Review

Cooperation for direct fitness benefits

Olof Leimar[1,3,*] and Peter Hammerstein[2]

[1]*Department of Zoology, Stockholm University, 10691 Stockholm, Sweden*
[2]*Institute for Theoretical Biology, Humboldt University Berlin, 10115 Berlin, Germany*
[3]*Wissenschaftskolleg zu Berlin, Wallotstrasse 19, 14193 Berlin, Germany*

Studies of the evolution of helping have traditionally used the explanatory frameworks of reciprocity and altruism towards relatives, but recently there has been an increasing interest in other kinds of explanations. We review the success or otherwise of work investigating alternative processes and mechanisms, most of which fall under the heading of cooperation for direct benefits. We evaluate to what extent concepts such as by-product benefits, pseudo-reciprocity, sanctions and partner choice, markets and the build-up of cross-species spatial trait correlations have contributed to the study of the evolution of cooperation. We conclude that these alternative ideas are successful and show potential to further increase our understanding of cooperation. We also bring up the origin and role of common interest in the evolution of cooperation, including the appearance of organisms. We note that there are still unresolved questions about the main processes contributing to the evolution of common interest. Commenting on the broader significance of the recent developments, we argue that they represent a justified balancing of the importance given to different major hypotheses for the evolution of cooperation. This balancing is beneficial because it widens considerably the range of phenomena addressed and, crucially, encourages empirical testing of important theoretical alternatives.

Keywords: biological markets; by-product benefits; common interest; mutualism; pseudo-reciprocity

1. INTRODUCTION

Following a period of many decades in which ideas about reciprocity and altruism towards relatives came to dominate the evolutionary study of helping behaviour, recent years have seen a rapidly increasing emphasis on explanations that lie outside these two categories. This is a beneficial development in the field, because it widens considerably the range of phenomena addressed and, crucially, encourages empirical testing of important theoretical alternatives. Our aim here is to evaluate the success or otherwise of these recent developments and to suggest important directions for the future. To what extent have concepts such as by-product benefits (Brown 1983), pseudo-reciprocity (Connor 1986), sanctions and partner choice (Murray 1985; Bull & Rice 1991), markets (Noë *et al.* 1991; Noë & Hammerstein 1994, 1995) and the build-up of cross-species spatial trait correlations (Frank 1994) proved their worth in the study of the evolution of cooperation?

In accordance with the historical development, our topic might be delineated in a negative fashion as the study of the evolution of helping beyond reciprocity and altruism towards relatives. The topic might also be referred to as cooperation for direct benefits,

in contrast to the indirect benefits associated with kin-selected altruism. Indirect benefits are important in the evolution of helping (Lehmann & Rousset 2010), but we do not deal with them here. The contrast with the traditional ideas of reciprocity (Trivers 1971; Axelrod & Hamilton 1981) is perhaps less sharp, and it seems natural to view this kind of reciprocity simply as one of several related categories of cooperation, which has been much studied in theoretical modelling but appears to be rare in nature (Hammerstein 2003; Clutton-Brock 2009). It is possible and useful to categorize the different mechanisms contributing to the evolution of cooperation in some way, for instance, by the pattern of costs and benefits of the exchanges between partners (e.g. Connor 2007; Bshary & Bergmüller 2008). In such schemes, reciprocity is characterized by an investment followed by a return investment, whereas the more common case of pseudo-reciprocity is characterized by an investment followed by a response that is in the immediate interest of the responder. One should keep in mind that several different mechanisms can contribute jointly and to varying degrees to the evolutionary outcome in a given interaction. This seems, for instance, to be the case for the relatively well-studied legume–rhizobium mutualism, where both post-association sanctions (Kiers *et al.* 2003; Simms *et al.* 2006; Kiers & Denison 2008) and pre-association partner choice (Heath & Tiffin 2009) may be important. Another example is the suggestion by

* Author for correspondence (olof.leimar@zoologi.su.se).

Leimar & Connor (2003) that mycorrhizal symbiosis, in which there can be investments by both plant and fungus in each other, is a case of mutual pseudo-reciprocity rather than reciprocity. A too simple accounting of costs and benefits could fail to distinguish these alternatives. In general, it is wise to remember that cooperation encompasses a rather diverse set of phenomena that only partially fit into any given framework.

Some of the mechanisms that influence the evolution of cooperation also play a role in exploitative manipulation, which has given rise to suggestions that cooperation and exploitation are phenomena that should be looked at jointly (Herre *et al*. 1999; Bronstein 2001; van Baalen & Jansen 2001; Oliver *et al*. 2009). The observation applies both to questions of the evolutionary origin and eventual fate of mutualistic interactions (Bronstein 2001, 2009; Sachs & Simms 2006; Edwards & Yu 2007; Kautz *et al*. 2009) and to the study of the coexistence of exploitative and mutualistic interactions (Bronstein 2001; Ferrière *et al*. 2007; Kautz *et al*. 2009; Little & Currie 2009). Furthermore, traits that function as sanctions in mutualisms may have originated as defences against exploitation by parasites or predators (Pellmyr & Huth 1994; West *et al*. 2002; Edwards *et al*. 2006; Edwards & Yu 2008; Herre *et al*. 2008; Oliver *et al*. 2009) and may also currently function as defences. So, for instance, the abortion of damaged fruit in yucca plants can be a way to avoid unproductive further investment into damaged tissue, but as an important side effect fruit abortion can also act as a sanction against excessive egg laying by pollinating yucca moths (Pellmyr & Huth 1994). As a general perspective, in many cases, it seems reasonable to view cooperation and mutualism as reciprocally exploitative interactions that provide net benefits, although this point of view becomes less compelling when there is substantial common interest among the partners.

