

## Primer

# Eusociality

David C. Queller<sup>1</sup> and Joan E. Strassmann

Most biologists devote their research careers to working out the intricacies of how their favorite organism functions, how it processes energy, transmits information from one place to another, regulates metabolites, gets rid of waste, builds itself, defends itself and reproduces itself. If one wants to step back and consider what it means to be an organism, it is obviously necessary to broaden one's scope and to consider the full range of organisms. But an even broader strategy is to consider entities that have organismal properties but are outside the realm of standard organisms. Man-made artifacts have long been mined for fruitful analogies about particular organisms and functions. Computer viruses and artificial life programs also capture some important similarities. But perhaps the best we can do in this area is to study eusocial colonies.

Eusociality is a term coined to cover ants, bees, wasps, and termites that have three properties: overlap of generations, cooperative rearing of young and non-reproducing worker castes. Other organisms that have these traits have since been added: some aphids and thrips, a beetle, some snapping shrimp and the naked mole rat. In eusocial species, non-reproductive workers care for the young of the reproductive queens (and sometimes kings). As such, workers are analogous to the somatic cells of an organism, which work for the transmission of their genes by proxy, via the germ line cells. Like the cells of an organism, the members of a eusocial colony have evolved elaborate mechanisms to enhance the survival and reproduction of the larger unit. The colony consisting of one or more queens and workers has been called a superorganism,

essentially a new kind of organism built up of organisms of the old kind.

Consider the famous honeybee waggle dance. This dance, performed by returning foragers, tells other workers the direction and distance of rich food sources. The colony benefits by exploiting the hard-won knowledge of those foragers that find food bonanzas. The dance is celebrated as a rare example of symbolic communication between individual organisms, but it can also be viewed as a part of a signaling cascade of the larger superorganism that regulates work according to the supply and demand. If the supply of food is great, there will be more waggle dancers stimulating more foraging to harvest it. But that is not the only adjustment necessary. Foragers, with their knowledge of valuable food sources, do not waste time processing the food, but hand it off to another set of bees inside the hive. If a forager has trouble finding a processor bee, she begins a different dance, the tremble dance, which both activates bees to become processors and inhibits waggle dancing. The result is a negative feedback system that allocates workers to foraging and processing tasks according to need (Figure 1). Additional links in the system include the needs of the brood and the degree to which storage capacity is filled. Such regulatory feedback systems operate in nearly every aspect of social insect colony functioning, just as they do in other organisms.

Besides the clear similarities between organisms and superorganismal colonies, there are some differences that show us that entities with organism-like functionality and integration can operate in unfamiliar ways. For example, the cells of organisms terminally differentiate into numerous specialized types, while social insect colonies have at most only a few terminally differentiated castes. Instead, much of the division of labor is carried out by means of a temporal specialization, often with the youngest adults tending the brood, older ones carrying out other activities in the

nest, and the oldest ones foraging outside the nest. Just as cells are more fixed in function, so are they more fixed in space. Social insects, in contrast, are not physically connected, and their colonies give us examples of organismal entities that are dispersed in space. A final important difference is the lack of centralized control in social insect colonies. Despite the controlling image conveyed by use of the term "queen", there is nothing like a colonial brain. No individual perceives the state of the entire colony and sends out instructions. Instead, actions are usually self organized by simple rules. Different individuals each have small pieces of information, which are integrated by the colony as a whole. A returning forager doesn't know how many foragers and processors are at work. Instead, she just experiences an indirect effect of those numbers — the time required to offload her nectar or pollen — and acts accordingly.

Despite these differences, the key defining similarity remains; colonies are like organisms, but unlike anything in the non-biological world, with respect to their degree of integration and cooperation for the good of the whole. The key question then is an evolutionary one. How did this organismal degree of cooperation evolve, given that the Darwinian norm is closer to a struggle of all against all? This is a question that doesn't trouble us much for most multicellular organisms. Genes in a macrophage can easily be selected to cause their cells to specialize on non-reproductive tasks, because they are the same genes that will be transmitted through the germ line. This is ensured by clonal descent from a single-celled zygote. William D. Hamilton showed that the same kind of explanation applies to eusocial insects, but in a less absolute way. Members of social insect colonies are relatives, sometimes just a single queen and her progeny. Therefore, though they are not clonal, they do share a large fraction of their genes. A gene causing self sacrifice can thus be favored by selection if it aids relatives who might bear copies of the gene, but the aid has to be large enough to

