

Theory of Cooperation

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Cooperation is defined as any adaptation that has evolved, at least in part, to increase the reproductive success of the actor's social partners. Inclusive fitness theory reveals that cooperation can be favoured by natural selection owing to either direct fitness benefits (mutually beneficial cooperation) or indirect fitness benefits (altruistic cooperation). Direct fitness benefits can arise as a simple by-product of cooperation, or else owing to the existence of enforcement mechanisms, which may be fixed or conditioned according to the individual's cooperative behaviour. Indirect fitness benefits can arise when cooperation occurs between genetically similar individuals, as a consequence of limited dispersal, kin discrimination or greenbeard mechanisms. These theoretical mechanisms are illustrated with empirical examples, from laboratory experiments to field studies.

The Problem of Cooperation

Adaptation is driven by natural selection, which has been described as the 'survival of the fittest'. Natural selection favours those individuals who achieve the greatest reproductive success relative to the rest of the population (Darwin, 1859; Fisher, 1930), and this has led to a view that nature is 'red in tooth and claw', and populated by Machiavellian individuals only interested in their own success. However, cooperative behaviour, which increases the reproductive success of individuals other than the actor, abounds in the natural world. All else being equal, cooperation decreases the relative reproductive success of the actor and hence would appear to be disfavoured by natural selection. Accordingly, explaining the selective value of cooperation is one of the greatest problems faced by evolutionary biologists (West *et al.*, 2007a).

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Article Contents

- The Problem of Cooperation
- Inclusive Fitness Theory
- Direct Fitness Benefits
- Indirect Fitness Benefits
- Future Directions

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More generally, the problem of why individuals cooperate poses a major challenge for sociologists, anthropologists, economists and philosophers. The problem is often encapsulated as the parable of the 'tragedy of the commons' (Hardin, 1968). Here, a community of herdsmen graze their cattle on a common pasture. At the level of the community, there will be an optimal level of exploitation of the pasture which balances both profits, in terms of fed animals that can be sold at market, and costs, in terms of sustainability of this shared resource. However, while the costs of overexploitation are shared among all individuals who graze their animals on the commons, the benefits of grazing additional livestock accrue directly to the individual herdsman. This leads to each individual deriving a net benefit from grazing more and more animals on the commons, until the pasture is destroyed from overgrazing – to everyone's detriment. Here, the problem is what stops – or could stop – the self-interested behaviour of the individual from damaging the interests of the group?

Inclusive Fitness Theory

Within evolutionary biology, an overview of possible solutions to the problem of cooperation is provided by inclusive fitness theory (Hamilton, 1964; Grafen, 2006; Gardner *et al.*, 2011). This theory is based on the understanding that adaptations function for the purpose of transmitting the underlying genes to future generations and that this can be achieved by either (1) increasing the reproductive success of the individual ('direct fitness' benefits) or else (2) increasing the reproductive success of other individuals who carry copies of the same genes ('indirect fitness' benefits). This insight is summarised by Hamilton's (1963, 1964) rule, which states that a behaviour (or indeed, any trait) will be favoured by natural selection provided that

$$rb - c > 0$$

where c is the fitness cost of the behaviour for the actor, b the fitness benefit for the recipient and r the genetic relatedness of the actor and the recipient. Here, the term $-c$ captures the direct fitness effect, and the term rb captures the indirect fitness effect, of the behaviour. The sum of these two effects, $rb - c$, is termed the 'inclusive fitness' effect (Figure 1). Note that the costs and benefits are measured in terms of lifetime reproductive success, or reproductive value, rather than short-term effects on fecundity or other vital rates. See also: [Hamilton, William Donald](#)