Common interest means, in its most extreme form, that reproductive success is fully linked among the interactants, so they stand or fall together. More generally, we can speak of varying degrees of overlap between the evolutionary interests. For the terminology to be worthwhile, common interest should refer to something more than the immediate benefits of cooperation, for instance, some circumstance that causes partners to stay together and depend on each other's success in the future, which is sometimes referred to as partner fidelity (Bull & Rice 1991). The overlap of interest can build up over evolutionary time, as exemplified by the emergence of the integrated complexity of cells and organisms. It would seem that several of the major transitions in evolution (Maynard Smith & Szathmáry 1995) involve and depend on an increase in common interest. It is also possible that common interest is undermined in evolution, although there are rather few well-established examples of this process (Sachs & Simms 2006). Changes in common interest may nevertheless be widespread, so that the study of these changes is worthwhile. We will briefly examine the role of common interest in the evolution of cooperation and exploitation. Finally, we will comment on the broader

significance of the developments we describe for the study of the evolution of cooperation.

2. THE RELEVANCE OF THE MARKET IDEA

Over the years, the process of partner choice (Bull & Rice 1991) and the concept of a biological market (Noë *et al*. 1991; Noë & Hammerstein 1994, 1995) have gained increasing prominence as explanations for the evolutionary stability of cooperation. Biological markets are of course different from the idealized view of a market in classical economics (Bowles & Hammerstein 2003), where there can be binding contracts between buyer and seller and where supply meets demand at an equilibrium price. It is only certain aspects of the concept of a market that have biological application. The most basic aspect is the choice between offers, and there is ample evidence for the relevance of this process in many cooperative interactions. Interspecific mutualisms often follow the pattern of 'hosts' offering food or shelter to 'visitors' while gaining benefits from the visits (Cushman & Beattie 1991), and the mobile visitors are then in a position to choose between hosts. In pollination biology, for instance, there is a long tradition of thinking in terms of market analogies, going back at least to von Frisch (1967), who writes about 'regulation of supply and demand on the flower market'. An extensive body of work lead to the conclusion that, on a relatively short time-scale, insect–flower systems may approach an equilibrium with approximately equal profitability for visitors to different hosts (Schaffer *et al*. 1983). Beyond such suggestions of market equilibration, it is clear that pollinator choosiness can dramatically influence the composition of host communities, such as when an invading plant outcompetes the residents, using a rich nectar to temp pollinators away from the native plants (Chittka & Schürkens 2001). There is also experimental evidence using artificial flowers showing the importance of rewards for pollinator visitation rates (Internicola *et al*. 2007). There are many other examples of systems where visitors choose among hosts, including ants visiting aphids (Völkl *et al*. 1999; Fisher *et al*. 2001) and client reef fish visiting cleaner wrasse stations (Bshary & Schäffer 2002; Bshary & Noë 2003).

The reverse situation, where a stationary individual chooses between incoming 'applicants' for a 'position', has been likened to a principal–agent problem from economics (Bowles & Hammerstein 2003). Among possible examples are bright-plumaged lazuli bunting males allowing less competitive dull-plumaged males to settle in nearby high-quality territories (Greene *et al*. 2000) and larger male fiddler crabs accepting smaller territorial neighbours, which they then assist in territorial defence (Backwell & Jennions 2004; Detto *et al*. 2010). In these cases, there is presumably an advantage for the stronger competitor to have a weaker competitor as a neighbour. There are also indications of choosiness by hosts in legume–rhizobium mutualism (Heath & Tiffin 2009), although the mechanisms by which a plant could recognize and choose a beneficial rhizobium strain before nodulation are currently unknown. The so-called sanctions, where

a host terminates an ongoing interaction with a less profitable visitor, is frequently thought of as a form of partner choice (Bull & Rice 1991; Kiers et al. 2003; Simms et al. 2006; Kiers & Denison 2008), even if the choosing only takes place after the interaction is established. The reason is that the overall effect of this type of sanctions is qualitatively similar to that of pre-interaction partner choice.

From the range of empirical data, there is little doubt that some form of choice in a market represents a widespread and basic mechanism acting to maintain cooperation in nature. An important characteristic of the mechanism is that it can in principle operate in situations where there is little or no common interest and where partners only meet in one-shot interactions (although real interactions may often be repeated or extend over time). Because choosiness and searching will be associated with various costs, there must be sufficient variability to choose from in order to offset such costs (McNamara & Leimar 2010).

The choices that drive biological markets are of course the result of particular traits of the interacting individuals. In order to understand the details of the interaction, one needs to appreciate the effects imposed by those traits. Social insect foraging is an important example with a strong influence on pollination biology (von Frisch 1967; Schaffer et al. 1983; Internicola et al. 2007) and on the many mutualisms between ants and their trophobionts. For instance, many associations between lycaenid butterfly larvae and ants are based on nutritional rewards delivered by lycaenid larvae in exchange for protective benefits of ant attendance. The larvae of some lycaenid species occur in aggregations and these species invariably associate with ants. Pierce et al. (1987) suggested that group living could be a way for the larvae to increase the protection from ant attendance and decrease the cost of the association. In a series of experiments, Axén & Pierce (1998) demonstrated that larvae of the group-living lycaenid *Jalmenus evagoras* modify the rate of reward delivery as a function of group size. A solitary larva secretes considerably more rewards than a group member (when controlling for the number of ants directly attending the larva). From the point of view of the ants, the larval aggregations seem disadvantageous, but ant foraging and tending behaviour results in a steady supply of ants to the aggregations, making these favourable for the larvae. Axén & Pierce (1998) estimated that ants would nearly triple their rewards if they were to break up naturally occurring aggregations into singletons (but the ants do not attempt this). The study indicates that larvae do not compete for ant attendance within a group. Nevertheless, larvae have to compete with other food sources of the ants, which could be other larval groups. Thus, the reason a singleton larva delivers more rewards should be to attract enough ants away from foraging elsewhere (see also Connor (2010) for a discussion of *n*-player cooperation).

