The Crafoord Prize 2007

The Royal Swedish Academy of Sciences has decided to award the Crafoord Prize in Biosciences for 2007 to ***ROBERT L. TRIVERS****, Rutgers University, New Brunswick, NJ, USA "for his fundamental analysis of social evolution, conflict and cooperation".*

Social evolution in the animal world – conflict and cooperation

In the early 1970s **Robert L. Trivers** presented pioneering ideas that connect the theory of evolution to the development of the social behaviour of animals. At that time, such ideas were controversial, but now they are established and form the basis of much of today's research on cooperation and conflict in the animal world.

Reciprocal altruism – services and services in return

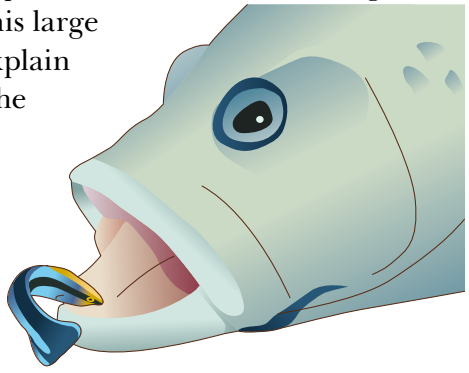
Blood-sucking bats in Costa Rica help each other with food. If one of them has not managed to quench its thirst during the night, it can beg a drink from one that has been more successful. Cooperation is important for bats: if they do not get blood every fiftieth hour, they die.

Services and services in return are common in the animal world. It is easy to imagine that flock animals obviously benefit from them. But how did this cooperation ever start?

According to Darwin's theory of evolution, the individuals that are most successful in various ways get most offspring, so their genes will live on. In the case of the bats, the most effective hunters that find most food should succeed best. An individual that shares its food should in fact not manage so well. So Darwin's classic theory does not explain how cooperation can arise.

The dilemma surrounding the origin of cooperation was something this year's Crafoord Prize winner for Biosciences, Robert Trivers, began to ponder as a biology student at Harvard in 1969. At that time, the connection between social behaviour and evolution was an unresearched area. Trivers's experience of ecology was in principle non-existent, but he based his studies quite simply on himself. Although he and his friends were not related, they helped each other; their self-sacrificial behaviour was reciprocal. Trivers called it reciprocal altruism.

Trivers also found examples from the animal world when he developed his theoretical model of reciprocal altruism. He had, for example, read about remarkable cooperation between different fish species: a small species rid another much larger species of parasites. It even cleaned the mouth of this large fish of prey. What Trivers found most difficult to explain was that when the large fish saw a prey, it warned the grooming fish. It opened and closed its mouth so that the grooming fish could escape.



Reciprocal altruism in practice. The cleaner fish enters the mouth of a host fish to clean its mouth of food remains and parasites. The cleaner benefits from the food, and the host may benefit from not eating the cleaner in the prospect of being cleaned again in the future by the same cleaner.

The other example Trivers used was of birds that sound a warning with a special, extremely clear note when a predator approaches the flock. Here he could also see cooperation between individuals: if I warn you when I see danger, you will warn me.

Trivers's model was that reciprocal altruism could develop if fish and birds recognised each other and interacted over long periods. Not until then could mutual help develop. He found, for example, that the same fish of prey and grooming fish often kept each other company. By recognising the fish of prey as a reliable individual, the grooming fish could survive.

Trivers's thoughts on reciprocal altruism have also been confirmed among bats in Costa Rica. Bats from the same place are more inclined to help each other; they recognise each other and need not be afraid of being cheated. Return services come sooner or later. Researchers have also seen that some bats cooperate in pairs and that this partnership can last for several years.

When Trivers published his model of reciprocal altruism in 1971, he created the basis for a field of research that is still active today. One example is the use of game theory – cheaters can win in the short run, but people who get to know each other and cooperate win in the long run.

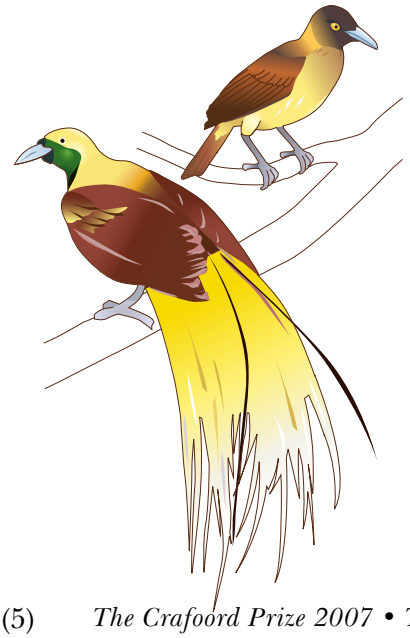
Trivers's work on reciprocal altruism met an immediate and warm response in the research community. But this was just the beginning of a very productive period for Trivers. Already in the following year, 1972, he published new ideas, this time about the connection between parental investment in their offspring and sexual selection.

Decisive care of offspring

Trivers's starting point was observations he had made of pigeons. His supervisor had advised him to study pigeons as they were too common and ugly to attract ornithologists. That is why not much was known about their behaviour. Trivers took on a group of pigeons that were nesting under the eaves of the house opposite where he lived. He followed with interest the interactions between males and females. Above all, he was fascinated by the way the males continuously watched their females.