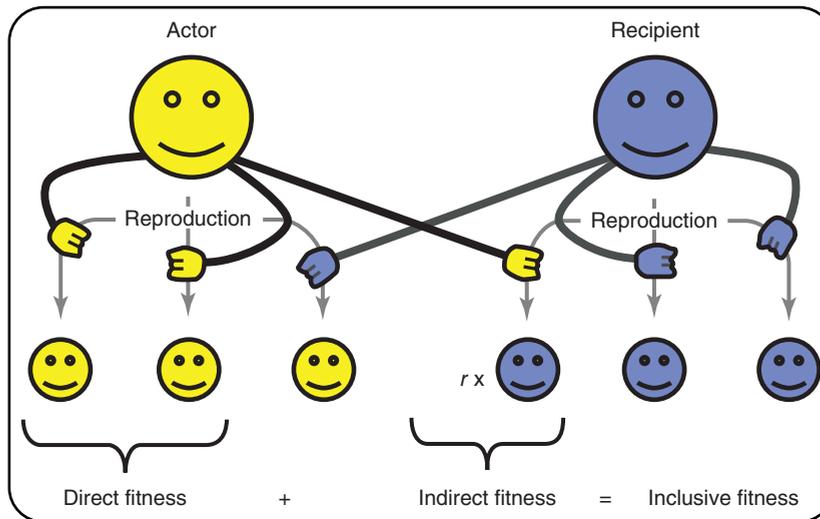


Figure 1 Inclusive fitness is the sum of direct fitness and indirect fitness. Social behaviours affect the reproductive success of individuals beyond the actor. The impact on the actor's own reproductive success is the direct fitness effect. The impact on the reproductive success of social partners, weighted by the relatedness of the actor to the recipient, is the indirect fitness effect. In particular, inclusive fitness does not include all the reproductive success of relatives, only that which is due to the behaviour of the actor (yellow hands). In addition, inclusive fitness does not include any of the reproductive success of the actor that is due to the actions of its social partners (blue hands). Reproduced from West *et al.* (2007a) © Elsevier.

This scheme allows a classification of the four basic types of social behaviour (Hamilton, 1964; West *et al.*, 2007a,b). A behaviour that incurs a fitness cost to the actor and a fitness benefit to the recipient ($b > 0$ & $c > 0$) is termed 'altruism'. A behaviour that benefits both the actor and the recipient ($b > 0$ & $c < 0$) is termed 'mutual benefit'. A behaviour that benefits the actor and incurs a cost for the recipient ($b < 0$ & $c < 0$) is termed 'selfishness'. And, finally, a behaviour that incurs a cost for both the actor and the recipient ($b < 0$ & $c > 0$) is termed 'spite'. More generally, we describe any behaviour that benefits the recipient ($b > 0$) as 'helping' (this includes both altruism and mutual benefit), and we describe any behaviour that incurs a cost for the recipient ($b < 0$) as 'harming' (this includes both selfishness and spite). Formally, cooperation is defined as a helping behaviour that has been favoured, at least in part, owing to the benefit it gives to the recipient. This includes all altruistic behaviours and any mutually beneficial behaviour in which the direct benefit to the actor follows as a consequence of the benefit to the recipient (West *et al.*, 2007a,b).

Direct Fitness Benefits

The first class of Darwinian explanations for cooperation are those that rely upon direct fitness benefits, that is, mutually beneficial cooperation (**Figure 2**). Here, we distinguish two basic types: by-product benefits, which arise as a basic consequence of otherwise self-interested behaviour of the actor, and enforcement, for example, where the actor is rewarded for cooperation or punished for noncooperation. Among the latter type, we distinguish fixed, behaviourally inflexible enforcement mechanisms from those that are conditionally adjusted in response to the actor's behaviour.

By-product benefits

Social partners may have a shared interest in cooperation (**Figure 2a**). For example, in many cooperative breeding vertebrates, such as meerkats, larger group size can provide a benefit to all the members of the group through an increase in factors such as survival, foraging success or the likelihood of winning between-group conflicts (Clutton-Brock, 2002). In this case, subordinate individuals can be selected to help rear offspring that are not their own, to increase group size ('group augmentation'; Kokko *et al.*, 2001). Selection for such helping is further increased if there is a chance that the subordinate will obtain dominance in the group at some later point, because they would then have a larger number of helpers themselves. These advantages of group augmentation would be greatest for the sex that is most likely to remain and breed in the natal group, which provides an explanation for why the level of helping is greatest in that sex for birds (males) and mammals (females) (Clutton-Brock *et al.*, 2002). Similar benefits of increased individual success in larger groups have been suggested to be important in a range of other cooperative organisms, including ants and social spiders (Avilés and Tufiño, 1998; Bernasconi and Strassmann, 1999). **See also: The Evolution and Ecology of Cooperative Breeding in Vertebrates**

Direct fitness benefits also appear to be important for cooperative breeding in the wasp *Polistes dominulus* (Queller *et al.*, 2000). In this species, colonies are initiated by one or a small number of foundress females who then form a dominance hierarchy with the dominant laying most of the eggs and the subordinates carrying out most of the more risky foraging. Eggs give rise to larvae, some of which are raised to become workers that forego reproduction in order to perform other tasks in the colony.