Even if biological markets depend on particular traits and processes of exchange, there are a number of examples of market dynamics or market adjustments that show a certain similarity to the influence of variation in supply and demand in idealized markets (Noë & Hammerstein 1994, 1995). So, for instance, in mutualisms where ants protect lycaenid larvae from parasitoids and other enemies, it has been found that a larva will sharply increase its delivery of food rewards when it perceives itself to be under attack from enemies or when ants return to it after an interruption in attendance (Leimar & Axén 1993; Axén et al. 1996; Agrawal & Fordyce 2000). The reactions illustrate the general importance of behavioural plasticity for the regulation of species interactions (Agrawal 2001), for instance, the use of signals to attract a mutualistic partner when the need for the partner is high (Axén et al. 1996; Agrawal & Fordyce 2000; Morales et al. 2008). This kind of influence of the availability or value of partners may also be present in cleaning mutualisms. For instance, 'local' clients for which long-distance moves are costly are cleaned less well than long-range travellers, who can easily switch between cleaning stations and thereby exert partner choice (Bshary & Noë 2003), which is exactly what one would expect from the economic theory of monopolistic competition: buyers with few alternative sources of supply will have less advantageous transactions than those who can shop around (Bowles & Hammerstein 2003). There are also data to suggest that cleaner service quality becomes better when clients are more scarce (Soares et al. 2008). Similarly, in the social behaviour of vervet monkeys, scarce food providers were found to receive more grooming (Fruteau et al. 2009). Such dynamics and adjustments represent potentially general properties of biological markets and are therefore of broad interest.

3. BY-PRODUCT MUTUALISM, PSEUDO-RECIPROCITY AND DEFENCES AGAINST EXPLOITATION

By-product effects are present when traits that benefit their bearers directly, additionally impose benefits or costs on other individuals. Such effects are likely to be among the most important and widespread facilitators of the evolution of cooperation. They frequently operate in conjunction with choices in biological markets, where they regulate the detailed post-choice transactions, such as pollen transfer and fertilization as a by-product of the collection of nectar and pollen by visiting mutualists. A reason to expect by-product effects to play significant roles, both for inter- and intraspecific cooperative interactions, is that they correspond to a broad set of circumstances, involving many kinds of interactions (Leimar & Connor 2003), and from this rich base, different kinds of cooperative relations can evolve. For instance, what are essentially defence traits can become either rewards (Oliver et al. 2009), sanctions (Murray 1985; Kiers & Denison 2008) or traits that otherwise limit exploitation (Herre et al. 2008). Thus, a traditional suggestion for the evolution of ant association with trophobionts, such as aphids and lycaenid larvae, is that the original function of the myrmecophilous traits was a reduction in the rate of predation by ants through appeasement (Atsatt 1981; Pierce et al. 2002; Oliver et al. 2009),

which was followed by or accompanied by ant protection from other enemies, such as parasitoids.

The work by Connor (1986, 1995) was instrumental in shifting the understanding of the role of by-product effects from the initial description of by-product mutualism as mutual incidental benefits derived from the partners' actions (Brown 1983), to also include further elaborations such as investments to obtain or enhance by-product benefits (i.e. pseudo-reciprocity). Such elaborations unfold a rich spectrum of possibilities. The applications range from a wealth of interspecific mutualisms (Connor 1995) to intraspecific interactions such as cooperative breeding and group living (Connor 1986; Kokko et al. 2001; Clutton-Brock 2009) and, possibly, joint predator inspection in fish (Connor 1996). Another intraspecific example is nuptial gift giving, where a male transfers resources to a female at mating, which is a form of male–female reproductive cooperation that is common in some groups of insects (Boggs 1990). The phenomenon can be interpreted as an investment of nutrient resources by a male to obtain the by-product benefit of delayed remating by the female, entailing enhanced fertilization success for the male (Leimar & Connor 2003).

Mutualistic interactions of the kind where each partner invests resources in the other would seem the likeliest candidates for the operation of reciprocity, but even in such cases there are good reasons to instead look for mutual investments in by-product benefits. A case in point is mycorrhizal symbiosis. Many species of vascular plants form mycorrhiza with fungal mycelium in the soil (Smith & Read 1997). The association is based on the transport of organic carbon from plant photosynthesis to the fungal partner as well as a transport of soil mineral nutrients, such as phosphorus, from fungus to plant. These transports often represent mutual investment of plant and fungus in each other. Leimar & Connor (2003) suggested that the interaction might be understood as an investment by the fungus in the by-product benefit of local new root growth of the plant, which the investing fungus would have a competitive advantage in colonizing, together with investment by the plant in the by-product benefit of conferring a competitive advantage in the soil to more beneficial fungi. Recent split-root experiments (Bever et al. 2009; Kennedy et al. 2009), investigating the dynamics of mycorrhizal symbiosis, tend to support these suggestions. Active pollination in yucca moths (Pellmyr 1997) and fig wasps (Jousselin et al. 2003), as well as interactions between *Acacia* ant plants and their mutualistic *Pseudomyrmex* ants (Heil et al. 2009), could be other examples where reciprocal investments are maintained through mutual by-product effects.

