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WASPS: THEY'RE NOT JUST FOR SOCIOBIOLOGISTS ANYMORE

Gess, Sarah K. 1996. **The pollen wasps: ecology and natural history of the Masarinae**. Harvard University Press, Cambridge, Massachusetts. x + 340 p. \$49.95, ISBN:0-674-68964-X (alk. paper).

Turillazzi, Stefano, and Mary Jane West-Eberhard (eds.). 1996. **Natural history and evolution of paper-wasps**. Oxford University Press, New York. xiv + 400 p. \$115.00, ISBN: 0-19-854947-4.

Ecologists often study ants and bees. Wasps are not so lucky. Menacing appearance, sometimes pointedly reinforced, constrains their initial appeal. I believe, however, that their role in ecological studies is restricted even more because "wasps" is a name that lumps ecologically and taxonomically diverse forms such as velvet ants, tarantula hawks, mud daubers, and paper wasps, along with many others that are less well known. In fact, ants and bees are wasps, too, albeit very distinctive ones. To distinguish a focal taxon for study enables

the accumulation of both data and aficionados that then enable further study. One group of wasps that has attracted a dedicated, if small, fraternity of devotees is the family Vespidae. It is a taxon that merits much greater attention from ecologists. Two recent books have the potential to bring knowledge of the Vespidae to a wider audience and to move study of these fascinating insects closer to the mainstream. Each focuses on one subfamily (of six) in the only insect family in which extant forms in a known phylogeny span the range from solitary to highly social.

The pollen wasps, by Sarah K. Gess, is the largest and finest single source of information ever assembled for the subfamily Masarinae. Masarines are one of two wasp taxa (bees are the other) to have adopted pollen as provision for their larvae. This means that masarines, like bees, have morphological specializations (some have tongues as long as, or longer than, many bees), flower preferences (most are oligolectic), and phenologies (most are seasonal in temperate arid lands) that reflect close ecological relationships with the plants that they visit. This means that masarines represent an evolution of specialized flower visitors (and probable pollinators) that is independent of, yet strongly convergent with, the better-known bees. Masarines thus offer an open invitation to pollination ecologists who would like to sort ecological from phylogenetic factors that affect the evolution and maintenance of pollination systems.

Gess has organized her book into eight substantive chapters plus a short, effective summary. Each of the chapters focuses on a selected aspect of masarine biology, and most have a similar structure. For example, the chapter on taxonomy begins with a detailed and historical review that may be a bit of a slog for the uninitiated, but it gives details a specialist would want while giving a general reader an appreciation of the breadth and quality of previous research; the chapter ends with James M. Carpenter's cladogram of genera in the subfamily, which is the state of current knowledge and the platform for future research. Chapters on biogeography, flower associations, and nesting have similarly detailed foreparts that undergird comfortably-resolved syntheses at the end. Of greatest interest to ecologists will be the chapters on flower associations and on pollen wasps as potential pollinators. A large appendix catalogs all known masarine-flower associations of the world; another catalogs all taxa known to visit flowers also visited by masarines in South Africa. Behaviorists will be drawn to the chapter on nesting (which is fascinating); evolutionists will turn to the chapter on life history to glean details relevant to the evolution of sociality in other subfamilies of Vespidae. A chapter on pollen wasps and land use is the only chapter that restricts its focus to Gess' native South Africa, but it is a salutary example of bringing topics on the conservation of one's focal taxon into the same forum as research results. It is lamentable that masarines are not backyard insects, but Gess' book makes it clear that their study will richly reward the effort required.

Natural history and evolution of paper-wasps, edited by Stefano Turillazzi and Mary Jane West-Eberhard, places its spotlight on the subfamily Polistinae. Polistines are those fascinating social wasps that span the range from the primitively social, independent-founding, cosmopolitan *Polistes* to highly social, swarm-founding genera found only in the

tropics. This book restricts its purview to the primitively social, independent-founding forms most commonly called paper wasps; greatest emphasis is placed on *Polistes*. The book is based on a workshop held in October 1993, although the references include literature as recent as 1995. Not all participants in the workshop contributed chapters to the volume, but those who did have given us a valuable compendium of information and perspectives on selected topics in the biology of paper wasps.

