JAMES H. HUNT

THE EVOLUTION OF SOCIAL WASPS

OXFORD
UNIVERSITY PRESS
2007

Foreword

It is not surprising that insect societies have long intrigued and fascinated people. Their colonial life with workers who help to rear the offspring of queens, caste system, division of labor, and communication—not to mention cooperation, altruism, and suicide—have unmistakable parallels with the achievements and predicaments of our own social lives. But evolutionary biologists have an important additional reason to be intrigued and fascinated by insect societies. The origin and persistence of the sterile worker caste is a major evolutionary puzzle, in many ways more puzzling than the evolution of the honey bee queen, capable of laying thousands of eggs per day, or the honey bee worker, capable of building perfectly hexagonal cells in a comb of wax during the first half of her life and estimating and communicating the distance and direction to newly discovered food sources by means of a symbolic dance language during the second half of her life. It is also more puzzling than the invention of agriculture through the cultivation of fungus gardens by leaf cutter ants 50 million years ago or the colonial organization of African army ants with more than 20 million workers weighing a total of more than 20 kg per colony. The reason for this is that sterility and self-sacrifice are the last things we expect natural selection to promote. Not surprisingly, the evolution of a worker caste is the quintessential problem of the evolution of sociality.

This problem can be approached in many different ways. At one extreme it can be approached as an abstract problem of how non-reproducing or more slowly reproducing units (e.g., cells, animals, or even robots) can increase in population relative to fertile or faster-reproducing entities. This approach was made possible due to W. D. Hamilton's inclusive fitness theory and requires mathematical skills and a deep understanding of population genetic principles.

It does not necessarily require familiarity with the biology of any particular group of social insects. (That W. D. Hamilton was a naturalist *par excellence* is another matter, however!) At the other extreme it can be approached by inquiring into the specific circumstances and historical sequence of events in the evolution of the worker caste in a particular evolutionary lineage. Although researchers have attempted to occupy all possible niches along this continuum, niches relatively close to the former extreme are better populated than those closer to the latter extreme. The closest anyone has gotten to the latter extreme is the author of the present book. Hunt's chosen group is the lineage of social wasps belonging to the family Vespidae, and what a wonderful choice it is.

If paleontologists trace evolutionary trajectories by holding a magnifying glass to rocks through real time (albeit in millions of years), Hunt's brand of evolutionary biology entails a microscopic examination of every aspect of the biology of all salient extant taxa. This is much harder work for at least two reasons. First, one has to cut-across disciplinary and taxonomic boundaries and understand and synthesize vast amounts of information about every taxon. Second, there is no help from carbon dating, so one has to do considerable detective work to sequence and date evolutionary events. Our knowledge of social wasps, let alone of other social insects, is extraordinarily sparse relative to what is needed for a satisfactory practice of this enterprise. Where information is inadequate, Hunt speculates, and where he feels that the current wisdom is at apparent loggerheads with known facts, he proposes radically new interpretations.

Perhaps Hunt's two most controversial points concern identification of the extant wasp taxon that can be considered to most closely resemble the solitary ancestor of social wasps and the number of times sociality has arisen independently in the family Vespidae. Here and elsewhere, Hunt's speculations and interpretations are bound to provoke, even anger, custodians of current wisdom, but because he provides powerful arguments for why current knowledge is inadequate to settle these questions, they are also sure to lead to more investigations and better understanding of wasp biology and phylogeny. But the single most important point of Hunt's synthesis is to argue that the life cycle of a social wasp such as *Polistes* is based on the underlying reproductive ground plan of a partially bivoltine solitary wasp. This argument, if true, suggests the need for altogether new lines of investigation at the morphological, physiological, and genomic levels and thus brings the hitherto esoteric field of social evolution in wasps to the doorsteps of diverse disciplines of modern biology. This is no mean achievement indeed.

Hunt offers us much more than a new perspective on and a new synthesis of our current understanding of the evolution of social wasps. He ends the book with a scathing attack on kin selection; inclusive fitness theory; sex ratio theory; behavioral ecology; the use of potentially loaded terms such as selfishness, altruism, worker policing, and even eusociality; and he questions the very validity of asking "why" questions in evolutionary biology. I expect that while, on the one hand, this will attract much attention among historians and philosophers of

science, it will also make most members of the criticized camps at first see red, then get defensive, and finally do much soul searching. Having taught behavioral ecology for more than 20 years, made inclusive fitness theory the center-stage of my life's research, and written one book on "why" questions in animal behavior and another book on the evolution of eusociality, I cannot now deny that I belong to the camp that Hunt so penetratingly strikes. All I can say after reading the book is that I could not have asked for a more competent "adversary!"

Raghavendra Gadagkar
Centre for Ecological Sciences,
Indian Institute of Science, Bangalore
National Academy of Sciences, USA