Social Insects

The social insects—the ants, termites, social bees, and social wasps—are important for reasons other than the clarity with which they exemplify social evolution. They also rank among the ecologically dominant animals of the land. Ants and termites in particular weigh more and utilize larger amounts of energy than all the birds and reptiles combined, they turn more soil than all the earthworms, and they also serve as very important predators and degraders of cellulose. If some catastrophe removed all the highly social vertebrates, including man, the remainder of the natural global ecosystem would scarcely register the perturbation; but if the social insects were exterminated, the result would be a major reorganization of the land environment.

For these reasons it is reasonable to speak of insect sociobiology as one of the relatively most underpopulated and undeveloped of the biological disciplines. Only several dozen specialists exist, not counting apiculturists, plus several hundred others who employ social insects marginally in more conventional aspects of biological research. On 25 to 27 February 1971, a group of 24 of the specialists gathered in Washington, D.C., for one of their infrequent convocations. The principal purpose was to honor a distinguished member, Caryl P. Haskins, on the occasion of his retirement as president of the Carnegie Institution of Washington. Coming from the United States, Europe, Israel, and South America, this group of insect sociobiologists examined recent advances in their field.

The symposium demonstrated that the discipline is advancing rapidly in both theoretical and experimental research. Among the participants, for example, was Warwick E. Kerr of Brazil, who showed how he and his associates have unraveled the complex interaction of genetic and environmental factors in caste determination in the stingless bees. In *Melipona*, a genetic queen is created when two loci are heterozygous for caste genes. Such individuals can always be distinguished by their smaller number of abdominal ganglia. However, they become full queens in other respects, including development of the reproductive system, only when "good times" provide the developing larvae with a favorable environment, including a rich supply of food. Otherwise larvae grow up into worker phenocopies and join the worker force. William D. Hamilton, of the University of London, elaborated on his genetic theory of altruistic evolution. Among his more important contributions has been to point out that the haplodiploid mode of sex determination in Hymenoptera results in sisters sharing three-fourths of their genes by common descent, whereas mothers and daughters continue to share one-half in the ordinary manner. Consequently it is more advantageous, in a Darwinian sense (and all other things being equal), for a hymenopteran female to care for her sisters than it is for her to try to rear daughters. Hamilton seems to have made real progress in explaining why higher social life is mostly limited to the Hymenoptera (namely, in the ants, bees, and wasps), why male hymenopterans behave like drones instead of industrious workers, and many other previously baffling details in the social life of insects.

Bert Hölldobler, from the University of Frankfurt and Harvard, described how social parasites have "broken the code" of ant communication and thus have succeeded in being accepted as members of the colonies they infest. Certain staphylinid beetles, to take the best understood case, secrete "appeasement substances" that halt attacking worker ants in their tracks. Later, the beetles offer "adoption substances," which mimic the identification pheromones of the ant larvae and cause the workers to carry them to the larval chambers. They obtain part of their food by imitating the begging movements of ant workers. By studying the adaptations of these parasites, Hölldobler has gone far in elucidating the minimal number of signals required to hold an ant colony together. Carl W. Rettenmeyer, of Kansas State University, described how the social parasites of army ants have carried the process of their specialization to what must surely be the outer limits of evolution. Among the extreme cases are mites that closely resemble various parts of the ant's body to which they are attached. One species, for example, fastens itself to the foot of the hind leg. It is shaped like a tarsal segment and, in fact, functions as an extra tarsal segment on which the ant walks.

Insect sociobiologists have made some of their most interesting recent discoveries by utilizing advanced techniques of biochemistry. Fred E. Regnier, of Purdue University, described his own efforts, and those of other biochemists, to perfect methods of microanalysis that permit the identification of pheromones ordinarily available only in microgram and nanogram quantities. With the level of resolution now steadily descending, it is becoming possible to fully characterize not only alarm-defense systems (in which the pheromones often exist in microgram quantities per individual) but also trail and reproductive behavior systems. Certain kinds of pheromones, however, such as recognition substances, have remained intractable and are deserving targets for the best efforts of chemists in the future. Jacob Ishay, of Tel-Aviv University, described the remarkable physiological division of labor which he and his associates have recently discovered in the hornet *Vespa orientalis*. The foraging workers collect insect prey but lack the enzymes to digest the protein. They feed fragments of fresh prey to the larvae, which digest the protein and utilize part of it for their own growth. Another part is converted into simple nutrients, including sugars, and fed back to the workers as a salivary discharge. The queen wasp also lives wholly on salivary discharges which she constantly "milks" from the willing larvae.

The history of sociobiology might be said to be divided into three phases: the natural history phase, in which species and phenomena are discovered and classified; the physiological phase, in which the phenomena are experimentally analyzed to elucidate proximate causation; and the population biology phase, in which the population consequences of the phenomena are analyzed to elucidate ultimate causation. As they unfold, these stages are seldom perfectly sequential. The Haskins Symposium revealed how, in this early growth of the discipline, all three kinds of research can be pursued with great profit, and preferably in a deliberately telescoped form.

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