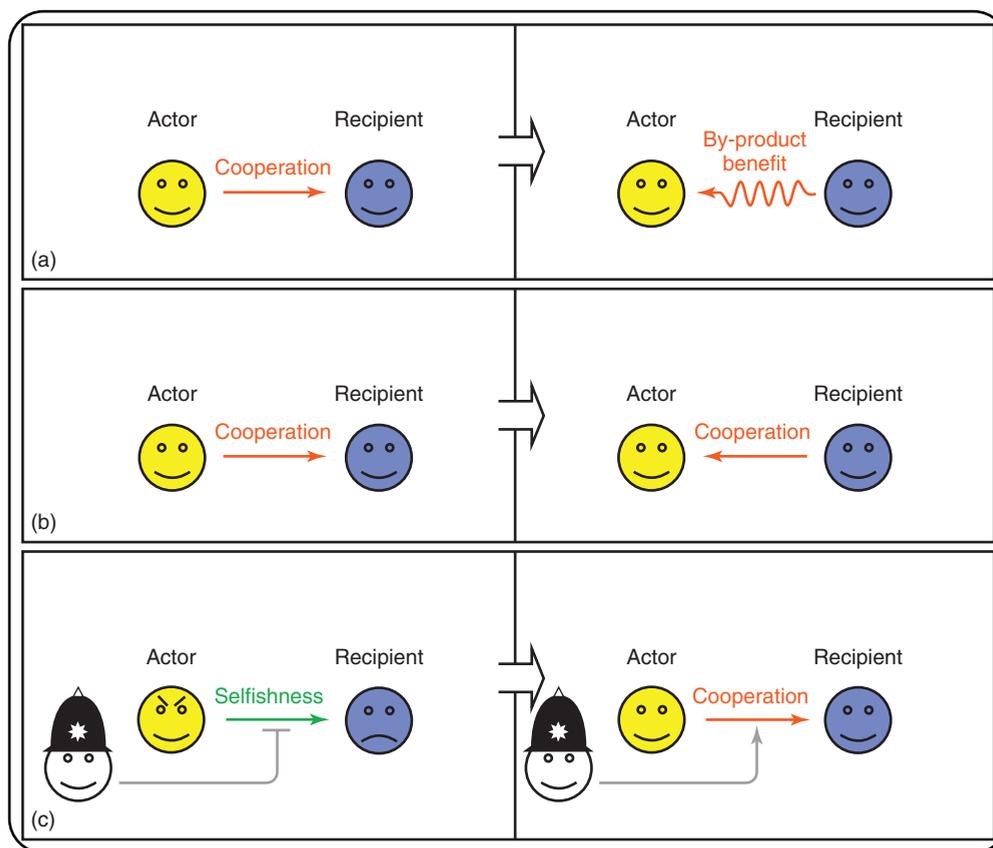


Figure 2 Mechanisms generating direct fitness benefits for cooperation. (a) By-product benefit. Helping a social partner may lead to increases in the overall fitness of all individuals in a social group; for example, in situations where larger social groups offer better protection against predators, the actor could benefit from helping its neighbours to reproduce (group augmentation). (b) Conditional enforcement (e.g. reciprocity). Helping may lead to a change in the behaviour of the recipient or a third party, in a way that leads to an overall direct fitness benefit for the actor; for example, direct reciprocity ensures that cooperators receive more cooperation than cheats, giving a direct benefit to cooperation even if each act involves an immediate cost. (c) Unconditional enforcement (e.g. policing). Helping may be the only option available to an individual, if the possibility for it to behave selfishly is ruled out by a successful system of policing.

