Encyclopedia of Social Insects

Christopher K. Starr
Editor

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With 491 Figures and 26 Tables

INTERNATIONAL UNION FOR IUSSI THE STUDY OF SOCIAL INSECTS

Springer

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Cover illustration: After a heavy rain, a *Synoeca cyanea* worker removes water from the nest envelope. Photo © Alex Wild.

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Foreword

The Biblical proverb, *Go to the ant, thou sluggard; consider her ways, and be wise*, epitomizes human attitude toward social insects throughout much of history. The societies of insects have inspired us to draw lessons, issue injunctions, influence politics, and formulate moral principles. And yet, much of this has been based on partially correct, incorrect, and sometimes dead-wrong ideas about the biology of social insects.

A particularly embarrassing example concerns the uncritical assumption, held by almost everyone until as recently as early eighteenth century, that the queen of the honey bee colony must be a king, and, to make matters worse, the use of that mistaken identity to deprive women of a place in public and political life. The "leader of the beehive" is neither a male nor indeed a leader, in almost any sense of the term. Most complex behavior in social insects is self-organized in a decentralized, bottom-up manner, with little scope or evidence of top-down control. The metaphoric transfer of power from the males to the females and from the royalty to the subjects is the result of two centuries of the scientific study of insect societies presented in this encyclopedia.

Social insects – ants, bees, wasps, termites, and a few aphids, thrips, and beetles – account for about 2% of the approximately one million species of insects described so far. Despite this modest taxonomic representation, social insects, especially ants and termites, are among the most evolutionarily successful and ecologically dominant species on earth, estimated to comprise up to three quarters of the total animal biomass in some tropical forests. They are found in virtually all land habitats worldwide where insects abound.

The Earth is estimated to harbor some 10 trillion ants that together weigh about as much as all 7.4 billion humans. The success of social insects is attributed to their ability to cooperate and form large colonies, with division of labor, 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. With few exceptions, members of a colony are not a clone, but they have nevertheless evolved elaborate mechanisms for conflict management.

One important reason for our interest in social insects is that we depend on some of them for our welfare. A third of our agriculture and food production, especially fruits, vegetables, and nuts, crucially depends on the pollination services rendered by honey bees and bumble bees (as well as many solitary

bees), the global economic value of which has been estimated at US$577 billion annually. In recent decades, bee populations have declined worldwide and therefore their services have been under great threat, endangering our food security and global peace, ironically caused by over-exploitation and mismanagement.

The blame for the havoc caused by importing the *Varroa destructor* mite to regions of the world where honey bees are not adapted to co-exist with it, and more generally for the so-called Colony Collapse Disorder, can be laid straight at our doorstep. We have unsuccessfully attempted to make honey bees live life in the fast lane, under crowded conditions, with frequent transportation over thousands of kilometers, exposed to multiple pesticides, faced with diminished diversity and abundance of nectar and pollen-producing plants, and forced to invest more in honey production than in colony maintenance and reproduction. We erroneously believe that we know best how honey bees should organize their lives and have only recently begun to understand how millions of years of evolution have shaped their sustainable lifestyles in the wild. It is time we learn from the bees rather than attempt to teach them. This will need learning much more than we know already and, more importantly, disseminating the little knowledge that we already have as widely as possible.

We are also interested in social insects because we fear them. Leafcutter ants have been important to the economy of Latin America since historical times to the present, being the most important herbivores in the region, devastating more vegetation than any other animals and causing destruction worth billions of dollars. The battle between humans and leafcutter ants is a unique one – the ants steal the products of our agriculture not just to feed on them but to use as raw material to sustain their own agriculture – making them the kind of enemies that demand our respect and admiration. Leafcutter ants have been practicing the cultivation of fungi in their gardens for over 50 million years. The secrets of their success in achieving sustainable agriculture, some of them worthy of emulation, are only now being discovered.