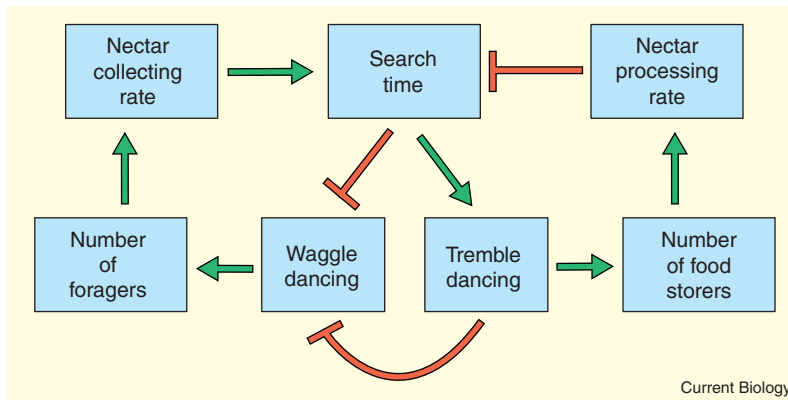


Figure 1. Regulatory network controlling allocation of honeybee workers to nectar gathering outside the hive and nectar processing within the hive. After Figure 6.14 of Seeley (1995).

compensate for the chance that the aided relative does not carry a copy of the gene. So honeybee workers can gain by stinging large vertebrate intruders, because they may save their whole colony full of relatives who pass on the genes for stinging. They have even evolved barbs on their stingers that increase the effectiveness of stinging by anchoring tightly in the victim, even though it also disembowels and kills the worker.

This selection via effects on relatives, known as kin selection, is quantified in Hamilton's rule, the simplest version of which is  $c < b \cdot r$ . The fitness cost for the altruist ( $c$ ) must be less than the fitness benefit to its relative ( $b$ ), multiplied by the relatedness ( $r$ ). In diploid species, the relatedness is 1/2 to mothers, fathers, children, and full siblings; it is 1/4 to half siblings, uncles, aunts, nephews and nieces, and so on. Hamilton also noticed that these relatedness values do not all apply to the ants, bees, and wasps. These taxa are members of the order Hymenoptera, which has a haplodiploid genetic system. Males develop from unfertilized eggs and are therefore haploid. Males bequeath their genes only to daughters, but they bequeath all of them, the usual halving due to meiosis being absent. As a result, the daughters are related among themselves by 3/4. So, Hamilton reasoned, a female could pass on more of her genes by trading her own offspring, related by 1/2, for the more related sisters. This seemed to explain why eusociality

had evolved over a dozen times in the Hymenoptera as against once or twice in the diploid termites, and also why workers are only female in the Hymenoptera, but both sexes in the termites.

This elegant hypothesis dominated discussions of the evolution of eusociality for many years, but has been weakened by further analysis. Once models incorporated all the details of reproductive value, sex ratios, and especially the fact that a female's high relatedness to sisters is countered by an unusually low relatedness to brothers, it became evident that any haplodiploid relatedness effect was not only smaller than had been thought, but transitory. Even though Hamilton's specific haplodiploid hypothesis has been weakened, his general theory of kin selection remains central to the understanding of the origin of eusociality. However, the focus has shifted from kin selection driven by unusually high relatedness to kin selection with normal relatedness, but driven by unusually high benefits to relatives. Specifically, if relatedness to one's mother's offspring is no higher than relatedness to one's own offspring, then a potential worker should help only if, for some reason, she can do more for her mother's offspring than for her own.

Perhaps the two most important classes of benefits to helping are those called fortress defense and life insurance. Fortress defenders are eusocial species that live and feed inside a protected area. As long as there is space for

expansion in this area, it may be better to stay at home and help than to take the risks of dispersing to find a new home. Fortress defenders would include aphids and thrips that live in plant galls, termites that inhabit wood, the social shrimp that live in sponges, and the naked mole rats in their extensive subterranean tunnel systems. In contrast, life insurers, which may include most ants, bees, and wasps, forage outside their nest to bring food back to their helpless young. This is a difficult lifestyle to follow as a solitary individual, because foraging entails risks of predation, and the death of the adult means the death of all her dependent young. It works much better when groups of adults share the risk; if one dies, her investments in young are not wasted because the surviving adults can carry on.

Despite the organismal quality of eusocial colonies, there are limits to cooperation. If the worker honeybee's use of her sting wins prizes for altruism, the young honeybee queen puts her sting to a strikingly different use. Honeybee colonies reproduce by splitting. The old queen departs with the majority of the worker force (Figure 2), leaving the remaining workers to await the emergence of several new queens, who have been developing in specially prepared cells. If the worker force is still quite large, the first new queen to emerge may also leave with some of them to start another colony. If, however, the worker force is smaller, the new queen stays and battles to the death with her sister queens for the right to set up housekeeping in the old colony. This too makes sense within the calculus of kin selection. If there are only enough workers to support one queen, then any queen that gets rid of her rivals will pass on more genes. The queens are related, which can limit selfishness, but only up to a point. If a queen's choice comes down to her own reproduction versus an equal amount of reproduction by her sister, who is related by 1/4, she will obviously pass on more genes if she can kill her sister.