In one study, it was found that 35% of subordinates were unrelated to the dominant. These subordinates gain significant direct fitness benefits from staying and helping on the nest because dominants suffer an appreciable mortality rate, and so there is approximately a 10% chance that a subordinate will become the dominant in the group, by the time the workers emerge (Queller *et al.*, 2000). It is unlikely that subordinates are merely helping nonrelatives by accident in this species, because there is sufficient between-individual variation in cuticular lipids (surface molecules employed in the recognition of nestmates) to allow subordinates to distinguish related nestmates from unrelated nestmates (Dani *et al.*, 2004), and so natural selection could have acted to reduce or remove cooperative behaviour when subordinates are on a colony with nonrelatives.

Enforced cooperation

Cooperation can be enforced if there is a mechanism for rewarding cooperators or punishing cheats (Trivers, 1971; Axelrod and Hamilton, 1981; Frank, 2003; **Figure 2b**). This was emphasised by Trivers (1971), who showed that cooperation

could be favoured in reciprocal interactions, with individuals preferentially aiding those that have helped them in the past. In this case, cooperation provides a direct fitness benefit, as it is only favoured if the short-term cost of being cooperative is outweighed by the long-term benefit of receiving cooperation (Lehmann and Keller, 2006). Trivers, 1971 termed this 'reciprocal altruism', but because it provides a direct fitness benefit, it is mutually beneficial and not truly altruistic. Consequently, 'reciprocity' or 'reciprocal cooperation' is the more appropriate term. Here, we use the term 'reciprocity' to mean the specific mechanism by which cooperation is preferentially directed at cooperative individuals, either directly (help those that help you) or indirectly (help those that help others).

Although such reciprocity has attracted a huge amount of theoretical attention, it is thought to be generally unimportant outside of humans (Hammerstein, 2003). A famous possible exception is food sharing in vampire bats, where successfully feeding individuals share their blood meals with less-successful social partners who shared with them on earlier occasions (Wilkinson, 1984), though even here the mechanism

is somewhat obscure (Stevens and Hauser, 2004). Our use of the term reciprocity differentiates it from other cases of enforcement that also rely on behavioural flexibility and which has been variously termed punishment, policing, sanctions, partner switching and partner choice (Frank, 2003; Sachs *et al.*, 2004). In some cases, the term ‘reciprocity’ is used more generally to cover all these cases (Lehmann and Keller, 2006).

Enforcement has been suggested to be important in a number of vertebrates. A particularly ruthless example is found in meerkats, where the dominant female suppresses reproduction in her subordinates (Young *et al.*, 2006). If a subordinate female becomes pregnant when the dominant is also pregnant, then the dominant is likely to subject the subordinate to aggressive attack and temporarily evict her from the group; this usually leads to abortion of the subordinate’s litter. In another cooperative breeding vertebrate, the white-fronted bee-eater, harassment both encourages cooperation and reduces competition (Emlen and Wrege, 1992). In this species, adults preferentially disrupt the breeding attempts of close relatives (offspring), and this harassment frequently leads to the offspring becoming a helper at the nest of the harasser. This strategy appears to work because the offspring gain approximately the same inclusive fitness return from helping at a nest as breeding independently and so have little to lose from becoming a helper, whereas the parents have a lot to gain from obtaining a helper (Emlen and Wrege, 1992).

Enforcement has also been suggested to be an important factor favouring cooperation in humans (Figure 3). In one study, students were split into groups of four to play a public goods game for cash prizes, where each person could contribute monetary units to a group project (Fehr and Gächter, 2002). For every unit invested in the group project, each of the four members of the group earned 0.4 units. This leads to the problem of cooperation because while investing increased the units available to the group, the investor was returned less than they invested. The

experiment was repeated with and without punishment; punishment was incorporated by allowing individuals to pay money to have units deducted from other players, after they were informed about each other’s investments. As expected, punishment led to higher levels of cooperation, as measured by higher investment in the group project (Fehr and Gächter, 2002).