As mentioned, by-product effects of defences against exploitation can be important in the evolution of cooperation. Thus, a response that acts as a sanction can directly benefit the individual imposing it, as when yuccas abort flowers that are heavily exploited by yucca moth oviposition (Pellmyr & Huth 1994), thereby avoiding investment in tissue with little or no fitness return. In such a case, the sanction occurs as a by-product effect. Legume–rhizobium mutualism is an example where, following the work by Denison (2000), the role of sanctions has been examined in some detail. Rhizobia are bacteria that fix atmospheric N_2 inside root nodules of leguminous plants. Different strains vary in the extent to which they provide this service, leading to the possibility that plants might senesce or otherwise limit investment into nodules containing low N_2-fixing rhizobia. Examining the trade-off for a plant between the amount of resource allocated to growth and the productivity of those resources, West et al. (2002) concluded that a plant may benefit directly by sanctioning less effective nodules. Experiments have shown that legumes in fact do sanction nodules that do not fix any N_2 (Kiers et al. 2003). Some subsequent work has contributed to the support for the role of sanctions (Simms et al. 2006), but other work has raised questions about the importance of sanctions as a regulating mechanism for less extreme, natural variation in the level of fixing of N_2 by rhizobia (Kiers & Denison 2008; Sachs & Simms 2008; Oono et al. 2009). There is also recent work suggesting that the role of sanctions is small (Marco et al. 2009), in accordance with Bronstein's (2001) claim that cheating often occurs in mutualisms without any punishment. A complementary suggestion is that genetic variability in plants and rhizobia together with partner choice may be more important than sanctions in maintaining legume–rhizobium mutualism (Heath & Tiffin 2007, 2009).

Results from studies of other mutualisms, for instance, figs and fig wasps (Herre et al. 2008; Wang et al. 2008; Jandér & Herre 2010) and ant plants and ants (Edwards et al. 2006; Nicklen & Wagner 2006; Edwards & Yu 2008), support the general idea that defences play an important role in the evolutionary maintenance of cooperation—if not always as sanctions then at least as a means of reducing the cost of being exploited. Overall, even though the question of the occurrence and interpretation of sanctions in legume–rhizobium mutualism is not settled, there seems to be little doubt that by-product effects have proven themselves as cornerstones for the understanding of the evolution of cooperation. Their seeming importance might even increase as more knowledge accumulates.

4. COMMON INTEREST

The basic idea of common interest is that organisms have a stake in the success of others or in the success of a joint 'project'. The joint project can be as simple as cooperative hunting in social carnivores or as elaborate as the contribution of different genes and regulatory elements to the development of a multicellular organism. Common interest often involves by-product benefits and investments, but it represents a different perspective on cooperation that includes ideas about the evolution of organisms and superorganisms (Queller & Strassmann 2009; Strassmann & Queller 2010). A general circumstance contributing to common interest is if partners are likely to stay together in the future, perhaps because of costs associated with partner change, resulting in partner fidelity.

Evolution of increased dependence of partners on each other is important for the generation of common interest. This is evident for the emergence of organisms, but it can also apply to less intimate associations. For instance, *Acacia* ant plants house mutualistic ants and provide them with extrafloral nectar. A notable property of the nectar is that it contains glucose and fructose but virtually no sucrose (Heil *et al.* 2005; Kautz *et al.* 2009), which makes it unattractive to ants in general, whose workers primarily respond to sucrose solution. The mutualistic *Pseudomyrmex* ants that are specialized to live on *Acacia* are, however, attracted to, and dependent on, the nectar, having lost the capacity to digest sucrose (Kautz *et al.* 2009). Presumably, the increased dependence evolved as a by-product of the advantage of the plant to be less attractive to non-mutualistic ants, together with the need for the mutualistic ants to adapt to and be efficient in their main habitat.

The suggestion by Frank (1994) that the build-up of cross-species trait correlations could play an important role in the origin and maintenance of cooperation between species started a new line of thinking about the evolution of mutualism. Nevertheless, the idea is a variation on a well-explored theme, exemplifying common interest. A major issue for the study of the origin of life has been, and continues to be, the problem of how different macromolecules came to cooperate in the execution of functions such as metabolism and replication. Eigen's hypercycles (Eigen & Schuster 1977) were an early attempt at solving the problem, by having supposedly mutualistic molecules interacting in random-encounter situations. The attempt was criticized by Maynard Smith (1979), who pointed out that a lack of statistical correlation between variants of the different types of molecules would seem to prevent the evolution of an improvement of the ability of one molecule to assist another. The now generally accepted solution to the dilemma is that in order for the evolution of mutualism to take place, the different molecules need to co-occur in circumstances that restrict their mobility, for instance, by being together in some form of compartment (Maynard Smith & Szathmáry 1995; Koonin & Martin 2005), which gives rise to common interest. This is in line with the arguments about partner fidelity (Bull & Rice 1991) and trait correlations in mutualism (Frank 1994).

The general validity of such arguments is not in doubt, and the applicability to spatial structure was further verified in the models by Doebeli & Knowlton (1998) and Yamamura *et al.* (2004). It is therefore of interest to inquire about the importance of processes of build-up of spatial trait correlations (Frank 1994), in comparison with other mechanisms contributing to the evolution of cooperation. Foster & Wenseleers (2006) argued that the need for several generations of cooperator association for the build-up of interspecies (genetic) trait correlations implies that they are likely to be of less importance than more directly acting effects. However, because of their generality, such processes might still represent an important influence on the evolution of mutualism, but at present there seems to be a lack of data bearing on the question.

