Social insects-All for one, and one for all

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Honey bees (Apis mellifera) have long been kept domestic for the honey. One bee cannot collect enough nectar to be in any interest by humans, but honey bees are not solitary. They live in colonies made up by thousands of individuals and perform a life strategy of highly advanced social structures which is called eusociality (box 1). In a bee hive the reproduction is limited to one or a few individuals in the nest while the rest of the colony, the workers, concentrates on taking care of the young, foraging for pollen and nectar as well as maintenance of the hive. The evolution of social insects troubled Darwin and the topic is still under debate. According to Darwin's idea of natural selection evolution should act upon individuals, where those well adapted to their environment would enjoy the greatest reproductive success. How come then, that individuals have given up their own reproduction to someone else's favor?

Cooperation-the key to success

All ants (Formicidae) and some species within wasps (Vaspoidea) and bees (Apoidea) are social insects belonging to the order Hymenoptera. Their colonies are made up of "castes", individuals with different tasks. The queen is the reproductive female caste. She mate only once and store the sperm in a special pocket within her body, which is called "spermateca". The queen can live to the respectable age of fifteen years in some ant species and the stored sperm is enough to fertilize the up to million eggs, which she will produce during her lifetime. Ants, wasps and bees have a sex determination system that turns all fertilized eggs into females and all non-fertilized eggs into males. As the males have no purpose after they mated with the queen, all the members in the colony are females made up from fertilized eggs. In the nest they take care of the brood, forage and defend the colony.

In order to perform all of these different tasks at the right time and at the right place, the members of the colony use a complex communication system. A honey bee forager who has found a good source of pollen and nectar displays a specific dance back in the nest, to get the attention from other foragers. A buzz with the wings at a certain frequency informs about the distance to the location and when the group head out to find it they follow the odor marks placed there by the forager who found it.

Box 1.

Eusociality is a highly advanced level of sociality, which is defined by the following criteria:

1. Several individuals sharing a nest.
2. Overlapping generations.
3. Members of the nest cooperate in taking care of the brood and the nest.
4. Reproduction is limited to a few individuals.

The theories diverge

The evolution of social insects has been under debate for several decades. Hamilton came up with a theory in 1964 of how unselfish behavior could be selected for, due to relationship. According to natural selection we expect individuals to fight for their own survival and reproduction so that their genes could carry on to the next generation. Frequently, in an ant's nest all of the members are sisters, daughters to the queen. Because of the sex determination system in these insects, full sisters get more related to each other. Humans got a double set of genes, one set from each parent. In ants, wasps and bees on the other hand the males only have one set of genes, because they only have one parent, their mother. As a male only have one set of genes to give their offspring, all of his daughters will most certainly have the same genes from him. These circumstances makes ant's sisters more related to each other than human sisters. Based on these facts Hamilton suggested that the cost of giving up reproduction could be overcome by the benefit of rearing sisters with whom they share more of their genes than they do with their own offspring. This is called the kin selection theory.

Recently, another theory has gained impact. The group selection theory, or multilevel selection, states that evolution can act upon groups as well as individuals. If insects tend to live in groups, then the groups containing most cooperative individuals should earn higher chances of survival and thus greater reproductive success. Unselfish behavior could therefore be selected for on a group level rather than an individual level. In this theory the high relatedness among social insects is rather a cause than a consequence. Siblings who stayed in the nest where they were born, specializing on different tasks such as reproduction or foraging, could enjoy higher survival rates.

Task specific appearances and behavior

The division of labor within the nest has led to different appearances, morphologies, in order to optimize an individual's specialization. In all social Hymenopterans you could tell a difference between a queen and a worker. The first is distinctly larger in size and have a well-developed oviduct and reproductive system. Ants also have differences in size and shape between workers (figure 1). The soldiers whose purpose is to protect the nest are large with disproportionately large heads to plug the entrances of the nest. The minor workers are often very small compared to the queen and soldier. Their main task is to take care of the brood and forage outside the nest.
In wasps and bees though, the division of tasks between workers are not to be revealed by appearance, but by behavior due to changes in endocrinology and gene expression. The young workers in a honey bee colony tend to stay in the hive as "nurses", taking care of the offspring, while older workers leave the hive to forage for pollen and nectar. This change in behavior is preceded by changes in hormonal activity. Juvenile hormone (JH) is found in all insects, but its function differs to some extent. In honey bees a low level of JH is correlated with nursing behaviors. As the bee gets older the JH level rises and initiates another kind of behavior, the foraging behavior.