The fire ant *Solenopsis invicta*, innocuous in its native South America, has become famously invasive in Southeastern United States, Australia, China, and Taiwan. It is a major health hazard in the USA requiring the expenditure of over $5 billion annually toward damage control, suppression, and medical treatment. In a failed attempt to breed a honey bee that combines the industriousness of the African bees with the gentleness of the European bees, scientists inadvertently produced and released, and/or let escape, a hybrid that is highly defensive toward humans and native bees. This hybrid bee spread through South and Central America in the 1990s at a rate of 300–500 km/year, reaching densities of 6 colonies per km that translate to about a trillion bees. Some termites are another kind of serious social insect pest, damaging buildings, wooden structures, and crops and requiring billions of dollars in expenditures, while also bringing about significant environmental pollution on account of the chemicals used to control them.

Beyond the love-hate relationship, most of us will admit to a sense of wonder and amazement at what our objects of study are capable of. Ant, bee, and wasp queens gather sperm from their mates, store and nourish them in their bodies for years and even decades, and then use them to make

daughters, or not use them, to make sons, giving them complete control over the sex of their offspring. The pheromone trails of ants guide them to distant locations of food and back to their nests.

When ants lacking trail pheromones have to relocate their nests, some of them spontaneously emerge as leaders carrying or tandem-running their nestmates to the new nest site. When ants, bees, and wasps walk or fly out in meandering paths, they continuously update information about their linear and angular displacement using the sun and other celestial cues, polarized light, and landmarks, after which they can walk or fly straight back to their nests.

Honey bees go a step further and communicate the distance and direction to food sources by means of a dance language, the discovery of which brought a Nobel Prize to social insect research. Honey bees also make the ultimate altruistic sacrifice in defense of their colonies – because they are unable to withdraw their barbed stings when attacking humans or other vertebrates, so that their abdomens rupture, fatally. The Argentine ant *Linepithema humile* forms supercolonies with billions of workers spread over 6000 km of coastline from Italy to Spain.

In addition to immune defenses of individual members of their colonies, social insects have a whole tool-kit of social immunity. The most remarkable feature may be the fine balance they achieve between their first line of defense – maintaining nest hygiene to prevent the spread of infection – and a final line of defense by killing and removing infected members.

Social insects have been at the forefront of the development of evolutionary theory. Charles Darwin worried about the "neuters" (i.e., workers) as a potential "insuperable difficulty" for his theory of evolution by natural selection. He proposed a way around it that is the forerunner of the modern theory of group selection. JBS Haldane, while contemplating how many brothers would he have to save from drowning in order to make it worthwhile to sacrifice his life, quickly turned his attention to honey bees and realized they might be more prone to sacrificial behavior.

William D. Hamilton drew inspiration from social insects, especially the social wasps that he observed in Brazil, to develop his theory of inclusive fitness, also known as kin selection. Recent controversies regarding the relative roles of individual, kin, and group selection have led to the development of multilevel selection theory. Because the evolution of altruism by natural selection remains a major unsolved paradox, social insects are still in the front lines of the elaboration of evolutionary theories, their controversies and their resolution, and will thereby throw much light on the rest of the living world.

Complex social behavior, including communication, transport, and the mind-boggling nest architecture so characteristic of many social insects, result not from superior conventional intelligence of individual members of their societies but through a process of decentralized self-organization – individual insects follow simple local rules that nevertheless result in the emergence of complexity. This knowledge has most surprisingly impacted science and technology well outside the social insect world and indeed outside biology.

The development and application of ant, bee, wasp, and termite-inspired procedures and algorithms in computer science, transportation,

telecommunications, the Internet, and robotics has been an unforeseen consequence of curiosity-driven research on social insects and their ways of solving their own day-to-day problems. To take another example, ant and honey bee queens can provide new insights for the study of ageing and senescence. While ant and honey bee workers have a natural life span in the order of a few weeks, their queens, who develop from the same genomes, can live for years and sometimes for decades. Even among honey bee workers, summer bees age faster than winter bees and forager bees faster than nurse bees. Their long and flexible life spans make social insects attractive and as yet poorly explored model systems for understanding the nutritional, physiological, and molecular modulation of ageing and senescence.

