Development of Social Relationships in Insects

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Social communities of ants, honey-bees, bumble-bees, wasps and termites have always been the source of wonder and amazement to people. Division of labour and cooperation of individuals in their tendering for the growth and development of the community reminded us of the relationships within the human society. There is, however, an important difference between the highly developed social insects and our society. Whereas the majority of people is fertile and can reproduce the majority of individuals in the insect family is barren and without offspring. Only males and fertile females reproduce, and the latter are few. As a rule, there is only one fertile female in an insect family. She is the mother to all workers in the nest and to the young sexual individuals who only occur in the family in a specific season. Workers are usually females, as a rule without developed ovaries. They spend their lives providing for the community, taking care of their younger brothers and sisters and the mother, who spends most of her time laying new eggs.

Even Charles Darwin admitted that the existence of infertile workers was the most difficult question to be explained by his theory of evolution or, as he called it, natural selection. How could traits distinguishing infertile individuals from sexual ones develop, if they do not leave descendants and cannot pass their genes to the next generation? Why workers selflessly care for their family and give up their own reproduction?

In past decades the kin selection theory, put forward by British biologist W.D. Hamilton, came into prominence. Eusociality, characterized by the division of sexual individuals from infertile workers as well as at least two generations living together, developed twelve times in insects and eleven times in the Hymenoptera. So he concluded some characteristics of hymenopterans must stimulate the evolution of sociality. A peculiarity of hymenopterans is the way how sex is determined in individuals. Males develop from infertilized eggs and are haploid, have only one set of chromosomes inherited from the mother, not two like females, which inherit one set from the mother and the other from the father. Because of this all sisters inherit the same father's genes, only by the mother's genes are they distinct from each other. On average, their genes are equal in 75 %. If females of bees, ants or wasps have daughters, they share only 50 % of their genes. So it should be better for them to help sisters, which are more related to them than daughters.

The theory prevailed probably also because it uses mathematics, which is a characteristic tool for sciences which can calculate all even before the phenomenon is observed (physics). People often reproach biology not to be true science if it is founded on observations only. But the kin selection theory has many deficiencies. The queen can mate with several males and her daughters (workers) are then less related. But this fact is not crucial to the theory. We can imagine that mating with several males evolved only after the sociality was already developed. It enables the colony to be more adaptable as different workers react differently to changes in the environment.

It is more important that only sisters are more related to the hymenopteran females than daughters. When young queen has descendants, they are less related to sisters helping the old queen than their own daughters would be. Descendants of the community, cared for selflessly by the workers, are therefore not related to them more than they would be in case the workers reproduced on their own. And only the next generation is importat to evolution.

In spite of attractiveness of the theory at first sight, it is not possible to imagine a selective mechanism favouring those descendants of the colony that would cooperate better only because they are related. If sisters are closely related, it is insignificant who among them will reproduce, in best instance. Those that care for the others and do not lay eggs by themselves cannot have influence on traits of the next generation. Only those females that reproduce in spite of relatedness, what means they are least adapted to social life, will have descendants. This does not lead to the development of sociality. Besides that, eusociality with infertile workers evolved also in termites, shrimps living in sponges and even in mammals mole-rats which all have diploid males.

A common feature to all animals living in eusocial communities is not the way sex is determined, but construction of nests or, respectively, dwellings in which they live and care for their progeny. Ants, bees, wasps, termites and mole-rats all build complicated burrows, combs, even several meters high residencies, and build their nests in hollows or cavities, which are usually rare in the environment. Sponges in which eusocial shrips live are also fewer than individuals. Construction of nests takes the majority of time and energy from animals building nests. Nests protect progeny and enable safe first steps in life for them. Such nests have to be protected from parasites, thieves of collected food and intruders. That is possible only in communities where only part of their members leave the nest to collect food. Initiation of new nests is a demanding and risky business because of shortage of suitable places, predators outside and great amount of energy, spent during construction by the female. More than half of solitary bee females die before their nest is finished. So it is better for them if they can use an already existing nest. Many bee and wasp species developed cleptoparasitic life. They do not build their own nests but lay their eggs in nests of other species, like cuckoos. In some species, however, females return to their natal nests and care for progeny of their mother or sister. A social community is formed.

Several forms of sociality can be found in bees. Most simple is a communal life. Females share a common entrance to the nest, but in it, each one of them prepares own brood cells and lays eggs on provisions. Quasisocial communities are similar, only the females cooperate in provisioning cells with food. In semisocial communities, however, one of them earns a dominant position. Usually it is the largest one who earns dominance by physical superiority. She stays in the nest, guards it and examines brood cells. If she finds an egg of her nestmate in them, she will eat it and lay her own egg in its place. In this way she succeeds to mother almost all descendants of her community in which other females, usually her sisters, fly to pastures for pollen and honeydew.

Communal life, quasisociality and semisociality can be understood also as steps in evolution leading to highly developed eusocial communities. But such development is not inevitable, it can stop at certain step or even return to solitary life of females, depending on conditions in the environment affecting each species specifically. Among halictid bees there are many solitary species and species with different kinds of sociality. Social life evolved several times in the group and several times returned to solitary life. That is the only explanation of the fact that in almost all large halictid genera some social and some solitary species exist.