In the abovementioned situation, enforcement of cooperation has involved facultative, or conditional, enforcement behaviour of social partners, which is adjusted in response to the behaviour of the focal individual. However, cooperation can also be enforced with fixed strategies that remove the incentive or opportunity for competition or cheating (Leigh, 1971; Frank, 2003; Figure 2c). If opportunities for competition or cheating are limited, then individuals can only increase their own success by increasing the success of their group (Frank, 2003) and receiving their fair share of this success. Consequently, any mechanism that aligns reproductive interests or represses competition within groups will select for higher levels of cooperation. Fair meiosis may be an example of such a mechanism and appears to have been favoured because it aligns the reproductive interests of genes in a genome (Leigh, 1971). Under the rules of fair Mendelian transmission, every gene in the genome has an equal probability of being passed onto the individual’s offspring, so it is in the interests of all genes to maximise the reproductive success of the individual. Although selfish genes (Mendelian outlaws) that increase their own transmission rate can arise and spread, there is often strong selection for them to be suppressed by the majority of genes elsewhere in the genome, and this policing prevents the genome dissolving into anarchy. This democratic tendency has been termed the ‘parliament of genes’ (Leigh, 1971). An example of a Mendelian outlaw is the *t* haplotype of mice, which derives a transmission advantage in the context of male reproduction by eliminating non-*t*-carrying sperm and hence increasing the fertilisation success of *t*-carrying sperm, and which has been

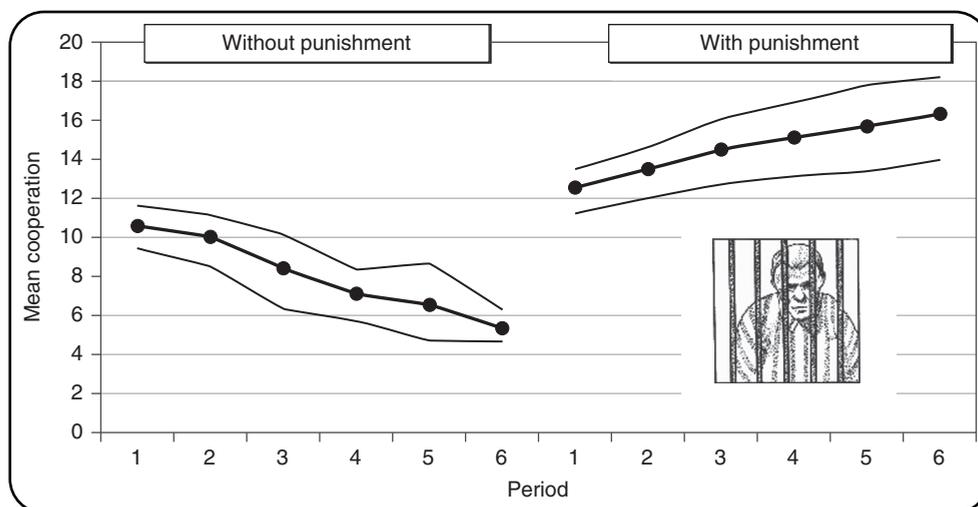


Figure 3 Cooperation and punishment in humans. Humans show higher levels of cooperation in economic games, when there are opportunities to punish individuals who do not cooperate (Fehr and Gächter, 2002). Thanks to E. Fehr for data and O. Henderson for illustration. Reproduced from West *et al.* (2007a) © Elsevier.

shown to be suppressed by other genes in laboratory populations of mice (reviewed by Burt and Trivers, 2006).

Why enforce?

While it is clear that behaviours such as punishment or policing favour cooperation, it is sometimes less obvious how punishment or policing can themselves be favoured by natural selection. To be favoured, behaviours such as punishment must provide a direct or an indirect fitness benefit to the punisher. The simplest way in which such behaviours could provide a direct fitness advantage is if they lead to the termination of interactions with relatively uncooperative individuals (ostracism) and hence allow interactions to be focused on more cooperative individuals (Axelrod and Hamilton, 1981; West *et al.*, 2002; Frank, 2003). In meerkats, pregnant subordinates will kill other young, even those of the dominant, and so the dominant increases the survival of her offspring by harassing and evicting pregnant subordinates (Young *et al.*, 2006). A more complicated possibility is that the punished individuals change their behaviour in response to punishment and are more likely to cooperate with the punisher in future interactions (Clutton-Brock and Parker, 1995). Finally, enforcement mechanisms may evolve for reasons that are unconnected with their consequences for cooperation. For example, honeybee workers can lay unfertilised eggs that will develop as males, but generally do not, as most worker-laid eggs are eaten by other workers – a form of enforcement that has been termed ‘worker policing’. However, this egg eating has not evolved for the purpose of maintaining cooperation, but rather because workers are less related to the sons of other workers (nephews) than they are to the queen’s sons (brothers), and so they are favoured to kill the former and rear only the latter. In other words, worker policing would continue to be favoured even if this did not lead to an increase in cooperation within the hive (Ratnieks, 1988; Ratnieks and Visscher, 1989; Wenseleers and Ratnieks, 2006).