An extreme form of cooperation is that of the genes operating in an organism. Even the most comprehensive survey on selfish genetic elements (Burt & Trivers 2006) expresses the view that most genes act most of the time to the benefit of the organism. Intragenomic cooperation is thus based on the genes' shared interest to 'keep the organism running' that carries them into the next generation and treats its passengers in a rather fair way. The eukaryotic organism's fair transmission of genes relates in particular to the organization of mitotic and meiotic cell divisions, where molecular devices such as the 'spindle check point' supervise 'passenger movements'. The emergence of such extreme common interest represents a major transition in evolution (Maynard Smith & Szathmáry 1995).

The idea that there may be general processes acting to increase common interest, both in the evolution of integrated organisms and more generally for groups and communities, was pursued by Leigh (1977, 1991, 2010). Frank (2003) reviewed the topic, claiming that the repression of competition within groups through mechanisms such as policing, which can be a source of common interest, is a major force shaping the evolution of cooperation. While this is an interesting and important possibility, we feel that it is not yet settled how large a role particular suggested mechanisms of suppression of competition might play in the generation of common interest. There is also the question of how phenomena such as policing should be interpreted, either as adaptations for the repression of competition or rather as side effects of other adaptations. This is still an area open to inquiry.

5. CONCLUSION

Keeping in mind the possibility that the enormous range of mutualistic species interactions and the truly impressive integrated complexity of cells and organisms are largely products of direct fitness benefits, it seems that the topic we have dealt with here is of major concern (Hammerstein & Leimar 2006). It is therefore a good sign that the level of interest in it is clearly increasing. We believe that a further balancing of the possible importance of different major hypotheses for the evolution of cooperation is called for. For instance, in a recent, frequently cited paper, Nowak (2006) presented five supposedly very basic principles of the evolution of cooperation. To a large extent, these principles are variants of ideas from the study of interactions between relatives and of reciprocity. The five principles show rather little overlap with the processes and mechanisms we have dealt with here and, furthermore, sometimes have a rather tenuous link to empirical observation outside humans (Brosnan *et al.* 2010; Connor 2010; Melis & Semmann 2010). We think that one of the major advantages of a broader view of the processes that may have contributed to the evolution of cooperation is that this encourages an increased contact with empirical observation (Leimar & Hammerstein 2006), by letting one kind of explanation compete with another. A desire to understand the traits that have evolved in real organisms is, after all, the major

reason for the interest in the evolution of cooperation. In our opinion, the time has come to put a stronger emphasis on work that brings theory and observation of cooperation into closer contact.

REFERENCES

Agrawal, A. A. 2001 Phenotypic plasticity in the interactions and evolution of species. *Science* **294**, 321–326. (doi:10.1126/science.1060701)

Agrawal, A. A. & Fordyce, J. A. 2000 Induced indirect defence in a lycaenid–ant association: the regulation of a resource in a mutualism. *Proc. R. Soc. Lond. B* **267**, 1857–1861. (doi:10.1098/rspb.2000.1221)

Atsatt, P. R. 1981 Lycaenid butterflies and ants: selection for enemy-free space. *Am. Nat.* **118**, 638–654. (doi:10.1086/283859)

Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)

Axén, A. H. & Pierce, N. E. 1998 Aggregation as a cost-reducing strategy for lycaenid larvae. *Behav. Ecol.* **9**, 109–115. (doi:10.1093/beheco/9.2.109)

Axén, A. H., Leimar, O. & Hoffman, V. 1996 Signalling in a mutualistic interaction. *Anim. Behav.* **52**, 321–333. (doi:10.1006/anbe.1996.0178)

Backwell, P. R. Y. & Jennions, M. D. 2004 Coalition among male fiddler crabs. *Nature* **430**, 417. (doi:10.1038/430417a)

Bever, J. D., Richardson, S. C., Lawrence, B. M., Holmes, J. & Watson, M. 2009 Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecol. Lett.* **12**, 13–21. (doi:10.1111/j.1461-0248.2008.01254.x)

Boggs, C. L. 1990 A general model of the role of male-donated nutrients in female insects' reproduction. *Am. Nat.* **136**, 598–617. (doi:10.1086/285118)

Bowles, S. & Hammerstein, P. 2003 Does market theory apply to biology? In *Genetical and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 153–165. Cambridge, MA: MIT Press.

Bronstein, J. L. 2001 The exploitation of mutualisms. *Ecol. Lett.* **4**, 277–287. (doi:10.1046/j.1461-0248.2001.00218.x)

Bronstein, J. L. 2009 The evolution of facilitation and mutualism. *J. Ecol.* **97**, 1160–1170. (doi:10.1111/j.1365-2745.2009.01566.x)

Brosnan, S. F., Salwiczek, L. & Bshary, R. 2010 The interplay of cognition and cooperation. *Phil. Trans. R. Soc. B* **365**, 2699–2710. (doi:10.1098/rstb.2010.0154)

Brown, J. L. 1983 Cooperation: a biologist's dilemma. *Adv. Study Behav.* **13**, 1–37. (doi:10.1016/S0065-3454(08)60284-3)

Bshary, R. & Bergmüller, R. 2008 Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* **21**, 405–420. (doi:10.1111/j.1420-9101.2007.01482.x)

Bshary, R. & Noë, R. 2003 The ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 167–184. Cambridge, MA: MIT Press.

