Quick guide

# Altruism

**Stuart A. West, Andy Gardner and Ashleigh S. Griffin**

***What is altruism?*** Altruism is a type of social behaviour. From an evolutionary point of view, a behaviour is social if it has consequences for both the actor and another individual — the recipient. Social behaviours can be categorized according to whether their consequences for the actor and recipient are beneficial, increasing fitness, or costly, decreasing fitness (Figure 1). Altruism is when a behaviour reduces the fitness of the actor, but increases the fitness of the recipient. This contrasts with the other forms of social behaviour: selfish, mutually beneficial and spiteful (Figure 1): a behaviour that increases the fitness of the actor is mutually beneficial if the recipient also benefits, and selfish if the recipient suffers a loss; a behaviour that reduces the fitness of both the actor and the recipient is spiteful.

***So what?*** Explaining altruism is a fundamental problem for evolutionary biology: why should an individual carry out a costly behaviour that benefits other individuals? This seems to go completely against the Darwinian idea of 'survival of the fittest'. Populations of altruists are vulnerable to invasion by cheaters who do not cooperate, but gain the benefit from others cooperating, so we would not expect altruistic behaviours to be maintained in a population — put formally, altruism should not be evolutionarily stable.

***How can altruism be explained?*** William D. Hamilton's kin selection theory provides an explanation for altruism between relatives. By helping a close relative reproduce, an individual still passes on its own genes to the next generation, albeit indirectly. So from the point of view of the gene, an altruistic behaviour can be selfish. This theory is encapsulated in a pleasingly simple form by Hamilton's rule that altruism is favoured when $rb - c > 0$; where $c$ is the fitness cost to the altruist, $b$ is the fitness benefit to the recipient and $r$ is their genetic relatedness. This predicts that altruism is favoured when r or b are higher and c lower.

Hamilton's theory is referred to in many ways. Hamilton called it 'inclusive fitness theory', but it is more often referred to as 'kin selection', a term coined by John Maynard Smith. Jerram Brown pointed out that the inclusive fitness of an individual is divided into two components: 'direct fitness' and 'indirect fitness'. Direct fitness is gained through the production of offspring, and indirect fitness through aiding the reproduction of nondescendent relatives. A behaviour is only altruistic if it leads to a decrease in direct fitness, so altruism can only be favoured when an indirect benefit outweighs this direct cost, as shown by Hamilton's rule.

***Are there any nice examples of altruism?*** Altruism can be found with ease in most gardens. A colony of ants is generally composed of one queen, who spends all her time laying eggs, and hundreds to thousands of workers who do all the other jobs, from rearing the eggs through to adulthood or foraging for food (Figure 2, middle). These workers are sterile, and therefore unable to reproduce themselves. They altruistically give up the opportunity for reproduction, and instead spend their time helping to rear the offspring of the queen. As the queen is usually their mother, they are rearing brothers and sisters, and so kin selection can explain this altruism. A similar life cycle occurs in the termites, many wasps and bees, as well as some aphids and thrips. Together, these social insects provide some of the clearest examples of altruism.

Altruism has also been demonstrated or suggested in numerous other contexts. At one end of the animal kingdom are several species of birds and mammals that breed cooperatively. In species such as African wild dogs, a dominant pair produces most of their offspring, whereas the cost of caring for offspring is shared by nonbreeding subordinates. In an even more extreme example, the naked molerat, a single female gives birth to pups in groups of up to 100 individuals. A complication here is that, although helping is clearly beneficial to the receiver, it can also provide direct benefits to the actor; for example, if helping leads to a larger group size, which increases the survival of everyone in the group, including the actor. So there is still much debate over the extent to which helping in cooperative breeding vertebrates is altruistic, explained by indirect fitness benefits, or mutually beneficial, explained by direct fitness benefits.