A key condition for the evolution of communities with infertile workers is exactly the achievement of dominant females in semisocial communities that enabled them to mother all descendents in their nests. Queens in eusocial colonies must, as they are the only individuals which transmit genes to the progeny, determine also features of future infertile workers with their genes, not only of future sex individuals. Queens, as well as workers, have all genes needed to become a queen or a worker. Which genes are expressed in certain individual depends on conditions in the environment in which it develops: available food, pheromones of the queen, or simply physical violence of the dominant female, causing stress in workers. The latter possibility is the most primitive, succeeded in evolution usually soon by chemical substances emitted by the queen – pheromones. The development of multicellular organism from a fertilized egg cell is similar. All cells formed by the division have the same genes, but some of them become skin cells, some liver cells, nerve cells and so on, all under influence of substances excreted by neighbouring cells. Also because of that we can look at an eusocial community as a superorganism. This conception was introduced by W.M. Wheeler already in 1911.

We observe semisocial communities most frequently as a step in the development of a halictid bee colony, *Halictus scabiosae* for example. In this species, sisters overwinter in their natal nest and renew it in spring. One of them becomes a functional queen. When her daughters grow up in the nest taking over the role of workers, she does not allow her sisters to enter the nest any more. Some of them excavate new nests in the vicinity and soon nestmates who do not like to dig a burrow join them. A new semisocial community is soon established, while in the old nest eusociality with infertile workers of the new generation formed.

The other path leading to eusocial communities also exists. Some solitary bees, members of the genus *Ceratina* for example, do not close brood cells and leave like other solitary species. They guard the nest and care for the progeny cleaning cells or bringing in additional food. Such community is called subsocial. In some species, a daughter can stay in the nest of her mother as a worker. As these bees are, like bumble-bees and honey-bees, members of the family Apidae, this could be the way leading to communities that we know in the domestic bee.

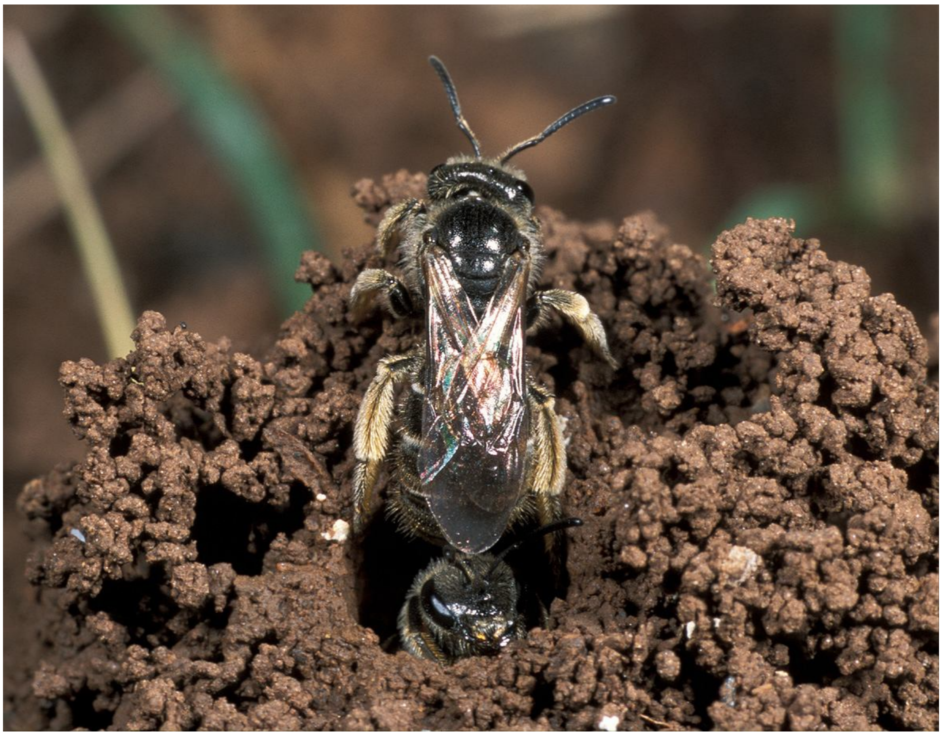
If only one female in a community has monopoly over reproduction, modified genes can accumulate in genomes of her descendants, determining behaviour and body shape of workers, as well as those genes determining features of fertile individuals. Workers distinguish often from queens not only by the behaviour, but also by size, colour, body shape and other traits. In many ants even several castes of workers exist that differ in size, shape and behaviour.

During competition among colonies (communities) of a species for food sources and during more or less successful nest construction and protection natural selection occurs. We can say that selection operates on better and less well adapted colonies or on better and worse genes of their queens and males that mated them. If we concentrate on the former viewpoint we talk about group selection, while the latter viewpoint instructs us that only the genomes of sex individuals are selected upon. If so, workers are only autonomous organs of the queen, detached from the body. Altruists are not by their own choice, but because that is beneficial to the community or in other words, it assures their parents a more successful reproduction.

Let as return to Darwin at the end. Although he knew nothing about mechanisms of inheritance, he correctly explained the origin of infertile workers and differences among them in his book *On the origin of species* (1859). He wrote: *…I believe the natural selection could, acting on fertile parents, form a species regularly rearing infertiles, only large ones or only little ones, and finally, a group of workers of the same size and constitution and at the same time another group of workers with a different size and constitution…*

A halictid bee *Lasioglossum xanthopus* is a solitary species.

Halictus scabiosae females live in semisocial and eusocial colonies. Sociable are even their males who gather in the evening to a collective rest.



Lasioglossum marginatum workers are leaving their underground nest. This species lives in perennial eusocial colonies with many workers.

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