How eusocial insects deal with conflict has been a major focus of

research in recent years. The fighting honey bee queens provide clues to both the cause of conflict and its control. The greatest potential source of conflict is the question of who gets to reproduce. Even though kin selected benefits can select for individuals helping rather than reproducing alone, it is better still to be the one being helped. The control of honeybee fighting is less visible, as you see it not in the fights observed, but rather in the peace that usually prevails. The fights are deadly but rare, because the number of new queens is limited to a few individuals at the time when they are needed. Queens are raised in special, large cells, and receive special food. Thus, the vast majority of females are forced to become workers and are morphologically unprepared to contest for the queen role. Nutritional control is at the root of queen-worker differentiation in most social insects.

What if this control was lacking? There are two natural 'experiments' that reveal the answer. The first comes from so-called primitively eusocial insects, like *Polistes* paper wasps. These have never evolved morphologically distinct queen-worker castes and in this respect presumably resemble a eusocial line early in its evolution. In a *Polistes* colony, there is still a dominant egg layer or queen, but her position is held by force or threat of force. Subordinate wasps challenge her, and if the queen weakens, the next wasp in the hierarchy supplants her.

The second natural experiment comes from the stingless bee genus *Melipona*, which belongs to the same family as honeybees. Here, queens and workers develop in sealed cells, on essentially equal provisions. They are, therefore, about the same size, but they have different proportions, with workers being larger at the work end of the body – the head and thorax – and queens larger at the reproduction end, the abdomen. Because feeding does not control caste choice, each developing female gets to decide on her own fate. As in honeybees, a new *Melipona* queen is needed only once in a

while, when the old queen dies or when the colony divides in two. The sensible strategy for the colony is the one followed by honeybees: produce just a queen or two at those times. But in a *Melipona* colony, about 20% of all females develop into queens. Nearly all of them fail to reproduce, but for each it is worth the risk for the small chance at the very high reproductive payoff of heading a colony. For other colony members, however, each excess queen is just a useless tax on colony resources, and so the workers kill them in order to minimize the losses.

Thus, physical control is employed in both cases that lack nutritional control. However, there is an important difference: In the small *Polistes* colonies, usually comprising no more than a few dozen individuals, the queen keeps her subordinates in line. This would be difficult in the larger colonies of *Melipona*, which can have many thousands of individuals; in this case it is the workers as a group that take charge of killing the excess queens. Likewise it is generally the workers who control food in species in which nutrition determines caste. This echoes the conclusion that we reached earlier about the regulation of task performance being accomplished only by the actions of numerous individuals, rather than by centralized control. Reproduction may be centralized in the queen, but in large colonies the control of who reproduces is exerted largely by the worker collective.

One might argue that these conflicts give lie to the assertion that eusocial colonies are organismal. After all, one neither expects nor observes such conflicts among the cells of a multicellular organism, because they are all clonal descendants of the zygote. But the study of cooperation and conflict in social insects has taught us that we can sometimes expect conflict in organisms. For example, there are organisms whose cells are not always clonal. In cellular slime molds such as *Dictyostelium discoideum*, multicellular fruiting bodies are formed by aggregation of starving cells, sometimes from different clones. This species



Figure 2.

A swarm of honeybees en route to founding a new colony. The old queen goes with the swarm, leaving young queens to fight over the old colony. Photo courtesy of Thomas D. Seeley.

shows both kin selected cooperation — formation of a sterile stalk to help the spores disperse — and cheating among different clones. Second, standard organisms have other conflicts, not between their cells, but between genes. For example, meiotic drive genes gain excess representation in gametes while imposing a cost on the organism as a whole. Organellar genes that pass through eggs but not sperm can bias sex ratios toward daughters, or sabotage male function in hermaphrodites. Transposons and other kinds of junk DNA can spread even if they are disadvantageous to the organism. Thus, eusocial insects have helped teach us that organismal cooperation is not a given, that it required the evolution of ways to control reproductive conflict, and that such control remains imperfect in all organisms.

#### Further reading

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<sup>1</sup>Department of Ecology and Evolutionary Biology MS-170, Rice University, P.O. Box 1892, Houston Texas 77005-1892, USA. E-mail: queller@rice.edu