At the other extreme, altruism has been observed in bacteria and other microorganisms. One of the clearest cases is in the social amoebae or slime molds, when forming fruiting bodies. Under harsh conditions, species such as *Dictyostelium discoideum* form fruiting bodies to disperse (Figure 2, left). Within these fruiting bodies, some cells become spores, whereas others sacrifice themselves and altruistically become non-viable stalk cells. The altruistic stalk raises the spores off the ground, aiding in their dispersal to more favourable environments. Clonal reproduction means that many of the cells in a fruiting body are

| | | Effect on recipient: + | Effect on recipient: – |
|---|---|---|---|
| Effect on actor | + | Mutual benefit | Selfishness |
| | – | Altruism | Spite |

Current Biology

Figure 1. Social behaviours.

Figure 2. Altruistic organisms.
Left: a fruiting body in the slime mold *Dictyostelium discoideum* (photo by Owen Gilbert). Middle: brood care in the ant *Myrmica scabrinodis* (photo by David Nash). Right: brood care in long-tailed tits (photo by Andrew MacColl).

genetically identical, and so again this behaviour can be explained by kin selection.

***But how does it really work?*** Altruistic behaviours are only favoured if directed towards relatives (*r*>0). Hamilton pointed out that this could happen in two ways. First, if there is some possibility for kin discrimination, with behaviours preferentially directed towards relatives. A clear example is in long-tailed tits (Figure 2, right), where non-breeders preferentially help at nests where close kin are breeding. Second, limited dispersal tends to keep relatives together. This could favour indiscriminate altruism as interacting individuals would on average be relatives. This type of mechanism is likely to be of huge importance in microorganisms such as slime molds where a single cell can colonise and grow clonally in a local area.

***Are all cooperative behaviours altruistic?*** The short answer is no. A full answer requires we clarify some points of semantic confusion. We use cooperation to mean a behaviour that benefits another individual (the receiver); cooperation can therefore be altruistic or mutually beneficial. This is how cooperation is used in the empirical literature. For example, it is not yet clear to what extent cooperative breeding in vertebrates is altruistic and explained by kin selection (indirect fitness benefits), or mutually beneficial and explained by direct fitness benefits; the answer is often likely to be a bit of both. Confusion can arise because cooperation is sometimes used more restrictively, to refer to behaviours that benefit both the actor and the receiver. In this case, behaviours that benefit the recipient would be either altruistic or cooperative. This usage is confusing because it could imply that direct fitness benefits are the only possible explanation for cooperative breeding in vertebrates or insects. The term ‘mutualism’ has also been used to describe behaviours that benefit both the actor and the receiver. This can be confusing, however, because many use mutualism to refer to the more specific case of cooperation between species, or specific types of direct fitness benefit. In his original papers, Hamilton did not give a term for behaviours that benefit both the actor and the receiver.

***Any more complications?*** It is often not appreciated that there can be significant relatedness, and thus the potential for altruism, between individuals who are not close kin. Relatedness describes a genetic association between social partners, which may be due to causes other than kinship. Hamilton (and later Richard Dawkins) illustrated this point by showing that a gene that both coded for a distinctive phenotype — such as a green beard — and also predisposed the individual towards altruism directed at other bearers of green beards could be favoured by selection, even when social partners are not close kin. This can be thought of as an extreme form of kin discrimination, acting at the gene level. But such examples are expected to be rare in the real world, as cheats that display the green beard without also being altruistic are able to take advantage and overrun the population. Nevertheless, this shows that the term kin selection can be somewhat misleading, as it emphasises the role of coancestry. Whilst coancestry is no doubt the most important mechanism that can lead to kin selection for altruism, it should be appreciated there are other possibilities.

***Where can I find out more?***

Dawkins, R. (1976). The Selfish Gene. Oxford University Press.
Griffin, A.S., and West, S.A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science *302*, 634–636.
Hamilton, W.D. (1964). The genetical evolution of social behaviour, I & II. J. Theor. Biol. *7*, 1–52.
Queller, D.C., and Strassman, J.E. (1998). Kin selection and social insects. Bioscience *48*, 165–175.
Rousset, F. (2004). Genetic structure and selection in subdivided populations. Princeton: Princeton University Press.
Sharp, S.P., McGowan, A., Wood, M.J., and Hatchwell, B.J. (2005). Learned kin recognition cues in a social bird. Nature *434*, 1127–1130.

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, King’s Buildings, Edinburgh EH9 3JT, UK.
E-mail: stu.west@ed.ac.uk