short-lived adult insects to assure care for their young throughout a long juvenile period. Reeve (chapter 4) persuasively argues that this explains why females found nests cooperatively in some *Polistes* species and not in others. But he also shows that the exact choice of an individual female is often more complicated, with optimum strategies differing according to her age, size relative to other colony members, season, and relatedness to brood.

The take-home lesson is that, although many females help, they may keep an eye out for chances to rear their own offspring. In this respect they seem remarkably similar to vertebrates with helping: numerous birds, wolves, lions, dwarf mongooses, and of course naked mole rats. The eusociality threshold, which has historically separated social insects from social vertebrates, is considerably fuzzier than it was before people started observing individual insects as if they were mockingbirds or vervets. In reality, the greatest claim to distinction of social insects is probably not eusociality itself but the degree to which some groups have progressed past the eusocial threshold. It is no accident that vertebrate groups have rarely been viewed as superorganisms, while the metaphor seems quite apt for certain social insects.

But how do small groups of competing individuals evolve into large superorganismic colonies? The question is significant in its own right and for what it might tell us about the emergence of higher levels of order and new units of selection (other examples, more difficult to study, include the eukaryotic cell and multicellularity). No clear answers are yet available, but some of the right questions are being asked. Why, for example, should workers require physical control by the queen in some societies while in others they peacefully respond to mere chemical hints from the queen? Starr (chapter 15) argues that the latter behavior will evolve only when it is in the workers' own genetic interests to respond, but what leads to such convergence of interest? Jeanne's discussion (chapter 11) of temporal castes (following West-Eberhard) shows the kind of thinking that needs to be applied. Even in species at the superorganismic end of the spectrum, workers begin life by performing safe chores at the nest and later switch to risky foraging, as if they were attempting to preserve their direct reproductive options as long as possible. By seeking the traces of individual conflict even within harmonious colonies, we may hope to understand how harmony comes about.

One clear lesson from the wasps is that there are multiple paths toward more advanced societies. The vespines are often seen as the pinnacle of wasp sociality by virtue of their single, morphologically distinct queens and the large, relatively peaceful colonies. But the swarm-founding polistines are more advanced in certain respects. Though they have multiple egg-layers and often lack morphological castes, they are the most obligately social wasps (lacking a solitary colony-founding stage) and have the most sophisticated division of labor. Additional systematic and behavioral studies should help reveal where and perhaps why these kinds of socially advanced traits have evolved.

Readers of The Social Biology of Wasps should be warned of the considerable overlap in coverage, particularly between early chapters organized by taxa and later ones organized by theme. Also, there is no overview chapter that collects the main themes and places wasps in a larger context. Those desiring such a chapter should turn to the recent review of eusociality by Alexander, Noonan, and Crespi in The Biology of the Naked Mole Rat, (P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, Eds., Princeton University Press, 1991). While we are only beginning to understand the complexity of sociality in wasps, The Social Biology of Wasps provides a thorough and up-to-date account. It is fertile ground for graduate students seeking thesis topics and a great resource for anyone attuned to the tension between conflict and cooperation that makes social animals so interesting.

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Engineer in the Making

The Idea Factory. Learning To Think at MIT. PEPPER WHITE. Dutton (Penguin), New York, 1991. xviii, 313 pp., illus. \$21.95.

The premise of this unabashedly autobiographical book is simple: a young man with a bachelor's degree in environmental engineering from Johns Hopkins and a year and a half of experience in Europe (including one year working at the von Kármán Institute in Belgium) goes to graduate school at MIT. Although admitted into the school's Technology and Policy Program, White transfers to "Course 2," which is mechanical engineering at MIT, even before classes begin. The bulk of the book is descriptive of various of the courses White takes (with varying degrees of success) and of graduate and undergraduate student life in Cambridge.

After his first semester White secures a research "assistanceship" on a project involv-

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Entries in a contest where "some weight had to go to the top of a ramp in twenty seconds, and with just a little tiny electric motor and two little tiny springs . . .". [From *The Idea Factory*]

ing a rapid-compression machine, for which it is his task to raise the compression ratio. Since his master's thesis work revolves about this project, it understandably plays a significant role in the story's development. In his second year, White moves into Senior House as a tutor, or resident assistant, and this position provides much of the focus for the book's descriptions of undergraduate life at MIT.

White's self-consciousness about what it means to be a student trying to distinguish himself, and an MIT student in particular, pervades *The Idea Factory*. This self-consciousness is especially explicit in an account of a televised contest in which a team of three MIT students is pitted against a team of three Berkeley students in attempting to explain the workings of an alleged perpetual motion machine. Tensions between concern for form and substance manifest themselves in how the students choose to dress and how they behave before the camera, but in the end it is the technical aspects of the competition that clearly determine the outcome.

Although The Idea Factory appears to be targeted toward a general readership, the technical detail White gets into in describing homework assignments in such courses as advanced fluid mechanics would seem to appeal to and be most accessible to a technically initiated readership of engineers and scientists. Indeed, this book provides a rare and welcome opportunity for more mature academic engineers and scientists to see materials and methods that have long become second nature to them from the point of view of a student. White's struggle with the concept of "model," for example, reveals how difficult it can be for some students to pick up even what might appear to be among the most fundamental aspects of the engineering and scientific method.

Many well-known personages are encountered in the pages of *The Idea Factory*, and the reader is given glimpses of the classroom style of several MIT professors. We spend an extended time in the labs of the legendary Doc Edgerton, to whom White goes for advice on the use of high-speed photography to capture the diesel fuel spray in the ignition chamber of the rapid compression machine. There is also much name-dropping in the book, and some of the names get damaged. Thus Vannevar Bush's name becomes "Vannebar" (on p. 7 and in the index, but not elsewhere), and Newton's Second Law is misnumbered the First (on p. 177). It is hard to know what to make of such lapses in technical detail in a book about technical detail, but they do give a touch of humanness to an account that at times borders on being overly mechanical.

The human side of the story of being a student in The Idea Factory is full of pathos, and White seems less sure of himself in trying to explain it. An awkward juxtaposition of personal tragedy and engineering calculation, for example, may leave the reader wondering if there really is something dehumanizing about technical education. But because White has, even with its flaws, told such a human and gripping story, it would be a disservice to potential readers of this book to reveal too much of the plot. Suffice it to say that in the end this is one articulate student's attempt to communicate across gaps in experience that have remained generally unbridged. White is to be applauded for his candid and hard-nosed account of his years at MIT, and his book is sure to reach a wide readership among those who have been through, at whatever level, the rigors of engineering and science education. Many will find this book hard to put down and will find much in it with which their own experiences can resonate.

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Children's Theories

Understanding the Representational Mind. JOSEF PERNER. MIT Press, Cambridge, MA, 1991. xiv, 348 pp., illus. \$35. A Bradford Book. Learning, Development, and Conceptual Change.

Most people, even most scientists, spend much of their time figuring out what other people think: "Why did the lecturer explode about that trivial question?" "What does the peculiar behavior of the grants officer mean?" "Does he really love me?" In asking and answering these questions we rely on an enormous store of ordinary, common-sense psychological knowledge. Where does this