

6. Read, J.C.A., and Cumming, B.G. (2005). The effect of interocular delay on disparity selective V1 neurons: relationship to stereoacuity and the Pulfrich effect. *J. Neurophysiol.* **94**, 1541–1553.
7. Menz, M.D., and Freeman, R.D. (2004). Temporal dynamics of binocular disparity processing in the central visual pathway. *J. Neurophysiol.* **91**, 1782–1793.
8. Tanabe, S., Haefner, R.M., and Cumming, B.G. (2011). Suppressive mechanisms in monkey V1 help to solve the stereo correspondence problem. *J. Neurosci.* **31**, 8295–8305.
9. Haefner, R.M., and Cumming, B.G. (2008). Adaptation to natural binocular disparities in primate V1 explained by a generalized energy model. *Neuron* **57**, 147–158.
10. Lippert, J., and Wagner, H. (2001). A threshold explains modulation of neural responses to opposite-contrast stereograms. *Neuroreport* **12**, 3205–3208.
11. Read, J.C.A., Parker, A.J., and Cumming, B.G. (2002). A simple model accounts for the reduced response of disparity-tuned V1 neurons to anti-correlated images. *Vis. Neurosci.* **19**, 735–753.
12. Tanaka, H., and Ohzawa, I. (2006). Neural basis for stereopsis from second-order contrast cues. *J. Neurosci.* **26**, 4370–4382.
13. Read, J.C.A., and Cumming, B.G. (2007). Sensors for impossible stimuli may solve the stereo correspondence problem. *Nat. Neurosci.* **10**, 1322–1328.
14. Tanabe, S., and Cumming, B.G. (2008). Mechanisms underlying the transformation of disparity signals from V1 to V2 in the macaque. *J. Neurosci.* **28**, 11304–11314.
15. Marr, D., and Poggio, T. (1976). Cooperative computation of stereo disparity. *Science* **194**, 283–287.
16. Julesz, B. (1971). *Foundations of Cyclopean Perception* (Chicago: University of Chicago Press).
17. Marr, D., and Poggio, T. (1979). A computational theory of human stereo vision. *Proc. R. Soc. Lond. B* **204**, 301–328.
18. Menz, M.D., and Freeman, R.D. (2003). Stereoscopic depth processing in the visual cortex: a coarse-to-fine mechanism. *Nat. Neurosci.* **6**, 59–65.
19. DeAngelis, G.C., Ohzawa, I., and Freeman, R.D. (1991). Depth is encoded in the visual cortex by a specialised receptive field structure. *Nature* **352**, 156–159.

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## Social Evolution: Reciprocity There Is

The theory of cooperation predicts that altruism can be established by reciprocity, yet empirical evidence from nature is contentious. Increasingly though, experimental results from social vertebrates challenge the nearly exclusive explanatory power of relatedness for the evolution of cooperation.

### Michael Taborsky

The theory of social evolution made big leaps in the sixties and seventies of the last century when behavioural biologists started to apply rigorous Darwinian thinking to the problems of competition and cooperation among conspecifics. William D. Hamilton detected and formalized the crucial importance of relatedness for the evolution of cooperation [1], John Maynard Smith developed evolutionary game theory as a tool to understand competitive interactions [2], and Robert Trivers figured out how cooperation might evolve also between unrelated social partners by reciprocal altruism, if received help enhances the recipient's cooperativeness [3]. Some forty years and hundreds of studies later, there is consensus among theoreticians and empiricists that assortment by relatedness is of paramount importance for the evolution of cooperative and competitive behaviour. There is general conviction also that animals cooperating or competing for resources use decision rules optimized by natural selection that can be adequately modelled with the help of evolutionary game theory. In contrast, there is less agreement about the importance of reciprocity for understanding interactions among

social partners. It has been questioned whether situations in nature are favourable for reciprocal altruism to evolve [4]. Nevertheless, new evidence from vampire bats shows that reciprocal exchange can indeed be more important for cooperation than relatedness [5].

It is easy to understand the grave doubts about the evolution of cooperation by reciprocity. Helping is costly to donors and beneficial to recipients, which reflects the essential meaning of altruistic behaviour; therefore, selection favours free-riders accepting help without return [3]. However, reciprocity can generate evolutionarily stable cooperation if costly help sufficiently increases the likelihood that donors obtain fitness benefits in return for helping, provided that the benefits more than compensate for the costs of initial investment. This means that the benefit from being helped must on average exceed the cost of helping, and that social interactions should be sufficiently frequent. At the proximate, mechanistic level, reciprocity involves considering information about the likelihood of getting adequate returns of any help provided to a social partner. Such information can be obtained from experience of previous interactions and can generate one of three decision rules: first, in the simplest case, an

individual will become more helpful if it received help. This rule — ‘help anyone if helped by someone’ — can generate evolutionarily stable levels of cooperation in a population [6,7], and such ‘generalized reciprocity’ is known to operate in rats and humans [8,9]. Second, if social partners interact repeatedly with each other, having received previous help from your social partner can make the recipient more helpful. This rule — ‘help someone who has helped you before’ — can again spawn stable cooperation [10], and experiments showed that such ‘direct reciprocity’ can be applied at least by mammals and birds [11–13]. Third, individuals might help a social partner depending on its helpfulness towards others, even if they themselves never received any help. Such ‘indirect reciprocity’ based on the reputation of social partners can create stable cooperation if individuals are capable of using the respective information [14], but the underlying decision rule ‘help someone who is helpful’ has been experimentally demonstrated only in humans [15].

