

## **Ultimate and Proximate Mechanisms of Cooperation in Animals**

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The widespread occurrence of cooperation in a competitive world is among the most remarkable aspects of biological evolution. Cooperation is responsible for the evolution of higher levels of organization, from microbes and cell components to highly structured animal societies. It has been suggested that cooperation should be added as a third fundamental principle of evolution, beside mutation and natural selection. However, despite the undisputed importance of cooperation for a comprehensive understanding of the living world, the mechanisms involved, both at evolutionary and causal levels, are only partly understood.

Due to synergistic effects, cooperation can evolve easily if the action itself generates an immediate fitness benefit to the actor (mutual benefits). However, often cooperative actions generate a net fitness cost to the actor at a benefit to a receiver. Such altruistic traits can evolve among related individuals by kin selection. Among both related *and* unrelated individuals, altruistic traits can be selected also by reciprocity, or when cooperation can be enforced by beneficiaries in case avoidance options of coerced actors are limited, or - under specific conditions - by group selection. Cooperation among non-kin is widespread in nature, but the conditions under which evolutionarily stable levels of altruism can be generated by group selection or coercion usually do not seem to be fulfilled. This suggests an important role of reciprocity. However, despite high expectations regarding the importance of this mechanism in social evolution, there is a disturbing discrepancy between the development of theoretical models explaining reciprocity and the information on reciprocity mechanisms actually causing cooperation among animals.

Our empirical work shows that reciprocity *does* indeed generate cooperation among animals, but the underlying behavioural mechanisms may be much simpler than hitherto assumed. Diverse modelling approaches suggest that 'generalized reciprocity' can establish evolutionarily stable levels of cooperation in a population without relying on advanced cognitive abilities, which provides ample scope for this mechanism to generate cooperation at various levels of biological organisation.