The book opens with a posthumously published essay by the eminent Italian entomologist Leo Pardi. Pardi, one of the pioneers of *Polistes*, gives an historical overview of the field, including personages, perspectives, and his own work on physiology. Next, James M. Carpenter gives a detailed cladistic analysis of subgenera and biogeography of *Polistes* that specialists will welcome for bringing order out of chaos and that ecologists will appreciate for the contextual simplicity it provides for future studies. The remaining chapters of the book, save the last, can be mined for ecological information and research ideas. The most explicit focus on ecology is by Sōichi Yamane, who catalogs life cycle variations in *Polistes* and some of the ecological factors that may affect them. I was disappointed in Yamane's chapter for its lack of synthesis between natural history and the perspectives of life history evolution, but John W. Wenzel, in an intelligently-written chapter on nesting behavior, points out that polistologists' preoccupation with relatedness has diverted attention from potentially fruitful avenues of ecological and life history research, and he cogently advocates such endeavors. Michael H. Hansell's chapter on nests exemplifies the potential value of ecological information for illuminating both constraints and opportunities in evolution. Robert L. Jeanne's chapter on exocrine glands shows how conceptual reorganization of information, breaking with traditional entomological approaches, can clarify existing knowledge and point the way for needed future study. Iniquilism (social parasitism) is a topic that unites a number of excellent chapters, and behavioral ecologists will find much of interest here.

An intriguing subtext that runs through several chapters is a tacit movement away from W. D. Hamilton's haplodiploidy hypothesis. Chapters on kin recognition and on the role of cuticular hydrocarbons show that nestmate recognition in paper wasps (which is abundantly documented) is based on a mechanism that cannot serve for intra-colonial kin discrimination in colonies of mixed maternity and/or paternity (which are commonplace); the mechanism therefore nullifies the possibility of kin-directed intra-colonial altruistic aid. Joan E. Strassmann compiles results of empirical studies that support the implied consequence of the nestmate recognition mechanism. David C. Queller and Raghavendra Gadagkar, prominent theorists on social evolution, each present models in which altruism in rearing nestmates of even very low relatedness can yield inclusive fitness benefits that exceed those that can be gained via haplodiploidy. Queller opens his chapter with an assertion, probably widely held to be true by sociobiologists, that workers "give up their own reproduction in order to help rear the offspring of relatives." Two authors question the postulate, implicit in Queller's assertion, that worker paper wasps are altruistic by choice. Pardi raises the question as a thoughtful skeptic; West-Eberhard, in her long

and insightful chapter, raises the question as a central thesis. She updates and expands her perspectives on intra-specific phenotype variability and its role in social evolution. Although her chapter does not incorporate the recent explosion of knowledge on regulatory genes in development, it is clear that West-Eberhard sees worker behavior as a consequence of development shaped by ecological factors and mediated by physiology, not as an expression of individual choice. Her chapter is an open invitation to ecological physiologists to bring their skills and insights to bear on the problem of caste in social insects.

The closing chapter, by philosopher of science Richard M. Burian, is bracing; I commend it to everyone. Turillazzi's chapter on *Belonogaster* and Stenogastrinae provides context for the discussions of *Polistes*; I only wished that he could have written more. Broader context on paper wasps can be found in *The social biology of wasps* (Ross, K. G., and R. W. Matthews (eds.), 1991. Cornell University Press, Ithaca, New York), and detailed information on yellowjackets and hornets

is given in *Biology of the vespine wasps* (Matsuura, M., and S. Yamane, 1990. Springer-Verlag, Berlin). Taken collectively with the two books reviewed here, a readily accessible, high quality, up-to-date literature on the Vespidae is becoming available. Book-length treatment of Eumeninae and Stenogastrinae would fill major lacunae in our knowledge, and the challenges posed by those subfamilies are open to current and future researchers. Soon, I hope, Vespidae will stand as peers of ants and bees in knowledge and value to science, including ecology, and they will be as widely known and widely loved (justifiably so, in my view). The two books reviewed here, both of which are excellent and of lasting value, mark a significant advance toward that goal.

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