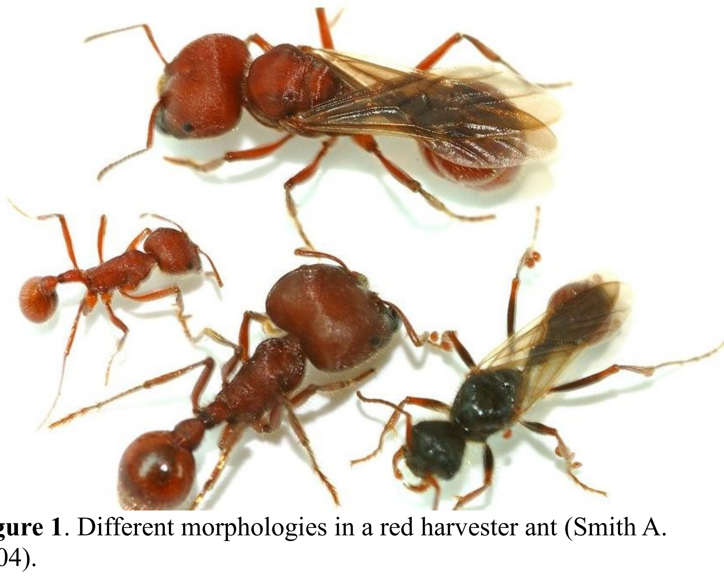

Figure 1. Different morphologies in a red harvester ant (Smith A. 2004).

Genetically or environmentally mediated influences?

The origin of separate castes is puzzling. How come that some eggs turn out to be queen larva, major worker larva or minor worker larva? It has long been thought that all larvae of social Hymenopterans had the possibility to develop into any caste and that their fate was determined by environmental factors such as food quality or quantity. In some species this is actually the case. In honey bees for example, the caste fate is socially regulated by the nurses in the hive. They feed the larvae different kinds of food depending on what caste they want the larva to have. The queen larvae are fed a nutritious mixture called “queen jelly” while worker larvae get “worker jelly”. In this manner, the adult individuals in the hive are able to regulate the caste ratios, so that not too many queens are born which would just be a waste of resources. High reproduction makes no use if there aren’t enough workers to maintain food storage and hive construction. Nature is complex though. It doesn’t always follow the models and theories made up by humans. In the Melipona bee caste fate is highly genetically determined. The eggs are enclosed in a hexagonal cell together with some food that is equally distributed among cells. The larvae then develop without any influence from their surroundings and they finally pupate and emerge as adult. As the caste fate is not socially regulated an excess number of queens are produced. In this species though, there is only one queen in each colony, so the excess is quickly executed by the adult workers in the hive.

Researchers today seem to agree upon the fact that both genetic and environmental factors influence caste fate. The one that has the greatest impact depends on the species. The origin though is still unclear. Kin selection proponents state that genetic factors are hardly credible as inherited sterility poses a problem. “If you don’t have kids, they won’t either”. Worker caste individuals unable to reproduce should therefore have been a matter of environmental factors at the time when the first social insect societies emerged. Genes, though, are not always obligately expressed. Sometimes a gene can be controlled by other genes in such a way that it’s hindered to be encoded. This kind of caste determination occurs in the red harvester ant (*Pogonomyrmex barbatus*). When a queen mates with a male from the same family, her eggs develop into other reproductive females. Genes from outside the family though, have an inhibitory effect on some of the queen’s caste determining genes, which turns her offspring into non reproductive females.

Very few genes interfering in social behavior and caste development have yet been identified, which is one of the reasons that the evolution of social insects is still widely debated. Have the genes been conserved and just slightly modified through solitary - to social insects? Or could new, “social” genes have popped up which are not to be found in social insects solitary ancestors? One conserved mechanism involving food search behavior in the fruit fly *Drosophila melanogaster* has been found in the honey bee, *Apis mellifera*. As been noted above, honey bees perform an age-regulated foraging behavior as adults. Young bees stay in the nest while older bees forage outside. These two different types of behavior have also been observed in fruit flies.

It is possible that future research will reveal that more than one theory have been right. Eusociality has arisen in different insect species and there is even one known case among mammals, the naked mole rat. Therefore it is, to some extent, an issue of convergent evolution. If all of the eusocial Hymenopterans have the same origin or not is to be told by future research. The evolutionary success of social insects will, most certainly, continue to fascinate people.

Recommended literature

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Pictures

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