To test which (if any) of these reciprocity mechanisms animals employ requires careful experimentation. Whether such mechanisms apply also in nature is an altogether different question. Cooperation among animals in the wild becomes particularly interesting if shown among unrelated individuals, because then its evolution cannot be explained by kin selection [1]. One prominent textbook example is the donation of blood among conspecifics in vampire bats (Figure 1). As Gerald Wilkinson had observed in a natural



Figure 1. The common vampire bat (*Desmodus rotundus*).

Vampire bats are known to donate blood to conspecifics. New work shows that reciprocity rather than relatedness is the foundation of this example of altruism (photo: iStockphoto, 10-29-08 ©Michael Lynch).

population of *Desmodus rotundus* in the early eighties, individuals in need of a blood meal receive the required donation not only from relatives, but also from individuals they have helped in a similar way before [16]. Wilkinson showed elegantly that the conditions for the evolution of such reciprocal exchange are favourable in these bats, because the costs and benefits of sharing blood are asymmetrical (Figure 2). A bat that has found a victim to bleed has plenty of precious blood to share with a companion. An unlucky starveling can thereby greatly increase its chances to survive until the next successful foray. As expected from the structure of bat groups, most transfers of blood occur between related roost mates, primarily reflecting maternal care. However, occasionally non-relatives were observed to exchange blood, and in four out of six cases in which reciprocation was experimentally enabled in a small captive group, previous blood donations were reciprocated more often than expected by chance.

The interpretation that reciprocity explained these donations has been challenged, however, because of the rather few observations of blood donations among non-relatives, and alternative explanations for this apparent reciprocal altruism

were proposed [4]. Sure, reciprocity can be an important proximate mechanism underlying exchanges among relatives as well, but is such exchange a result of selection for reciprocal altruism, a product of kin selection, or is cooperation even

enforced by demanding receivers? This question has been tackled in a recent study by Gerald Wilkinson and Gerald Carter [5]. They starved 20 common vampire bats experimentally and induced blood sharing in a laboratory colony consisting of related and unrelated roost mates. They found that across blood donation dyads, food previously received from a partner predicted donations 8.5 times better than relatedness. In fact, food received, allogrooming (i.e. grooming by another individual) received and the donor's sex predicted the presence of food sharing in 312 measured dyads, but relatedness did not (Figure 2). Relatedness did affect the positive correlation between food donated and food previously received, although in an unexpected direction; dyads of related individuals showed even higher symmetrical reciprocation than unrelated ones, which was apparently mainly due to frequent bilateral exchanges of blood between mothers and offspring. In contrast, coercion by prospective receivers did not explain altruistic donations.

Fasted bats were usually fed by four donors, which in total made up for about 20% of the mass lost during previous starvation. Furthermore, food sharing networks remained stable over the six month test period, and the amounts given and received correlated

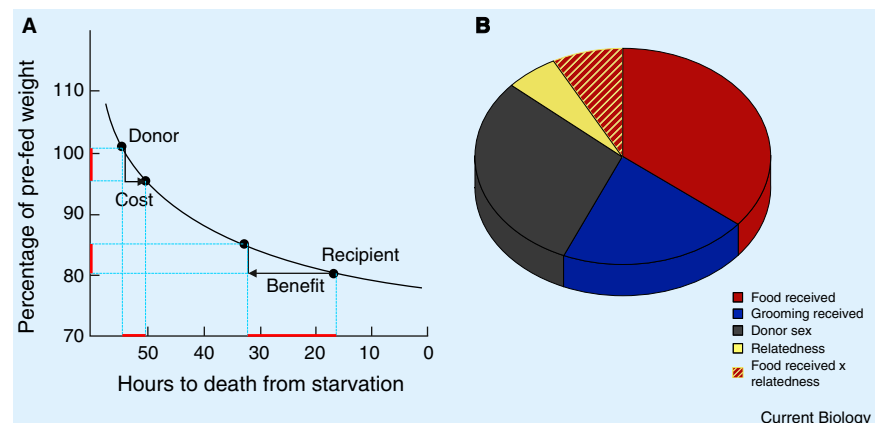


Figure 2. Costs and benefits of blood sharing in vampire bats.