Bshary, R. & Schäffer, D. 2002 Choosy reef fish select cleaner fish that provide high-quality service. *Anim. Behav.* **63**, 557–564. (doi:10.1006/anbe.2001.1923)

Bull, J. J. & Rice, W. R. 1991 Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* **149**, 63–74. (doi:10.1016/S0022-5193(05)80072-4)

Burt, A. & Trivers, R. 2006 *Genes in conflict: the biology of selfish elements.* Cambridge, MA: Harvard University Press.

Chittka, L. & Schürkens, S. 2001 Successful invasion of a flower market. *Nature* **411**, 653. (doi:10.1038/35079676)

Clutton-Brock, T. H. 2009 Cooperation between non-kin in animal societies. *Nature* **462**, 51–57. (doi:10.1038/nature08366)

Connor, R. C. 1986 Pseudo-reciprocity: investing in mutualism. *Anim. Behav.* **34**, 1562–1566. (doi:10.1016/S0003-3472(86)80225-1)

Connor, R. C. 1995 The benefits of mutualism: a conceptual framework. *Biol. Rev.* **70**, 427–457. (doi:10.1111/j.1469-185X.1995.tb01196.x)

Connor, R. C. 1996 Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Anim. Behav.* **51**, 451–454. (doi:10.1006/anbe.1996.0042)

Connor, R. C. 2007 Invested, extracted and byproduct benefits: a modified scheme for the evolution of cooperation. *Behav. Proc.* **76**, 109–113. (doi:10.1016/j.beproc.2007.01.014)

Connor, R. C. 2010 Cooperation beyond the dyad: on simple models and a complex society. *Phil. Trans. R. Soc. B* **365**, 2687–2697. (doi:10.1098/rstb.2010.0150)

Cushman, J. H. & Beattie, A. J. 1991 Mutualisms: assessing the benefits to hosts and visitors. *Trends. Ecol. Evol.* **6**, 193–195. (doi:10.1016/0169-5347(91)90213-H)

Denison, R. F. 2000 Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *Am. Nat.* **156**, 567–576. (doi:10.1086/316994)

Detto, T., Jennions, M. D. & Backwell, P. R. Y. 2010 When and why do territorial coalitions occur? Experimental evidence for a fiddler crab. *Am. Nat.* **175**, E119–E125. (doi:10.1086/651588)

Doebeli, M. & Knowlton, N. 1998 The evolution of inter-specific mutualisms. *Proc. Natl Acad. Sci. USA* **95**, 8676–8680. (doi:10.1073/pnas.95.15.8676)

Edwards, D. P. & Yu, D. W. 2007 The roles of sensory traps in the origin, maintenance, and breakdown of mutualism. *Behav. Ecol. Sociobiol.* **61**, 1321–1327. (doi:10.1007/s00265-007-0369-3)

Edwards, D. P. & Yu, D. W. 2008 Tolerating castration by hiding flowers in plain sight. *Behav. Ecol. Sociobiol.* **63**, 95–102. (doi:10.1007/s00265-008-0639-8)

Edwards, D. P., Hassall, M., Sutherland, W. J. & Yu, D. W. 2006 Selection for protection in an ant-plant mutualism: host sanctions, host modularity and the principal–agent game. *Proc. R. Soc. B* **273**, 595–602. (doi:10.1098/rspb.2005.3273)

Eigen, M. & Schuster, P. 1977 The hypercycle. A principle of natural self-organization. Part A: emergence of the hypercycle. *Naturwissenschaften* **64**, 541–565. (doi:10.1007/BF00450633)

Ferrière, R., Gauduchon, M. & Bronstein, J. L. 2007 Evolution and persistence of obligate mutualists: competition for partners and evolutionary immunization. *Ecol. Lett.* **10**, 115–126. (doi:10.1111/j.1461-0248.2006.01008.x)

Fischer, M. K., Hoffmann, K. H. & Völkl, W. 2001 Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. *Oikos* **92**, 531–541. (doi:10.1034/j.1600-0706.2001.920314.x)

Foster, K. R. & Wenseleers, T. 2006 A general model for the evolution of mutualisms. *J. Evol. Biol.* **19**, 1283–1293. (doi:10.1111/j.1420-9101.2005.01073.x)

Frank, S. A. 1994 Genetics of mutualism: the evolution of altruism between species. *J. Theor. Biol.* **170**, 393–400. (doi:10.1006/jtbi.1994.1200)

Frank, S. A. 2003 Repression of competition and the evolution of cooperation. *Evolution* **57**, 693–705.

Fruteau, C., Voelkl, B., van Damme, E. & Noë, R. 2009 Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc. Natl Acad. Sci. USA* **106**, 12 007–12 012. (doi:10.1073/pnas.0812280106)

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L. & Boag, P. T. 2000 Disruptive sexual selection for plumage coloration in a passerine bird. *Nature* **407**, 1000–1003. (doi:10.1038/35039500)

Hammerstein, P. 2003 Why is reciprocity so rare in social animals? A protestant appeal. In *Genetical and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 83–93. Cambridge, MA: MIT Press.

