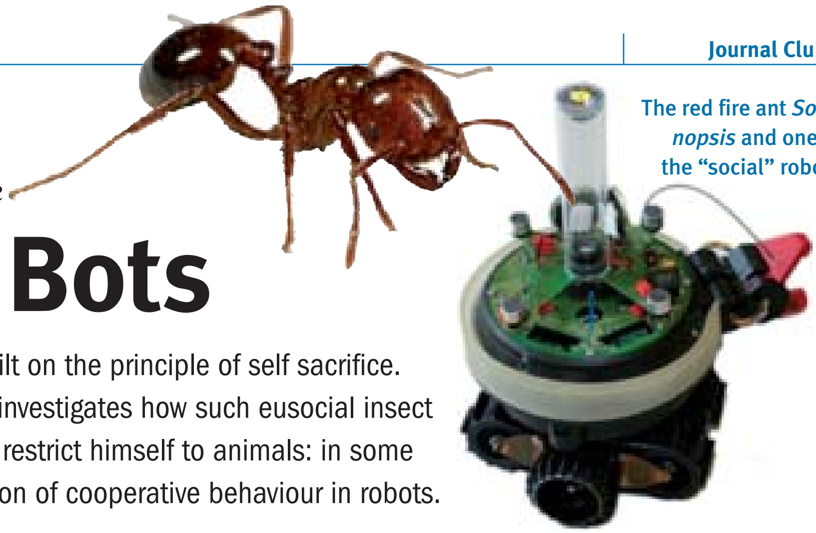
Evolution of social behaviour in Lausanne

Of Ants and Bots



The red fire ant *Solenopsis* and one of the "social" robots

Ant societies are strictly organised. They are built on the principle of self sacrifice. Laurent Keller from the University of Lausanne investigates how such eusocial insect systems might have developed. But he doesn't restrict himself to animals: in some of his experiments, he can even see the evolution of cooperative behaviour in robots.

Ant workers live a selfless life. They clean and feed their mothers' brood with no opportunity to reproduce. Ant societies are strictly stratified into monarchs with full rights and comforts and workers or food gatherers with no such rights at all. Why do animals help each other? Why do they give up their own evolutionary success for that of group?

Some theories try to explain the origin of altruism by going back to the principle of reciprocity. But for the self sacrificing individuals in insect colonies, William Donald Hamilton's theory of kin selection seems more plausible. The answer this theory gives is that selfless behaviour might arise when individuals share genes. Ant workers share 50% of their genes with the offspring of the colony queen. By helping their sisters and brothers they increase the probability of reproducing parts of their own genomes. That's why altruism should be adaptive. Of course, the real origin of the phenomenon is still unclear. And the origin of the complexity of ant social structure might be even harder to understand.

"I have been fascinated by the social systems of ants ever since my career started", says Laurent Keller from the University of Lausanne. Since the 1980s he has tackled the mystery of cooperational systems in the animal kingdom in more than 200 original papers, several books and book chapters and a bunch of reviews and other publications. Today, he and his colleagues from the Department of Ecology and Evolution do not only combine classical experiments with genetic, molecular and theoretical methods. In cooperation with computational engineers they also develop experiments on robots with artificial genomes and test hypotheses on the evolution of social traits.

The "ants' friend" Laurent Keller

The Keller group's scientific interests are very diverse. The origin of altruism is only one of them. What is the genetic basis of social behaviour? How are insect castes determined? Why do ant queens become much older than their workers? These are only a few of the questions that the Keller group tries to answer. Some of their latest publications show a good cross section of their scientific achievements.

Keller and his colleagues have been investigating the social systems of various ant species all over the world. They found, for example, that social structures are very variable even within one single species. One example is the fire ant Solenopsis invicta, which forms two kinds of colonies: one with a single queen and the second with multiple queens. Keller and his team revealed that this differential social behaviour is coupled to a single allelic variation of the gene Gp-9, which codes for the Odorant Binding Protein (OBP), a member of the pheromone signalling system (*PLoS Genet.* 4(7):e1000127). Workers in monogyne colonies have two identical copies of the gene whereas workers in polygyne colonies have two different copies. A direct influence of the OBP coding gene on the colony structure is possible because workers accept their queens collectively on the basis of chemical signals. In one of their recent papers Keller and his colleagues showed additional ways in which Gp-9 might work.

On the one hand, the composition of Gp-9 alleles seems to be directly linked to the activity of some 30 other genes. Applying expression analyses, Keller and Co. proved that some genes are expressed differently in the homo- and the heterozygous workers of polygyne colonies. Some of these genes are involved in the pheromone signalling system, as is Gp-9 itself. They might push workers towards the establishment of single or multiple queens by influencing chemical communication.