Indirect Fitness Benefits

The second class of adaptive explanations for cooperation are those that rely upon indirect fitness benefits, that is, altruistic cooperation. Three major mechanisms for generating indirect fitness benefits – which rely on the improvements to reproductive success preferentially accruing to other carriers of the actor’s genes – have been identified (**Figure 4**). These are limited dispersal, in which populations are not well mixed and so neighbouring individuals tend to be closely related; kin discrimination, in which individuals respond to cues that indicate that their social partner is a close relative and the greenbeard effect, in which the gene for cooperation directly detects copies of itself among the actor’s social partners.

Limited dispersal

Perhaps, the simplest mechanism for generating positive relatedness between social partners is limited dispersal – also termed ‘population viscosity’ – which ensures that genetic similarity of individuals is correlated with their spatial proximity (Hamilton,

1964; **Figure 4a**), so that even indiscriminate cooperation with one’s neighbours could be favoured via indirect fitness benefits. Because this mechanism does not require complicated cognitive faculties, it has the potential to apply very generally, at all levels of biological organisation. Empirical support for this idea has been found in experimental manipulations of bacterial populations (Griffin *et al.*, 2004). *Pseudomonas aeruginosa* bacteria cooperate by producing iron-scavenging molecules, called siderophores, that they secrete into their environment. Because the siderophores are costly to produce and can be used by any cell in the local population, they represent a form of ‘public goods’ cooperation, which would appear to be vulnerable to invasion by cheats who do not produce their fair share of siderophores but which free-ride on the contributions made by their social partners. When the population of bacteria is well mixed, cooperation is indeed disfavoured and cheats accumulate in the population. However, when the population is structured, with little exchange of individual cells between subpopulations, then the high local relatedness can favour cooperation over cheating.

A complication with this mechanism is that limited dispersal can also lead to an intensifying of competition for resources between social partners, and this can reduce or even completely negate the benefits of cooperation (Queller, 1992; West *et al.*, 2002). For example, helping a sibling to achieve greater reproductive success might not be favoured if their offspring end up competing with the offspring of one’s other siblings. In the simplest scenario, these two effects exactly cancel, so that cooperation is as readily favoured (or disfavoured) in a viscous population as it is in a fully mixed population (Taylor, 1992). One solution to this problem is ‘budding’ dispersal, where social groups undergo fission and dispersal but where there is only limited exchange of individuals between groups (Gardner and West, 2006). This eases resource competition, but maintains high relatedness between social partners and has been shown to favour cooperation in selection experiments with *P. aeruginosa* (Kümmerli *et al.*, 2009). More generally, many aspects of life history and demography may interact with limited dispersal to promote the evolution of cooperation (Lehmann and Rousset, 2010).

Kin discrimination

Another mechanism that can promote the evolution of cooperation is kin discrimination, when an individual can distinguish its kin from nonkin and preferentially direct aid towards the former (**Figure 4b**; Hamilton, 1964). Because kin tend to share genes in common, this nepotism can lead to an appreciable genetic relatedness between the individual and its beneficiaries, favouring the evolution of altruistic cooperation. This has been demonstrated in many cooperatively breeding vertebrates such as long-tailed tits, where individuals that fail to breed independently and, owing to low survival between breeding seasons, have little prospect of pursuing their own future reproduction, preferentially help at the nest of closer relatives (**Figure 5**; Russell and Hatchwell, 2001). In this species, individuals distinguish between relatives and non-relatives on the basis of vocal contact cues, which are learned from adults during the nesting period (associative learning). This leads to the situation where individuals tend to help relatives with whom they have been associated during the nestling phase.