Hammerstein, P. & Leimar, O. 2006 Cooperating for direct fitness benefits. *J. Evol. Biol.* **19**, 1400–1402. (doi:10.1111/j.1420-9101.2006.01160.x)

Heath, K. D. & Tiffin, P. D. 2007 Context dependence in the evolution of plant and rhizobial mutualists. *Proc. R. Soc. B* **274**, 1905–1912. (doi:10.1098/rspb.2007.0495)

Heath, K. D. & Tiffin, P. D. 2009 Stabilizing mechanisms in a legume–rhizobium mutualism. *Evolution* **63**, 652–662. (doi:10.1111/j.1558-5646.2008.00582.x)

Heil, M., Rattke, J. & Boland, W. 2005 Postsecretory hydrolysis of nectar sucrose and specialization in ant/plant mutualism. *Science* **308**, 560–563. (doi:10.1126/science.1107536)

Heil, M., Gonzalez-Teuber, M., Clement, L. W., Kautz, S., Verhaagh, M. & Bueno, J. C. S. 2009 Divergent investment strategies of *Acacia* myrmecophytes and the coexistence of mutualists and exploiters. *Proc. Natl Acad. Sci. USA* **106**, 18 091–18 096. (doi:10.1073/pnas.0904304106)

Herre, E. A., Knowlton, N., Mueller, U. G. & Rehner, S. A. 1999 The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* **14**, 49–53. (doi:10.1016/S0169-5347(98)01529-8)

Herre, E. A., Jandér, K. C. & Machado, C. A. 2008 Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Ann. Rev. Evol. Ecol. Syst.* **39**, 439–458. (doi:10.1146/annurev.ecolsys.37.091305.110232)

Internicola, A. I., Page, P. A., Bernasconi, G. & Gigord, L. D. B. 2007 Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: an experimental test of the effects of floral colour similarity and spatial mingling. *Funct. Ecol.* **21**, 864–872. (doi:10.1111/j.1365-2435.2007.01303.x)

Jandér, K. C. & Herre, E. A. 2010 Host sanctions and pollinator cheating in the fig tree–fig wasp mutualism. *Proc. R. Soc. B* **277**, 1481–1488. (doi:10.1098/rspb.2009.2157)

Jousselin, E., Hossaert-McKay, M., Herre, E. A. & Kjellnberg, F. 2003 Why do fig wasps actively pollinate monoecious figs? *Oecologia* **134**, 381–387.

Kautz, S., Lumbsch, H. T., Ward, P. S. & Heil, M. 2009 How to prevent cheating: a digestive specialization ties mutualistic plant-ants to their ant-plant partners. *Evolution* **63**, 839–853. (doi:10.1111/j.1558-5646.2008.00594.x)

Kennedy, P. G., Peay, K. G. & Bruns, T. D. 2009 Root tip competition among ectomycorrhizal fungi: are priority effects a rule or an exception? *Ecology* **90**, 2098–2107. (doi:10.1890/08-1291.1)

Kiers, E. T. & Denison, R. F. 2008 Sanctions, cooperation, and the stability of plant–rhizosphere mutualisms. *Ann. Rev. Ecol. Evol. Syst.* **39**, 215–236. (doi:10.1146/annurev.ecolsys.39.110707.173423)

Kiers, E. T., Rousseau, R. A., West, S. A. & Denison, R. F. 2003 Host sanctions and the legume–rhizobium mutualism. *Nature* **425**, 78–81. (doi:10.1038/nature01931)

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196. (doi:10.1098/rspb.2000.1349)

Koonin, E. V. & Martin, W. 2005 On the origin of genomes and cells within inorganic compartments. *Trends Genet.* **21**, 647–654. (doi:10.1016/j.tig.2005.09.006)

Lehmann, L. & Rousset, F. 2010 How life history and demography promote or inhibit the evolution of helping behaviours. *Phil. Trans. R. Soc. B* **365**, 2599–2617. (doi:10.1098/rstb.2010.0138)

Leigh Jr, E. G. 1977 How does selection reconcile individual advantage with the good of the group? *Proc. Natl Acad. Sci. USA* **74**, 4542–4546. (doi:10.1073/pnas.74.10.4542)

Leigh Jr, E. G. 1991 Genes, bees and ecosystems: the evolution of common interest among individuals. *Trends Ecol. Evol.* **8**, 257–262.

Leigh Jr, E. G. 2010 The group selection controversy. *J. Evol. Biol.* **23**, 6–19.

Leimar, O. & Axén, A. H. 1993 Strategic behaviour in an interspecific mutualism: interactions between lycaenid larvae and ants. *Anim. Behav.* **46**, 1177–1182. (doi:10.1006/anbe.1993.1307)

Leimar, O. & Connor, R. C. 2003 By-product benefits, reciprocity, and pseudoreciprocity in mutualism. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 203–222. Cambridge, MA: MIT Press.

Leimar, O. & Hammerstein, P. 2006 Facing the facts. *J. Evol. Biol.* **19**, 1403–1405. (doi:10.1111/j.1420-9101.2006.01156.x)

Little, A. E. F. & Currie, C. R. 2009 Parasites may help stabilize cooperative relationships. *BMC Evol. Biol.* **9**, 124. (doi:10.1186/1471-2148-9-124)

Marco, D. E., Pérez-Arnedo, R., Hidalgo-Perea, Á., Olivares, J., Ruiz-Sainz, J. E. & Sanjúan, J. 2009 A mechanistic molecular test of the plant-sanction hypothesis in legume–rhizobia mutualism. *Acta. Oecol.* **35**, 664–667. (doi:10.1016/j.actao.2009.06.005)

Maynard Smith, J. 1979 Hypercycles and the origin of life. *Nature* **280**, 445–446.

Maynard Smith, J. & Szathmáry, E. 1995 *The major transitions in evolution*. Oxford, UK: Oxford University Press.