One single gene is enough

On the other hand, Gp-9 seems to have an indirect influence, too. Apparently, the composition of Gp-9 alleles in the surrounding individuals affects the decision making of an individual even more than the allelic pattern of the individual itself. Workers show different expression patterns of about 90 genes depending on the type of colony in which they live. "In the future we would like to sequence the genome of *Solenopsis invicta* in order to find further genes that are linked to Gp-9", says Keller. "Then we can try to find out how it exerts its influence."

The fact that the social organisation of ant colonies is influenced by single genetic factors is exciting. But even more exciting is the phenomenon of eusociality. In many other papers Keller and colleagues have been elucidating this problem. One of their most recent publications provides a particularly good example (*Oecologia* 157(4):717-23). In the corresponding study, the researchers showed that social behaviour does not necessarily presume direct relations between workers and their queens. Keller and his group tested whether colonies of the wood ant Formica exsecta would accept foreign queens and if the intruders would succeed in having offspring. Formica exsecta forms monogyne and polygyne colonies, as does Solenopsis invicta. Young ant queens either found their own colonies after mating or can be adopted by already established colonies. The latter results in a colony type where workers are confronted with the closely related brood of their mother and, at the same time, with offspring of foreign origin. How did they react?

In their experiments, Keller and Co. introduced foreign queens into colonies raised in the lab. They measured the survival of these foreign queens over more than 130 days. And they ruled out the extent to which the queens were able to have their own offspring. It turned out that the intruders survived as long as resident monarchs. Furthermore, the resident workers not only accepted the strangers in their nests but even allowed them to have offspring. There was, however, a quantitative difference: foreign queens raised fewer pupae than resident ones. Whether the workers reared the foreign eggs to a lower extent or whether the foreign eggs suffered from greater mortality is unclear.

But still, foreign queens were cared for and were even helped to have eggs. This result contradicts the kin selection theory which presumes relatedness between altruistic individuals, doesn't it? "No, it doesn't", says Keller. "The young queens of *Formica exsecta* usually travel only 50 to 80 metres away from their home colonies after mating. The probability of relatedness to their new hosts is not that low." The phenomenon of population viscosity – the low dispersal rate of related individuals – might be the reason for the evolution of altruistic behaviour between individuals from different colonies. Their genomes still remain closely related.

Four robots communicate by blue light that they have found a food source

Of course, whether the principle of kin selection leads to the evolution of altruism or eusocial behaviour is a question to which only indirect access is possible. Researchers cannot travel back in time and observe the birth of an insect system. That's why modern robotics could help – in particular, since this field offers the opportunity to model the very first steps in the evolution of social systems. For this reason, Keller and his colleagues collaborated with the Laboratory of Intelligent Systems at the EPFL in Lausanne, whose members have the expertise and the hardware to conduct helpful experiments.

In 2007, the team published a paper in *Current Biology* (vol. 17(6):514-9) that provided an example for the artificial evolution of social behaviour. The researchers first designed colonies of individual agents *in silico* and constructed real robots afterwards. Both, simulated and real robots, were set loose in an arena with two kinds of objects – one classified as poison and the other as food. Each bot had a built-in attraction to food and aversion to poison. They also had a randomly-generated set of parameters, "genomes", defining the way they moved, flashed a blue light, as a useful tool for communication, and processed sensory information.

The simulated bots were allowed to explore their surroundings. After that, the researchers recombined the genomes of those bots that found food and avoided poison most efficiently. In simple words: they played natural selection. The genomes were combined and randomised in a way designed to simulate mating and mutation in nature. In this way, five hundred generations were evolved. In some experiments, however, Keller and his colleagues implemented the genomes in such a way that they were highly related to each other. Robots harbouring these genomes were kin, whereas in the other experiments the robots were completely unrelated. In addition, the researchers chose two different levels of selection: in the individual-level selection group, the genomes of the 20% of robots with the highest individual performance were selected to form the next generation, whereas in the colony-level selection group, Keller and Co. randomly selected all robots from the 20% of most efficient colonies, independent of individual performance.

"The robots started with completely random behaviour," Keller explains. "All they could do is discriminate food from poison. But then they evolved and started getting better and better." After a while sophisticated social systems developed. Some robots flashed their blue lights to signal the position of food or poison to the others.

Robots are fine, but nature is more fascinating

What role did kin structure and the level of selection play? Closely related individuals under colony-level selection cooperated best. In contrast, individually selected and therefore unrelated robots failed to act socially. In some cases they even developed deception strategies, flashing their lights as far away as possible from the food and thus misleading their conspecifics. It seems that kin selection on the colony level, as is given in ant colonies, is very beneficial to the evolution of cooperation and communication.

Future robot experiments might elucidate further aspects of social activity. Keller and his group might learn to understand how altruistic insect systems develop, where sterile workers give up their chance to reproduce for the good of the colony. But will these simple robots be able to mimic ant societies in all their complexity one day? Keller surely wouldn't want to give up his tiny scramblers entirely. There is nothing more fascinating about nature than nature itself, he says.

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