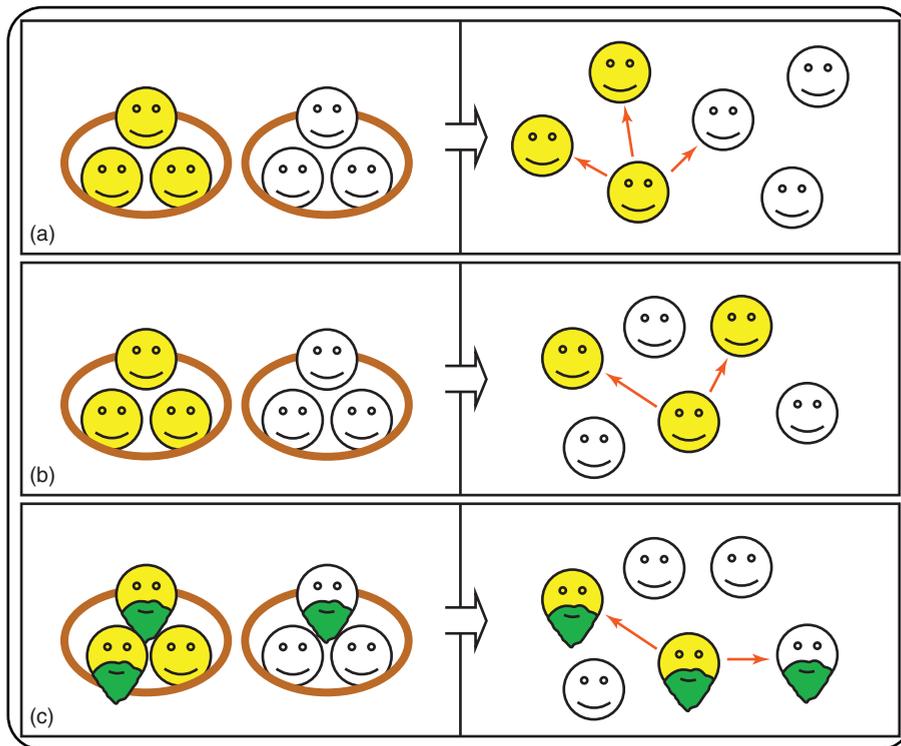


Figure 4 Mechanisms generating indirect fitness benefits for cooperation. (a) Limited dispersal. If individuals do not move far during their lifetime, then they will tend to be surrounded by kin (shaded) and hence even indiscriminate altruism could be directed primarily towards kin rather than nonkin. (b) Kin discrimination. For example, if the actor can remember those individuals it shared a nest with when young and discriminate these kin (shaded) from nonkin (unshaded) after leaving the nest, then cooperation can be directed primarily towards genetic relatives. (c) Greenbeard. If the gene-controlling altruism is also associated with a phenotypic marker, such as a green beard, then green-bearded individuals can identify which of their neighbours carries a copy of the gene. Altruism directed at genetic relatives can be favoured by natural selection, even if these are not genealogical relatives (kin).

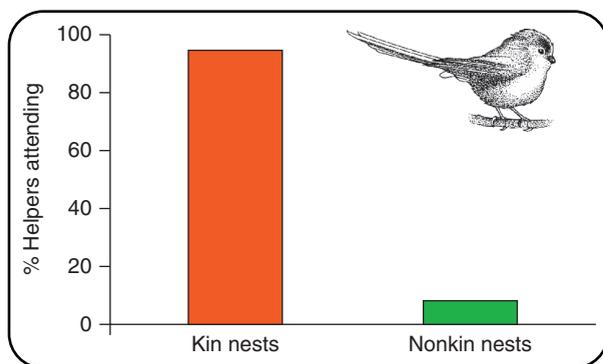


Figure 5 Kin discrimination in long-tailed tits. Ninety-four percent of helpers prefer to help at nests containing related chicks when they have the choice of where to invest their efforts (Russell and Hatchwell, 2001). Thanks to O. Henderson for illustration. Reproduced from West *et al.* (2007a) © Elsevier.

Inclusive fitness theory not only explains kin discrimination, but also explains variation in the level of kin discrimination across species (Griffin and West, 2003). In contrast to the long-tailed tit example given earlier, some cooperative breeding vertebrates, such as meerkats (Clutton-Brock *et al.*, 2000), have subordinates

that do not show kin discrimination when helping. This is presumably because there are direct fitness benefits of helping, as discussed earlier. Clearly, the advantage of kin discrimination will be positively correlated with the benefit provided by cooperation. In the extreme, if a supposedly 'helpful' behaviour provides little or no benefit to the recipients, then there is little or no advantage in directing it preferentially towards closer relatives. This leads to the prediction that kin discrimination should be greater in those species where cooperation provides a larger benefit for the recipient, and this pattern is indeed observed across cooperatively breeding vertebrate species (Griffin and West, 2003).