Social insect science is poised to make even greater contributions to the growth of knowledge and technology in many different areas of human activity. To facilitate this, we need to provide easy access to our growing understanding of the world of insect societies to a wide audience who may never care to call themselves biologists, let alone entomologists. The *Encyclopedia of Social Insects* is designed to fill this very need. In a decentralized, self-organized manner, befitting the insect societies, the International Union for the Study of Social Insects (IUSSI) has undertaken as a community project the production of this compendium of our current knowledge about social insects, as well as social spiders, the result of which you now have before you. Perhaps it's time to rephrase the Biblical proverb and say: *Go to the Encyclopedia of Social Insects, thou curious one; consider its contents, and be enlightened.*

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Raghavendra Gadagkar

Preface

Scientific societies in our time largely restrict their activities to organizing conferences and publishing journals. The International Union for the Study of Social Insects (IUSSI) does all of this, but in addition we have produced this comprehensive reference work on our subject. It is intended to treat the full breadth of the scientific study of social insects and arachnids, from the molecular to the ecosystem level and is unrivaled by anything now available in any language.

The book before you is designed to serve as a very accessible yet authoritative reference work on the biology and systematics of the subject. This is the first general treatise on this broad field since those of Edward O. Wilson in 1971 and Henry R. Hermann (ed.) in 1979–1982. The entries are in alphabetic order according to taxon (e.g., stingless bees) or concept (e.g., kin recognition). There are no biographical entries, but some identify major contributors to the topic.

In the spirit of Diderot & D'Alembert's encyclopedia of the Enlightenment period, it is hoped that this reference work will not only summarize present knowledge but will also draw sharp attention to areas of ignorance and growing points that can be expected to yield major discoveries in the coming period. In this way it will serve to shape our discipline by giving direction to younger researchers at the same time as it informs the broader mass of the curious what we think we already know.

The encyclopedia is produced in three formats: dynamic (Living Reference), print, and e-book (static) editions. The print edition and (static) e-book have the same content. The Living e-book version allows for changes over time, including updating of entries and the inclusion of new entries not present in the print and static e-book edition. Both make provision for abundant cross-referencing among entries.

This is a true community project, reflective of the IUSSI as a whole. The more than 200 authors are drawn from 29 countries in all regions of the world where insects abound.

To my immense gratitude, the project has been guided throughout by an Advisory Panel of 23 experts whose collective expertise embraces the discipline as a whole:

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A note about the references. While the individual entries resemble review articles in scope and focus (although much shorter), the references at the end of each are mainly intended to direct motivated readers to further reading. They are seldom included just in order to indicate the source of particular findings or to support statements. This restriction has its drawbacks, to be sure, but it was taken in order to keep the focus on sources to deepen the reader's understanding of the topic.

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Christopher K. Starr
Editor

About the Editor

Christopher K. Starr was born in 1949 and educated in Canada, the USA, and Germany. He has lived and worked in Canada, the USA, the Philippines, Taiwan, and Trinidad & Tobago. Depending on how you look at it, this could mean either that (a) he has a rich and varied background or (b) he can't hold down a job. His introduction to insects came rather sharply one day in 1954 when his grandmother asked "Christopher, would thee like to go bug collecting?" He said yes and has never turned back. In 1972 – just in time to appreciate Edward O. Wilson's *The Insect Societies* (1971) – he reached the unshakable view of social insects as the most interesting aspect of the universe. His main focus since then has been social wasps, but he is one of very few scientists to have published original biological observations on all four major groups of social insects. After retiring as Professor of Entomology at the University of the West Indies, he continues to live and work in tropical Trinidad & Tobago. It is noteworthy that these tiny islands harbor 38 species of native social wasps, while all of Canada, with 2000 times the land area, has half that many. Besides, in his early years he was exposed to a lifetime's worth of snow, something he hopes never again to experience.

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