BOOKS & ARTS

Colonies that conquer

A landmark book documents how social insects form highly successful colonies that mimic a single organism, explains Manfred Milinski.

The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies
by Bert Hölldobler and E. O. Wilson
W. W. Norton: 2008. 576 pp.
$55.00, £30.00

Being just one cell, a bacterium has to be a jack-of-all-trades. By contrast, multicellular organisms, such as humans, profit from a division of labour between their specialized organs. The digestive, immune, circulatory and other systems all cooperate to help the gonads to maximize the reproductive success of that organism in competition with other organisms. Would a village of human inhabitants, in competition with other villages, profit similarly if its foragers, defenders and communicators volunteered to help the reproducers maximize their reproductive success? Certainly not. But many social insects do just this, as Bert Hölldobler and Edward Wilson beautifully portray in their new masterpiece *The Superorganism*.

Darwin200

A scientist from another planet would describe the most widespread, highly social form on Earth as having six legs, two antennae and three body parts, living in groups of up to 20 million members. Ants, bees and termites have evolved into superorganisms — colonies with a strict division of labour, in which one or a few individuals reproduce while many nonbreeding workers with various specializations carry out tasks altruistically.

Eighteen years after their Pulitzer prize-winning book *The Ants*, the authors have put together a wealth of new research to present the rich and diverse natural history facts that define a superorganism's traits — the colony as a self-organized entity and a subject of natural selection.

Most of us are familiar with the colony life of honeybees. One female, the queen, is the mother of all offspring, including her 'busy as a bee' worker daughters who build, clean and guard the nest, feeding the larvae to raise many sisters and brothers in competition with other colonies. Worker bees all look alike, each practising all professions sequentially, except reproduction. Many ants, however, have castes of workers with different morphologies; one example is the worldwide ant genus *Pheidole*, with its unusually large-headed soldiers and many minor workers.

Cooperation in colonies can be very sophisticated. The aerial pavilions of the weaver ant *Oecophylla* are constructed of leaves bound together by silk. One group of workers cooperates to pull the edges of the leaves together. Another group brings out large, larval sisters and wags them bodily back and forth across the newly created seams. With each sweep, the larvae emit sticky threads of silk over the seams to hold the leaves in place. Hölldobler and Wilson present numerous further fantastic examples.

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Royal servants: the queen bee (centre) produces offspring while her worker daughters do the rest.

The evolution of this division of labour is a fascinating topic. All colony members have the same genotype for caste formation, but in response to environmental conditions, these genes turn growth on and off specifically towards one caste or another. That which is needed is produced, dictated by colony economy.

Why are insect workers so altruistic that they give up their own reproduction to help others to reproduce? Natural selection favours traits that help their possessor to have more offspring. Thus, organisms that help others at the expense of their own offspring are difficult to explain. Why should the brain cells of an organism help her gonads to produce offspring? Simply, because the genes of brain cells and gonad cells are identical — there is no conflict of interest among cells of an organism about which cells should reproduce. Any division of labour that boosts reproductive success should evolve. Human inhabitants of a village, however, differ in their genes and would not agree on who should reproduce and who should raise the reproducers' offspring.

Colonies of social insects are similar to the cells of an organism; they start as a family. Being altruistic has low costs because helping the mother to produce more siblings is genetically equivalent to producing one's own offspring. The former strategy can be more efficient through division of labour. The basic


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Seamless cooperation between weaver-ant workers allows them to build elegant aerial nests using leaves.

idea that altruism towards kin should evolve goes back to the founding fathers of population genetics, Ronald Fisher and J. B. S. Haldane. They proposed that altruism is more likely to evolve the more the helper and helped are related, and the more efficient that help is. William D. Hamilton's seminal work on inclusive fitness theory made the idea explicit.

Most superorganisms are found among the Hymenoptera, or bees and ants. Owing to their special sex-determining mechanism, females develop from fertilized eggs and males from unfertilized eggs. Because their father has only one set of chromosomes, the sisters are 75% related to each other instead of the usual 50%. Sisters are less related both to their brothers (25%) and to their own offspring (50%), if they had any. This explains why, in all hymenopteran colonies, workers are the daughters and never the sons of the queen. This high relatedness among sisters is, as Hölldobler and Wilson point out, not a necessary but a helpful prerequisite for crossing the so-called eusociality threshold, when a worker propagates more of her own genes through related sisters by staying in the colony and helping than by trying on her own. Termites and even one mammal, the naked mole-rat, have become superorganisms despite their normal mode of reproduction. Maximizing efficiency through division of labour is of key importance besides relatedness. Thus, organized groups beat solitary individuals in competition for resources, and large groups beat smaller ones of the same species. After the point of no return — when an anatomically distinct worker caste exists — a lower level of within-colony relatedness can be tolerated, as long as this is higher than the level of relatedness between colonies.

Hölldobler and Wilson present a thorough account of the selective forces that led to the evolutionary construction of superorganisms. They favour 'multilevel selection', a combination of within-colony selection on individuals helping their relatives and between-colony selection, so-called group selection. Colonies compete and the best adapted win. The logic of group selection — groups with altruists are more productive than those without — is compelling. However, the conditions that allow altruists to survive within large groups are still annoyingly demanding. The trick of superorganisms may be that altruists benefit anyway through efficient sister production. Recently, a fierce debate has started among theorists, questioning whether inclusive fitness models can easily incorporate all mathematical intricacies of multilevel selection. Whatever the solution might be, superorganisms certainly have it.

Communication is highly evolved in superorganisms. Besides the celebrated dance language of honeybees, ants have become the insect geniuses of chemical communication with numerous pheromones. This and many other fascinating topics — such as the combined phylogenetic and ecological explanation for the immense diversity of ants, or the beauty and functionality of ant nest architecture — are presented in depth, but always in a lucid, entertaining language combined with magnificent line drawings and photographs. My favourite chapter highlights the leafcutter ants, "Earth's ultimate superorganisms". As well as having the most complex communication system known in animals, they have the most elaborate caste systems, build air-conditioned nests, and made the transition from a hunter-gatherer existence to agriculture — by growing their fungal food source in their nests using elaborate techniques — long before humans did.

This monograph is a state-of-the-art review of the organization and evolution of social insect societies. Detailed references on almost every page help to track information back to its roots. This book will fascinate everybody interested in biology, social sciences, economy or simply natural history. ■

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