

Polistine passions

I have taken a deep breath and decided to introduce this issue on *Polistes* with a somewhat personal appreciation, a kind of love letter for an insect. People who only read about wasps may find this odd or even perverse, but anyone who has observed *Polistes* closely in the field will certainly understand. Anyone, that is, except the most cold and detached observer, and such an observer might not see beyond superficial appearances to appreciate what *Polistes* has to offer the curious mind.

Nearly fifty years ago, Howard Evans recognized *Polistes* as a “key genus” for understanding the evolution of social behavior. Species in this genus have an intermediate form of social organization, more complex than that of group-living species that lack a reproductive division of labor between workers and queens, and less highly derived than that of the specialized species with morphologically distinctive queens and workers. Not only are *Polistes* wasps easy to observe, playing out their social lives in full view on a stage-like unenveloped nest, but the more than 200 species, including three that are workerless social parasites of other *Polistes* species, provide ample material for comparative study.

George Gaylord Simpson wrote of tempo and mode in evolution. There is tempo and mode in social behavior too. *Polistes* females have just the right tempo of activity and mode of social organization to reward research on virtually any topic relating to the evolution of sociality. In tempo, they are always active, always doing something interesting. This is not true of all social wasps. The genus *Mischocyttarus*, for example, resembles *Polistes* in having simple, open nests that invite observation, and a great variety of nest architectures that suggest behavioral diversity. But I have found *Mischocyttarus* to be disappointingly dull compared with *Polistes*. The females are relatively inactive and their nests relatively slow to grow. The males of some species spend entire days, month after month, scent-marking and patrolling the same sunlit bushes in search of females that seem never to appear, confirming my impression that success with *Mischocyttarus* females demands extraordinary patience. Studying such a wasp is like being stuck with a bore at a party, when you could be spending your time with a wasp like *Polistes*, alert with colorful behavior and verve, always busy, each species with some revealing variant on the themes of social competition, communication and cooperation. As for social mode, the intermediate type of colony organization seen in *Polistes* combines individuality and sociality in a way that is especially conducive to understanding key questions in research on social evolution — indeed, in research on evolution in general, for reproductive competition within populations is at the center of all Darwinian evolution.

For these reasons and others, the genus *Polistes* has emerged as a truly *model* model organism. The concept of model organism is finally beginning to expand beyond “the fruitfly” *Drosophila*, “the worm” *Caenorhabditis*, “the frog” *Xenopus*, and “the mouse” *Mus*. But the model-organism craze has diminished the usefulness of the term, which sometimes means little more than “the organism I use in my research.” For studies of social evolution, however, *Polistes* deserves to be called a model organism. It is the subject of a large body of information that now spans more than a century and a great variety of relevant facts. Substantial knowledge of *Polistes* sociality began to grow in the early 1900s, with the natural history studies of, especially, Phil Rau whose many publications on *Polistes* spanned the period 1918–1948. Some of the earliest research on *Polistes* natural history was done in Japan, by K. Iwata and J. Yoshikawa. Later research on the physiological and behavioral underpinnings of caste determination by scientists in France (e.g., Deleurance, Strambi), Italy (L. Pardi), and later in Germany (P.-F. Röseler) and the U.S. (M. Bohm) combined laboratory studies of hormones and

reproductive morphology with observations of behavior. Primed by direct references to *Polistes* in seminal papers on kin selection by Hamilton in the early 1960s, and by a series of doctoral theses that focused on evolutionary aspects (e.g. by M. J. West (West-Eberhard), D. Gibo, J. Strassmann, R. Metcalf, J. Klahn, K. Noonan) *Polistes* soon grew in prominence, as evolutionary ecologists and animal behaviorists attempted to disentangle the roles of mutualism, kin selection, and social competition in the evolution of sociality. Because *Polistes* was featured in widely read books by E. O. Wilson on the insect societies (1971: *The insect societies*, Belknap Press of Harvard Univ. Press, Cambridge, MA.) and sociobiology (1975: *Sociobiology: the new synthesis*, Belknap Press of Harvard Univ. Press, Cambridge, MA), and broadly oriented articles by students of *Polistes* on the evolution of sociality, its use in evolutionary hypothesis-testing spread beyond the realm of social insect studies, and continues in a new age when adaptive evolution has come to include developmental phenomena as well as genetics (for example, see articles in this issue by S. Sumner, and J. Hunt).

