

18 January 2007



Advanced information on the Crafoord Prize i Biosciences 2007

## **Social evolution: Cooperation and conflict**

## Social evolution

Social behaviour in animals presents some of the most fascinating and challenging problems in evolutionary biology. For example, large complex societies, to which many individuals contribute their life's efforts without having a chance of reproducing; highly elaborate and costly sexual signals, often expressed only in one sex; and complex family interactions between mates and between parents and offspring, involving cooperation in some cases, conflict in others. How have such traits and interactions come about?

The evolution of social behaviour was made a subject of scientific study already by Darwin (1859, 1871). Yet, in spite of its great inherent interest to scientists and laypersons alike, the field was largely dormant for about a century, until seeded by a number of theoretical advances (e.g. Hamilton 1964, Williams 1966, Trivers 1971-74, Maynard Smith and Price 1973, Wilson 1975). They led to a rich harvest of observational, experimental and comparative studies of sociality and social behaviour, often in the natural environment to which animal behaviour can be expected to be adapted.

The theoretical revolution was brought about by a small number of researchers, among which Robert Trivers is one of the foremost. Four others are W.D. Hamilton, G. C. Williams, E.O. Wilson and J. Maynard Smith (all of them previous Crafoord Laureates for these or other contributions). Together they were the main theoretical architects of the initially controversial research field (Segerstråle 2000) that came to be known as sociobiology, part of the broader subject of behavioural ecology (cf. Dawkins 1976; Krebs and Davies 1978; King's College Sociobiology Group 1982).

The selection and evolution of sociality and social behaviour involves not only cooperation and mutual benefit but, because selection at the level of the individual and below is strong, also a great deal of conflict. This applies also among kin, even though relatedness is a major catalyst of sociality (Hamilton 1964, reviewed by Dugatkin 1997). In a remarkably creative period during the early 1970s, Robert Trivers produced a series of outstandingly original, bold and profound papers dealing with cooperation and conflict in the evolution of sociality, laying theoretical foundations for huge areas of research, which are still highly active today.

Cooperation and altruism among unrelated individuals presents a puzzle to evolutionary biologists, as natural selection is usually strongest at the individual level. How, then, can actions that are risky or detrimental to the actor but beneficial to an unrelated recipient evolve by natural selection? Trivers (1971) suggested that in addition to kin selection (Hamilton 1964), which involves relatives other than offspring, and hence collateral gene propagation, there is another social mechanism, *reciprocal altruism*, that can favour altruistic behaviour also between non-kin. A problem for its evolution is the possibility of cheaters, which reap the benefit of receiving help, but avoid cost by not reciprocating. Trivers suggested the problem can be overcome if there is individual recognition and long-term repeated interactions between the parties. Genetical evolution of altruism may then take place if individuals reserve help to others who in turn reciprocate.

These ideas started a new research area that is still very active (Dugatkin 1997). Game theory modelling, based on various forms of the 'prisoner's dilemma' game (e.g. Axelrod and Hamilton 1981), has been crucial in further clarifying how reciprocal altruism can become established as an evolutionarily stable strategy (Maynard Smith 1982). 'Tit for tat' strategies, copying the partner's previous move, can be robust in an iterated prisoner's dilemma game. Empirical examples of reciprocal altruism have been found, from baboons taking turns grooming each other and removing parasites (Silk et al. 1999) to vampire bats sharing blood meals (Wilkinson 1984). Building on foundations laid by Bateman (1948) and Williams (1966), Trivers (1972) in a

second highly influential paper clarified the relations between *parental investment* and *sexual selection*, and integrated the two in a comprehensive theory. This is one of the most widely cited papers ever in evolutionary biology, inspiring a wealth of research (reviewed e.g. by Clutton-Brock 1991, Andersson 1994).

Trivers defined PI as investment in an individual offspring that increases its chances of surviving and reproducing, at the cost of the parent's ability to invest in other offspring. He pointed out that the relative parental investment by males and females controls the relative strength of competition over mates in the two sexes, i.e. the strength of sexual selection, favouring traits used in sexual competition. In most animals, males invest less resources in their offspring than do females, so sexual selection and the traits it favours are usually more pronounced in the male sex.

Sex allocation theory (Charnov 1982) is another highly successful topic in evolutionary ecology, producing a wealth of stringent theoretical modeling and critical empirical testing (reviewed in Hardy 2002). In a third pioneering work, on *parental ability to vary the sex ratio of offspring*, Trivers and Willard (1973) suggested that it might be adaptive for parents to adjust their relative investment in sons versus daughters to resource availability and parental condition. If resources allocated to offspring of one sex result in greater fitness returns, parents will benefit from biasing their investment towards that sex. For example, in many birds and mammals, breeding success increases more rapidly with body size in males than in females. Parents might then rear sons when resources and parental condition are high and permit rapid growth of offspring, and daughters in the opposite situation. There is now empirical evidence for parental sex ratio adjustment in many species, and the theory has been further developed and improved in various ways (Hardy 2002).

The following year, Trivers (1974) published the paper that launched the evolutionary study of *parent-offspring conflict*. He pointed out that as a parent and its offspring are not genetically identical, there will be conflict between them over the level of parental investment. For a current offspring receiving PI, its optimal level may be greater than the optimal level from the parent's point of view. For example, when a current offspring approaches the age of independence and the parent can save its investment for future offspring, the current offspring will still benefit if it can obtain further parental investment – hence a conflict between parent and offspring. There is now much empirical evidence for parent-offspring conflict, and the theory has been extended in a number of directions (reviewed by Clutton-Brock 1991).