Together with previously published work by the biologists Angus Bateman (1948) and George C. Williams (1966), Trivers's observations of pigeons formed the basis of his new theory. This is that the sexes develop different behaviour patterns and traits depending on the amount of time and energy they invest in their offspring.

In certain species, for example, one sex takes care of the offspring much more than the other. In the animal world, it is often the females that take the greater responsibility. The males then get the opportunity to have many more offspring if they manage to attract more females. That is why the males develop traits that are not actually necessary for survival, but that the females appreciate: beautiful plumage, a large body or the white spot on the forehead of a male flycatcher.



In order to attract as many females as possible, the males of the Lesser bird of paradise have developed impressive plumage and an eye-catching courtship behaviour that they display when they compete for the females´ favour at the lek. Once mated, the females nest-build, incubate and provision their young unaided by the male.

Among species in which both sexes invest about the same amount of time and energy in their offspring, other behaviour is encouraged. For example, the male will watch jealously over the female so that she is not unfaithful, because if the female gives birth to the young of another male, the male will waste time and energy on the "wrong" genes. The male pigeons on the roof opposite Trivers's house, for example, did everything to stop their females from even sitting close to another male in the flock.

Trivers's publication "Parental Investment and Sexual Selection" is now one of those most frequently quoted in evolutionary biology.

Parental ability to vary the sex ratio of offspring

The next natural phenomenon Trivers studied is less well known. In some species, there are born at times more males than females, and vice versa. In 1973, Trivers provided a theoretical explanation of how differences in sex ratio might arise. In his opinion, during the course of evolution, parents had developed an ability to decide their offspring's sex depending on what suited that time best. If, for example, male young had to grow bigger than female young, it is advantageous to have males at a time when it is easy to find food.

This prediction has proved to be correct. For example, researchers have shown that female red deer that are in good condition give birth to more male calves. If they are in poor condition, they have more female offspring.

Natural teenage conflicts

In 1974 Trivers published his fourth pioneering work in as many years. This time he questioned the harmonious view of nature that was predominant among biologists at that time. Instead, he revealed the conflicts that arise naturally between parents and young. Trivers had seen how both young pigeons and young monkeys that were a little older were treated harshly by their parents. At the same time, the older young harassed their parents to get food and attention. According to Darwin's theory, it is natural for parents to invest as much effort as possible in their young so that they thrive and survive. But according to Trivers, there is a limit to this; when the young are old enough to take care of themselves, the parents gain by kicking the young ones out and getting one or several new ones. The young ones, on the other hand, want to exploit their parents' care as long as possible so as to grow strong.

Worker ants are feminists

The fifth work for which Trivers is awarded the Crafoord Prize was developed from his knowledge of ants, bees and wasps. These species are special since the females are born from fertilised eggs and have a double (diploid) set of genes, whereas the males are born from unfertilised eggs and have a simple (haploid) set of genes. That is why, in an ant community with a queen, the workers, which are females, share on average three quarters * of their genetic set with each other, while they share on average only one quarter with their brothers.

From this, Trivers concluded that the workers, which bring up all the queen's young, ought to devote three times as much of their resources to their sisters as to their brothers. Consequently, there ought to be three times as many swarming, reproductive

females as males in a colony. When Trivers began to investigate what ant researchers knew about the relationships between females and males in different species of ants, he discovered to his disappointment that there were often more males in a colony. But his colleague, the evolutionary biologist and ant expert Edward O. Wilson (who was awarded the Crafoord Prize in 1990) reassured him by telling him that the females are always larger. That is why Trivers weighed males and females from a species of ants, Prenolepsis imparis, in which it was known that there were eight times more males than females. The females turned out to be 25 times heavier! 25 divided by 8 is about 3. So the workers had invested three times as many resources to get females rather than males.

The next species Trivers investigated together with experimentalists had as many males as females, but the females weighed 3.5 times more. All in all, Trivers saw the same phenomenon in 20 different species of ants. When he and a colleague published "Haplodiploidy and the Evolution of the Social Insects" in 1976, in the well-reputed journal "Science", his theory immediately had a great impact.

Thus, together with the previous Crafoord prize winners William D. Hamilton, George C. Williams, Edward O. Wilson and John Maynard Smith, Robert Trivers has laid the theoretical foundation for research on the evolution of social behaviour patterns in animals, a field that is known today as sociobiology and which is part of the larger field of behavioural ecology. For example, he has recently published the book "Genes in Conflict" together with Austin Burt, and he plans next to tackle explaining the evolution of deceit and self-deception – two human and biological phenomena that have long held his interest.

Footnote:
* Half come from the father's sperm, which are all genetically identical since the father is haploid. Half of the other half come from the part of the egg's genome that comes from the common mother.

LINKS AND FURTHER READING

Article:
Advanced information on the Crafoord Prize in Biosciences 2007

Books:
Robert L. Trivers, Social Biology (1985)
Robert L. Trivers, Natural Selection and Social Evolution (2004)
Edward O. Wilson, Sociobiology (1975)
Richard Dawkins, The selfish gene (1976 och omtryckt senast 2006)
Tim Clutton-Broch, The evolution of parental care (1991)
John Krebs & Nick Davies, An introduction to Animal Behaviour (1993)
Malte Andersson, Sexual selection (1994)
Lee Dugatkin, Principles of animal behavior (2004)
John Alcock, Animal behavior (2005)

Links:
http://anthro.rutgers.edu/faculty/trivers.shtml
www.edge.org/3rd_culture/bios/trivers.html

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