Furthermore — and this is crucial for an aspiring model taxon — the systematics and phylogeny of *Polistes* species have been analysed by a long series of productive systematists, including H. de Saussure, A. Ducke, K. Zimmermann, J. Bequaert, J. van der Vecht, O. W. Richards, S. Yamane, J. Kojima, R. Snelling, D. Guiglia, and J. M. Carpenter. In this attention from taxonomists, *Polistes* researchers have been extremely fortunate: prospects for expansion of model-organism research into comparisons of related species, as prognosticated by expanding genome projects, will be frustrated if systematics, including alpha taxonomy, falls into neglect.

This issue is a timely report on the state of *Polistes* research today. It shows that investigations of *Polistes* continue to generate a healthy mixture of theory, controversy, and new information. This issue contains new theory on conflict over sex ratio and male production (K. Tsuchida and T. Suzuki), the origin of the worker caste (J. H. Hunt), and the maintenance of alternative behavioral tactics during nest foundation (P. T. Starks and N. Fefferman). And it contains new critical analyses of older ideas, on skew theory (P. Nonacs), and social evolution, from a phylogenetic perspective (K. M. Pickett, J. M. Carpenter and W. C. Wheeler). There are new findings on the manipulation of *Polistes* worker behavior by a strepsipteran parasite (L. Beani); on the social interactions in pre-hibernation aggregations (L. Dapporto and E. Palagi); and on the communicative functions of facial color patterns (E. A. Tibbetts), venom components (S. Turillazzi), and cuticular lipids (F. R. Dani), all topics that advance understanding of social evolution.

Particular topics of general interest are the subject of major authoritative reviews. Polistine social parasites are now one of the best understood examples of social-parasite evolution in the social insects, so the overview of this topic by R. Cervo is of particular interest, as is the analysis of chemical strategies of the parasitic species by M. C. Lorenzi. The subject of social dominance, pioneered more than fifty years ago by L. Pardi using *Polistes*, is seen as part of a broader picture in the article by T. Monnin on chemical cues of dominance in social insects.

Beyond the strictly social lives of the wasps, a highly qualified group of experts on *Polistes* (A. E. Liebert, G. J. Gamboa, N. E. Stamp, T. R. Curtis, K. M. Monnet, S. Turillazzi and P. T. Starks) has joined together to attempt to understand the dramatic invasion of a European species, *P. dominulus*, into the American northeast and middle west, where it has spread rapidly and seems to threaten to displace and possibly drive to local extinction a native species, *P. fuscatus*. This article is of special interest because the collaborating authors include one set of specialists deeply familiar with the behavior and ecology of the invader in its native Europe, and another with comparable knowledge of both the invader on foreign soil and the native species being displaced.

Why does *Polistes* serve so well as a model organism in social and evolutionary biology? And will it continue to be useful in future research? In my opinion the genus has risen to prominence because it is so transparently Darwinian. Females are socially competitive and, to use an American slang expression, they let it all hang out, displaying their competitive interactions, as well as their cooperation and sexual behavior, in plain view. They are also manageable as laboratory animals. Early behavioral observations of kinship relations have been supported and improved with modern genetic analyses

and experimental studies of kin recognition. And because *Polistes* females are markedly individualistic as well as obligatorily group living they illuminate some of the major transitions in evolution, those between individual and group life, and beyond that to the reproductive divisions of labor that characterize highly evolved societies and multicellular organisms. All of this makes *Polistes* eminently qualified for continued deep studies of sociality and evolution. These insects are increasingly valuable because there is a great fund of fundamental knowledge already in place, which means a multiplier effect for any effort devoted to future research.

I have never seen a love letter to *Drosophila* or a nematode worm, or even a sign of warm regard. But mass reared, overfed members of an inbred strain do not readily inspire affection. A personal relationship with the sting-wielding *Polistes* is a love affair at a distance. But I find it satisfying to work with an organism that inspires respect, and a subject — social biology — that demands respect for natural conditions. Researchers on *Polistes*, whose decades of research justify the stature of *Polistes* as a model organism, have at the same time enjoyed a relationship with *Polistes* as a living organism, one capable of self defense and life in its own peculiar world. It is a world of gleaming larvae, intricate interaction, and artful hexagonal cells. Seeing the beauty of that world is one of the enduring rewards of research on *Polistes*.

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