One of these other directions was laid out by Trivers and Hare (1976), in a seminal paper on *haplo-diploidy and the evolution of social insects*. In hymenopterans (wasps, ants and bees among others), the female can control the primary sex of an offspring by laying a fertilized or an unfertilized egg. Sons are produced from unfertilized eggs and are therefore genetically haploid, with a single set of chromosomes, whereas fertilised eggs produce diploid daughters. Therefore, if you think about it, in a hymenopteran society with one monogamously mated queen, the workers, which are females, on average will share 3/4 of their genes with their sisters, but only 1/4 with brothers. Combining Hamilton's (1964) kin selection theory with Fisher's (1930) sex ratio theory, Trivers and Hare showed that sterile workers in social hymenopterans are therefore expected to bias their sex allocation towards sisters among the reproductive siblings they help raise until they leave the colony by swarming. More precisely, the workers are predicted to favour a 3 times larger investment in reproductive sisters than in reproductive brothers. On the other hand, the queen who produces the eggs has an optimal offspring sex ratio of 1:1. This creates queen-worker (parent-offspring) conflict over colony sex ratio. Testing the predictions in a number of ant species, Trivers and Hare found that sex allocation in most cases was closer to 3:1, showing that workers usually win the conflict.

The theory and tests in this field have since been elaborated to great sophistication, often corroborating the predictions in remarkable detail (reviewed by Bourke and Franks 1995, Crozier and Pamilo 1996). The field is still developing, and the seeds sown by Trivers and Hare (1976) are bearing rich fruit.

All this pioneering work, for which Dr Trivers is awarded the Crafoord prize, was done in the 1970s. This in no way means that he has given up research. On the contrary, Dr Trivers is also unusual in carrying out highly creative and original research still in his sixties. He has, however, changed research fields, and his main work now concerns fluctuating asymmetry and intra-genomic conflict. His basic approach is still that of a selection-oriented evolutionary biologist, harvesting fascinating new insights from pioneering research. For example, in their long-term study of fluctuating asymmetry in Jamaican children, Dr Trivers and his colleagues have shown in a recent article in *Nature* that “Dance reveals symmetry especially in young men” (Brown et al. 2005). And last year, Robert Trivers and Austin Burt published the first synthesis in book form of the burgeoning field of intra-genomic conflict (Burt and Trivers 2006), an area of great importance to our understanding of evolutionary genetics as well as several medical genetic aspects. This year’s winner of the Crafoord prize has therefore made crucial contributions to a remarkably wide range of important subjects in evolutionary biology.

## References

- Andersson, M. 1994. *Sexual Selection*. Princeton Univ. Press.
- Axelrod, R. and Hamilton, W.D. 1981. The evolution of cooperation. *Science* 211, 1390-1396.
- Bateman, A. 1948. Intrasexual selection in *Drosophila*. *Heredity* 2: 349-368.
- Bourke, A.F.G. and N.R. Franks. 1995. *Social Evolution in Ants*. Princeton Univ. Press.
- Brown, W.M, L. Cronk, K. Grochow, A. Jacobson, C.K. Lu, Z. Popovic and R. Trivers. 2005. Dance reveals symmetry especially in young men. *Nature* 438: 1148-1150.
- Burt, A. and R. Trivers. 2006. *Genes in conflict*. Belknap Press of Harvard Univ. Press.
- Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton Univ. Press.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton Univ. Press.
- Crozier, R.H. and P. Pamilo. 1996. *Evolution of Social Insect Colonies. Sex Allocation and Kin Selection*. Oxford Univ. Press.
- Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. Murray, London.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. Murray, London.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford Univ. Press, Oxford.
- Dugatkin, L.A. 1997. *Cooperation among animals: an evolutionary perspective*. Oxford Univ. Press, New York.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour. *Journal of theoretical Biology* 7, 1-52.
- Hardy, I.C.W. 2002. *Sex Ratios: Concepts and Research Methods*. Cambridge Univ. Press.
- King's College Sociobiology Group 1982. *Current problems in Sociobiology*. Cambridge Univ. Press, Cambridge
- Krebs, J.R. and Davies, N.B. 1978 (eds.) *Behavioural ecology an evolutionary approach*. Blackwell, Oxford.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge Univ. Press, Cambridge.
- Maynard Smith, J. and G. R. Price 1973. The logic of animal conflict. *Nature* 246: 15-18.
- Seegerstråle, U. 2000. *Defenders of the Truth: the Battle for Science in the Sociobiology Debate and Beyond*. Oxford Univ. Press
- Silk, J.B., R.M. Seyfarth and D.L. Cheney. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour* 136: 679-703.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology* 46:35-57.
- Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell, ed., *Sexual Selection and the Descent of Man 1871-1971*, 136-179. Heinemann, London.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 14: 249-264.
- Trivers, R. L. 1985. *Social Evolution*. Benjamin/Cummings, Menlo Park.
- Trivers, R. L. and D. E. Willard 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90-92.
- Trivers, R. L. and Hare, H. 1976. Haplodiploidy and the evolution of the social insects. *Science* 191: 249-263.
- Wilkinson, G.S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308: 181 – 184.
- Williams, G. C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton Univ. Press, Princeton.
- Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Harvard Univ. Press, Cambridge, Mass. 2007