(A) The loss of reserves in vampire bats follows a negative exponential function. For this reason, the amount of blood delivered by a donor has a smaller effect on its risk of starvation than it has on the receiver's risk of starvation (Adapted from [16] with permission from Nature Publishing Group). (B) Predictors of food donated to a starved social partner. The relative explanatory power is shown for the variables: food and allogrooming previously received from the recipient, the donor's sex, the relatedness between donor and recipient, and the interaction between food received and relatedness (hatched). The complete statistical model explained 37.2% of the variation in donated food, with significant effects of food received, allogrooming received, donor sex, and the interaction between food received and relatedness, but no significant effect of relatedness itself. After data provided in [5].

positively both for blood donations and for allogrooming. These long-term associations between individual bats seem to be stabilized also by frequent reciprocal grooming. Frequent dyadic interactions ensure favourable conditions for direct reciprocity. Whether bats use decision rules of direct or generalized reciprocity was not tested, however, because this would require manipulation of both the helping experience and the identity of the helper [13].

One might ask how unique this kind of reciprocal sharing is among animals in nature. Food sharing occurs also in many other species, particularly in primates [17], but the most frequent reciprocal interactions observed in nature involve grooming [4]. It has been argued that allogrooming might be too 'cheap' to classify as altruistic behaviour, but several studies have shown that such hygienic behaviour does involve considerable costs, including time effort, energy expenditure, and risk of predation and parasite transmission [18]. Furthermore, reciprocal aid is often not confined to one commodity, as demonstrated in vampire bats and many primates, where grooming is exchanged for other amenities such as access to food or partners [5,17]. Reciprocal commodity trading may be much more frequent than currently assumed, both between related and unrelated social partners. It can explain, for instance, that in cooperatively breeding cichlids,

unrelated helpers invest more in altruistic brood care than related ones, thereby paying for access to resources and a safe territory [19]. In contrast to vampire bats, here relatedness was shown to *reduce* the propensity of individuals to cooperate.

The difficulty of demonstrating the components of reciprocity experimentally and in a nearly natural context is probably mainly responsible for the fact that reciprocal altruism has yet received comparably little attention as an evolutionary mechanism responsible for cooperation [20]. However, as the study of vampire bats suggests [5], we should not thoughtlessly reject the possibility of reciprocal altruism occurring among social partners in nature — the absence of evidence should not be mistaken for evidence of absence [17].

#### References

1. Hamilton, W.D. (1964). The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* 7, 1–52.
2. Maynard Smith, J., and Price, G.R. (1973). The logic of animal conflict. *Nature* 246, 15–18.
3. Trivers, R.L. (1971). The evolution of reciprocal altruism. *Qu. Rev. Biol.* 46, 35–57.
4. Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature* 462, 51–57.
5. Carter, G.G., and Wilkinson, G.S. (2013). Food sharing in vampire bats, reciprocal help predicts donations more than relatedness or harassment. *Proc. R. Soc. B Biol. Sci.* 280, 20122573.
6. Rankin, D.J., and Taborsky, M. (2009). Assortment and the evolution of generalized reciprocity. *Evolution* 63, 1913–1922.
7. Barta, Z., McNamara, J.M., Huszar, D.B., and Taborsky, M. (2011). Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proc. R. Soc. B Biol. Sci.* 278, 843–848.
8. Rutte, C., and Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biol.* 5, 1421–1425.
9. Stanca, L. (2009). Measuring indirect reciprocity, Whose back do we scratch? *J. Econ. Psych.* 30, 190–202.
10. Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. *Science* 211, 1390–1396.
11. Hauser, M.D., Chen, M.K., Chen, F., Chuang, E., and Chuang, E. (2003). Give unto others, genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. R. Soc. B Biol. Sci.* 270, 2363–2370.
12. Krams, I., Krama, T., Igaune, K., and Maend, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav. Ecol. Sociobiol.* 62, 599–605.
13. Rutte, C., and Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*), direct vs generalised reciprocity. *Behav. Ecol. Sociobiol.* 62, 499–505.
14. Nowak, M.A., and Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
15. Wedekind, C., and Milinski, M. (2000). Cooperation through image scoring in humans. *Science* 288, 850–852.
16. Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. *Nature* 308, 181–184.
17. Silk, J.B. (2007). The strategic dynamics of cooperation in primate groups. *Adv. Study Behav.* 37, 1–41.
18. Hawlena, H., Bashary, D., Abramsky, Z., and Krasnov, B.R. (2007). Benefits, costs and constraints of anti-parasitic grooming in adult and juvenile rodents. *Ethology* 113, 394–402.
19. Zöttl, M., Heg, D., Chervet, N., and Taborsky, M. (2013). Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nat. Comm.* 4, 1341.
20. Cheney, D.L., Moscovice, L.R., Heesen, M., Mundry, R., and Seyfarth, R.M. (2010). Contingent cooperation between wild female baboons. *Proc. Natl. Acad. Sci. USA* 107, 9562–9566.

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