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1

What are insect societies?



Many species of insects, such as ants, bees, wasps, and termites, organize themselves into social groupings that we may legitimately call societies. Although insect societies have captured the imagination of humans since antiquity, the modern study of insect sociobiology can be said to have begun in 1923, with the publication of William Morton Wheeler's *Social Life among the Insects*.¹⁻³ The next milestone was the publication of *The Insect Societies* by E. O. Wilson nearly 50 years later.⁴ For my generation of insect sociobiologists, *The Insect Societies* has been a great source of inspiration and the go-to place for information and ideas, while *Social Life among the Insects* has been a legacy of great pride.

Today, the best-known insect societies are those of ants,⁵⁻⁷ bees,^{8,9} and wasps¹⁰⁻¹² in the insect order Hymenoptera, and termites¹³⁻¹⁵ in the insect order Isoptera (color plates 1 and 2).

Within the insect orders Hymenoptera and Isoptera and beyond, we find so many shades of social behavior^{16,17} that a unified consideration of insect sociality and its evolutionary origin and progression is difficult. Among the numerous contributions of *The Insect Societies*, perhaps the

most useful one was Wilson's effort to bring order into this chaos. Drawing on earlier authors, especially Wheeler¹⁸ and Michener,¹⁹ Wilson clearly delineated well-defined grades of progressively more sophisticated sociality, starting from the solitary, progressing through subsocial and parasocial (including the communal, quasisocial, and semisocial), and moving finally to the pinnacle of sociality—the eusocial (or truly social). He defined eusocial insects as follows:

Insects that can be distinguished as a group by their common possession of three traits: individuals of the same species cooperate in caring for the young; there is a reproductive division of labor, with more or less sterile individuals working on behalf of fecund individuals; and there is an overlap of at least two generations in life stages capable of contributing to colony labor so that offspring assist parents during some period of their life.

The term *eusocial* was originally coined by Suzanne Batra to describe the halictine bees she was studying in India but has now been adopted to describe all species at the pinnacle of social evolution, including the termites, ants, honey bees, many other social wasps and bees, and also Batra's halictine bees.^{20–22} Further subdivision of the eusocial species into the advanced or highly eusocial and the primitively eusocial has also been very helpful, as these terms represent very different levels of social evolution and lend themselves as exemplary model systems for studying different phenomena. But it is important to remember that primitive does not mean old and inferior; it simply means that the societies retain more features from the (solitary) ancestral state. Similarly, advanced does not mean new and superior; it is merely that they retain less resemblance to the ancestral state.²³

Advanced eusocial species generally maintain relatively large colonies, sometimes with hundreds of thousands of individuals, such as honey bees, and even a million or more individuals, such as some leaf-cutter ants. Their queens use pheromones to maintain reproductive monopoly, and their workers generally regulate their activities through a bottom-up, decentralized self-organization. Caste differentiation into fertile reproductives and sterile workers takes place in the pre-imaginal

(early larval) stage through a process of developmental regulation, and division of labor is well developed, usually with a component of age polyethism (individuals change tasks as they age).

In contrast, primitively eusocial species maintain small colonies (often fewer than 100 individuals, as in many polistine wasps and halictine bees), and queens generally resort to behavioral dominance to maintain reproductive monopoly and may even regulate the nonreproductive activities of the workers in a top-down manner. Caste differentiation takes place in the adult stage through a process of behavioral regulation, and division of labor can be rudimentary and flexible, making it possible for workers to readily replace existing queens, or to leave to found their own new colonies.

The delineation of different levels of sociality and the clear-cut definition of eusociality have had another exciting consequence: the search for species outside the traditional taxa for newer species that may qualify as eusocial. While all known termites are eusocial, eusociality in the Hymenoptera was traditionally thought to be limited to the families Apidae (honey bees and bumble bees), Halictidae (stingless bees), Formicidae (ants), and Vespidae (wasps). We now know that eusociality also occurs in a sphecid wasp.^{24–26} The discovery of eusocial aphids (Hemiptera) marked the first discovery of eusociality outside the orders Hymenoptera and Isoptera.^{27–31} This was followed by the discovery of eusociality in thrips,^{27,32–34} a beetle,^{35–37} a coral-reef shrimp,^{27,38} and even a plant.^{39–41} However, the most dramatic expansion of the reach of eusociality occurred when a eusocial mammal, the naked mole rat, was discovered.^{42–44} A eusocial vertebrate was unexpected, yet it had been predicted beforehand that if one ever existed, it would have the exact features of the species that was eventually discovered.^{21,45} The discovery of several independent evolutionary lineages of eusocial species is now making it possible to take a holistic view of social evolution and to compare with the equally interesting social birds and mammals, though not technically eusocial.^{16,46–48}

The insect societies represent only some 2% of the approximately one million species of insects described so far. Yet they are among Earth's most evolutionarily successful and ecologically dominant

species, estimated to make up as much as three-quarters of the total animal biomass in some tropical forests. They are found in virtually all land habitats worldwide where insects abound.⁴⁹ A recent study estimates that Earth may harbor as many as 20 quadrillion (2×10^{16}) ants—that's about 12 Mt of dry carbon, more than the biomass of all wild birds and mammals combined, and, if you are still not impressed, the biomass of all ants is about 20% of that of all humans put together.⁵⁰ Another study suggests that the biomass of termites in the soil may far exceed even that of ants.⁵¹

The insect societies are frequently thought of as superorganisms with an emergent level of organizational complexity that sets them apart from other organisms,^{52–56} making possible new kinds of evolutionary processes, such as co-opting old genes for new social functions and creating new networks of old genes.^{57–60} As might be expected, superorganismality is more evident in highly eusocial insect societies than in primitively eusocial ones, but the latter might be the place to look to understand the origins of this phenomenon. I will say more about this when we compare *Ropalidia cyathiformis*, a typical primitively eusocial species, with its sister species, *R. marginata*, a somewhat advanced primitively eusocial species.

The success of the insect societies can be attributed to their ability to cooperate and form large colonies, with division of labor and communication and the propensity for individual members to sacrifice their reproductive success and even their lives in the interests of the colony. Equally important is their ability to build elaborate nests and achieve impressive climate control, and to defend themselves.⁶¹ With few exceptions, members of a colony are not clones, but they have nevertheless evolved elaborate mechanisms for conflict management. Conflict is more prevalent in primitively eusocial species because adult workers can also become future queens, making the management of conflict acuter and more interesting, a topic that will loom large in the rest of this book.

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