Greenbeard effect

The final mechanism for generating indirect fitness benefits for cooperation is the greenbeard effect. This is similar to kin discrimination, but involves the actor identifying which of its social partners share the gene for cooperation, and preferentially interacting with those individuals, even if they are neither close relatives nor genetically similar at other loci (Hamilton, 1964; Gardner and West, 2010; **Figure 4c**). The mechanism gets its name from a hypothetical example, proposed by Dawkins (1976), in which a gene causes individuals to grow a green beard, and to act altruistically only towards other individuals who have green

beards – thus looking out for its own interests. This highlights that genetic relatedness is distinct from genealogical relationship. Greenbeard genes are vulnerable to cheating by individuals who wear a beard but do not exhibit altruism (falsebeard) and so are expected to be rare in the natural world (Gardner and West, 2010). One of the few cases where a cooperative greenbeard does occur is in the slime mould *Dictyostelium discoideum*, which forms fruiting bodies in a very similar way to *Dictyostelium purpureum*. In *D. discoideum*, individuals with the *csa* cell-adhesion gene adhere to each other in aggregation streams, excluding mutants who do not, and cooperatively form fruiting bodies (Queller *et al.*, 2003). Here, cell adhesion commits an amoeba to the possibility of becoming a stalk cell, but is also required to be included in the fruiting body and hence to have a chance at successful spore formation. **See also: *Dictyostelium: Cell Sorting and Patterning***

Future Directions

We have seen that there is a well-developed theoretical overview for tackling the problem of cooperation in evolutionary biology. Adaptive explanations of cooperation involve inclusive fitness benefits, which can be subdivided into direct fitness and indirect fitness categories. In addition, in broad outline, there is a good understanding of the types of mechanisms that can deliver such benefits. However, the relative importance of direct and indirect fitness benefits, in explaining cooperation as it occurs across the whole of the diversity of life, is far from being properly understood. We suggest three directions that will be crucial for further development of the field.

First, we need better integration between theory and empirical work. Much theoretical work is aimed at developing very general models that can be difficult to apply to real systems. Greater emphasis is needed on the development of models that can be applied to and tested in specific systems and which make predictions for how the level of cooperation should vary, not just whether it should occur. The usefulness of this approach is clearly demonstrated by the fact that the most successful branches of social evolution theory are those, such as sex ratio evolution, where there has been the greatest integration of theory and empirical work (West, 2009). The need for testable predictions is particularly great for many direct fitness explanations for cooperation, which are often only invoked when indirect fitness explanations apparently fail and not as a competing hypothesis.

Second, the possible advantages of less-traditional study systems need to be exploited. Previous empirical work has focused on animals, and within them, the *Hymenoptera* (ants, bees and wasps) and the cooperatively breeding vertebrates. Far less attention is applied to other possibilities such as social cockroaches (termites), social spiders or aphids. Beyond the animal world, the amazing opportunities offered by bacteria and other microbes have only recently come to be exploited (West *et al.*, 2006). Different taxa offer different advantages. For example, while bacteria are useful for genetic manipulations and multigeneration selection experiments, insects and vertebrates are more useful for field studies. Furthermore, apart from work on selfish genetic elements and their suppressors, far less attention has been paid to the problems of cooperation that occupy lower levels among the

major evolutionary transitions, such as the evolution of multicellularity (Queller and Strassmann, 2012).

Third, there is a strong need for greater unification across taxa. In some cases, there is surprisingly little interaction between empirical workers and theoreticians in different areas. For example, one could be forgiven for thinking that the human, primate and social insect literatures on cooperation concerned completely different topics, rather than attempts to develop and test the same body of theory. This lack of unification has led to much semantic confusion and unnecessary reinvention of theory. Inclusive fitness (Hamilton, 1964) provides a relatively unified body of theory on the evolution of cooperation (Frank, 2003; Sachs *et al.*, 2004; Grafen, 2006; West *et al.*, 2007a; Bourke, 2014), and the major aim for the future should be to show how this links different explanations for cooperation across various taxa and levels of biological organisation.

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