McNamara, J. M. & Leimar, O. 2010 Variation and the response to variation as a basis for successful cooperation. *Phil. Trans. R. Soc. B* **365**, 2627–2633. (doi:10.1098/rstb.2010.0159)

Melis, A. P. & Semmann, D. 2010 How is human cooperation different? *Phil. Trans. R. Soc. B* **365**, 2663–2674. (doi:10.1098/rstb.2010.0157)

Morales, M. A., Barone, J. L. & Henry, C. S. 2008 Acoustic alarm signalling facilitates predator protection of treehoppers by mutualist ant bodyguards. *Proc. R. Soc. B* **275**, 1935–1941. (doi:10.1098/rspb.2008.0410)

Murray, M. G. 1985 Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol. J. Linn. Soc.* **26**, 69–81. (doi:10.1111/j.1095-8312.1985.tb01552.x)

Nicklen, E. F. & Wagner, D. 2006 Conflict resolution in an ant-plant interaction: *Acacia constricta* traits reduce ant costs to reproduction. *Oecologia* **148**, 81–87. (doi:10.1007/s00442-006-0359-6)

Noë, R. & Hammerstein, P. 1994 Biological markets: supply and demand determine the effect of partner choice in co-operation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**, 1–11. (doi:10.1007/BF00167053)

Noë, R. & Hammerstein, P. 1995 Biological markets. *Trends Ecol. Evol.* **10**, 336–339. (doi:10.1016/S0169-5347(00)89123-5)

Noë, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. 1991 The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology* **87**, 97–118. (doi:10.1111/j.1439-0310.1991.tb01192.x)

Nowak, M. A. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560–1563. (doi:10.1126/science.1133755)

Oliver, T. H., Leather, S. R. & Cook, J. M. 2009 Tolerance traits and the stability of mutualism. *Oikos* **118**, 346–352. (doi:10.1111/j.1600-0706.2008.17045.x)

Oono, R., Denison, R. F. & Kiers, E. T. 2009 Controlling the reproductive fate of rhizobia: how universal are legume sanctions? *New Phytol.* **183**, 967–979. (doi:10.1111/j.1469-8137.2009.02941.x)

Pellmyr, O. 1997 Pollinating seed eaters: why is active pollination so rare? *Ecology* **78**, 1655–1660. (doi:10.1890/0012-9658(1997)078[1655:PSEWIA]2.0.CO;2)

Pellmyr, O. & Huth, C. J. 1994 Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**, 257–260. (doi:10.1038/372257a0)

Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J. & Benbow, K. F. 1987 The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* **21**, 237–248. (doi:10.1007/BF00292505)

Pierce, N. E., Heath, A., Lohman, D. J., Mathew, J., Rand, D. B. & Travassos, M. A. 2002 The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Ann. Rev. Entomol.* **47**, 733–771. (doi:10.1146/annurev.ento.47.091201.145257)

Queller, D. C. & Strassmann, J. E. 2009 Beyond society: the evolution of organismality. *Phil. Trans. R. Soc. B* **364**, 3143–3155. (doi:10.1098/rstb.2009.0095)

Sachs, J. L. & Simms, E. L. 2006 Pathways to mutualism breakdown. *Trends Ecol. Evol.* **21**, 585–592. (doi:10.1016/j.tree.2006.06.018)

Sachs, J. L. & Simms, E. L. 2008 The origins of uncooperative rhizobia. *Oikos* **117**, 961–966. (doi:10.1111/j.0030-1299.2008.16606.x)

Schaffer, W. M., Zeh, D. W., Buchmann, S. L., Kleinhans, S., Schaffer, M. W. & Antrim, J. 1983 Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* **64**, 564–577. (doi:10.2307/1939976)

Simms, E. L., Taylor, D. L., Provich, J., Shefferson, R. P., Sachs, J. L., Urbina, M. & Tauszik, Y. 2006 An empirical test of partner choice mechanisms in a wild legume–rhizobium interaction. *Proc. R. Soc. B* **273**, 77–81. (doi:10.1098/rspb.2005.3292)

Smith, S. E. & Read, D. J. 1997 *Mycorrhizal symbiosis*. San Diego, CA: Academic Press.

Soares, M. C., Bshary, R., Cardoso, S. C. & Côté, I. 2008 Does competition for clients increase service quality in cleaning gobies? *Ethology* **114**, 625–632. (doi:10.1111/j.1439-0310.2008.01510.x)

Strassmann, J. E. & Queller, D. C. 2010 The social organism: congresses, parties, and committees. *Evolution* **64**, 605–616. (doi:10.1111/j.1558-5646.2009.00929.x)

Trivers, R. L. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 33–57.

van Baalen, M. & Jansen, V. A. A. 2001 Dangerous liaisons: the ecology of private interest and common good. *Oikos* **95**, 211–224. (doi:10.1034/j.1600-0706.2001.950203.x)

Völkl, W., Woodring, J., Fischer, M., Lorentz, M. W. & Hoffmann, K. H. 1999 Ant–aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia* **118**, 483–491.

von Frisch, K. 1967 *The dance language and orientation of the bees*. Cambridge, MA: Harvard University Press.

Wang, R. W., Shi, L., Ai, S. M. & Zheng, Q. 2008 Trade-off between reciprocal mutualists: local resource availability-oriented interaction in fig/fig wasp mutualism. *J. Anim. Ecol.* **77**, 616–623. (doi:10.1111/j.1365-2656.2008.01359.x)

West, S. A., Kiers, E. T., Pen, I. & Denison, R. F. 2002 Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? *J. Evol. Biol.* **15**, 830–837. (doi:10.1046/j.1420-9101.2002.00441.x)

Yamamura, N., Higashi, M., Behera, N. & Wakano, J. Y. 2004 Evolution of mutualism through spatial effects. *J. Theor. Biol.* **226**, 421–428. (doi:10.1016/j.jtbi.2003.09.016)