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## Altruism



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### Origins of Altruism

The earliest conceptualization of altruism can be traced back to the Ancient Greeks and forward to more contemporary behaviorists (Rushton and Sorrentino 1981 for review). The first view was from some of the writers of the old and new testaments and Freud who thought of human nature as essentially bad. A second view was popular among Socrates, Aristotle, and Carl Rogers, who thought of human nature as essentially moral and altruistic. The third view was commonly held by Plato, Locke, Watson, and Skinner who believed that human nature was neutral.

The term “altruism” was coined by French sociologist Auguste Comte (1858) in a description of his ethical doctrine indicating that individuals had a moral obligation to renounce self-interest and love for all others. Not long after Comte coined the term altruism, Darwin published his *Descent of Man* (1871), in which he proposed that humans are biologically disposed to behave socially, cooperatively, and helpful to one another. He speculated that it was “moral sense” that distinguished

humans most from nonhuman animals, and it was composed of intellectual power and sociability. Interestingly, while Darwin described examples of altruism in nonhuman animal species, he identified a paradox in the way altruism evolved in natural selection. Specifically, he noted that, if the most altruistic members of a group were willing to die for others, sacrificing themselves, there would be fewer offspring of altruistic individuals to pass on the altruism trait.

Around the mid-1960s, in his book entitled *Animal Dispersion in Relation to Social Behavior*, Wynne-Edwards suggested that evolution occurred through group selection, at the level of the species (Wynne-Edwards 1962). He argued that many behaviors evolved for the good of the species as a whole, rather than at a lower level of organization. His arguments were strongly criticized by George C. Williams, an evolutionary biologist, in *Adaptation and Natural Selection* (Williams 1966), in which he argued on the basis of mathematical models that individuals would not altruistically sacrifice fitness for the sake of a group. He persuaded the majority of biologists that group selection did not occur, other than in special situations such as the haplodiploid social insects like honeybees (Hymenoptera), where kin selection was possible. To support his stance, Williams used the popular lemming example, in which some lemmings take it upon themselves to commit suicide to relieve pressure on critical food resources. The

classic scenario is one in which a population of lemmings is jumping off a cliff into treacherous water on a suicide mission but one individual wears a life preserver around its waist. In such a case, group selection would be said to favor the allele(s) for suicidal behavior. However, Williams argued that altruism could not have evolved through group selection because selection among individuals will usually have a stronger effect than group selection in shaping the genetic makeup of the population. Additionally, he argued that groups of altruists would have to prevail over groups of selfish individuals at a faster rate than the selfish individuals within the groups and group selection is much slower than individual selection.

## Types of Altruism

### Hamiltonian Altruism and Kin Selection

Charles Darwin discussed the concept of kin selection in his 1859 book, *The Origin of Species* in which he questions the altruistic behavior of sterile social insects, such as honeybees who leave reproduction to their mothers. He also describes how populations evolve across many generations through natural selection. Under natural selection, a gene encoding a trait that enhances the fitness of each individual carrying it, should increase in frequency within the population, and conversely, a gene that lowers the individual fitness of its carriers, should be eliminated. A gene that prompts behavior that enhances fitness of relatives but lowers the individual carrying it, should increase in frequency within a population because relatives often carry the same gene. The enhanced fitness of relatives would more than compensate for the fitness loss incurred by the individuals, making kin selection possible. In 1975, Harvard biologist, E.O. Wilson published *Sociobiology*, which re-launched the debate about nurture versus nature and proposed that social behavior, such as altruism was often genetically programmed and that these genes were subject to natural selection. Relatively recently, Wilson recanted this explanation for altruism (discussed below and Nowak et al. 2010).

Maynard Smith (1964) coined the term “kin selection” to describe how helping relatives to reproduce resulted in indirect fitness benefits, the reproduction of nondescendent kin. Hamilton (1964) described kin selection more specifically stating that because genetically related individuals were likely to carry the copies of the same alleles, they would be more likely to help their kin to ensure that copies of their alleles were passed on. The prominent biologist, J. B. S. Haldane (1932) popularized the math involved in kin selection by stating that he was willing to lay down his life for two brothers or eight cousins. It was Hamilton who later expressed the conditions under which such altruism would evolve through the following equation:  $r \times b > c$  where  $r$  denotes the relatedness of the individuals,  $b$  denotes the benefit to the recipient of the altruistic act, and  $c$  denotes the cost to the altruist (Hamilton 1964). The equation predicts that altruistic behavior would more likely occur among individuals that are closely related kin. Cooperation is favored by natural selection if relatedness is greater than the cost to benefit ratio. Hamilton also coined the term “inclusive fitness” to refer to the total genetic success of an individual based on personal reproduction (direct fitness) and the effects on reproduction of nondescendent kin (indirect fitness). Inclusive fitness is a defining feature of kin selection.

### Examples of Kin Selection

One popular example of kin selection is in the Polistes, paper wasp (Hamilton 1964). The female wasps mate with unrelated male wasps during the breeding season and then spend the winter hibernating in a shelter. In the spring, they emerge and start a nest that contains a single egg. Other females join the foundress female and a hierarchy is established. The dominant female reproduces and the subordinates help rear the larvae and protect the nest against predators and parasites. The queen wasp uses sperm stored from last fall’s copulation to fertilize the eggs that were laid early in the season. These eggs are destined to become daughters. When it is adaptive to produce sons, she lays unfertilized eggs.

When the first females emerge, they help their mother raise more daughters (both full and half sister) rather than fly off and start their own colonies. The queen continues to produce more eggs. As summer progresses, some of the females that the queen produces, stop working and start taking food from their sisters. Later, males emerge for the first time and they also do nothing to help the colony. The latter females and males fly off together and mate, the males die, and the females hibernate through the winter to start the cycle all over again.

The daughters of the queen wasp serve in helper roles for life because they may not have the option to reproduce and by helping their sisters such that they increase their fitness indirectly. Females and males who do not take on the helper role may be acting to increase their fitness directly by increasing their personal chance of reproductive success.

Another example of kin selection is in the Belding's ground squirrels. These squirrels produce a whistle-like alarm call when they see a terrestrial predator, such as a coyote or badger. Paul Sherman (1985) observed predators capture and kill alarm callers at a higher rate than non-calling, fleeing squirrels and investigated the mechanisms underlying the alarm calling. He found that the caller may serve to enhance its own personal chances of reproductive success by alerting its neighbors so that together they create a chaotic mass that confuses the predator and allows them to run away safely. But in addition, while the caller may reduce its chances for reproductive success, it increases its inclusive fitness by alerting its relatives. Females are more likely to give calls than males. They may be increasing the chances of survival of their offspring but also because females live with many relatives compared to more solitary males, females could be increasing the survival of their relatives. Females with living relatives nearby call more frequently than females without living relatives as neighbors.

Evidence of gene bias in humans is suggested by the phenomenon of mother's brother (Alexander 1974). The phenomenon suggests that if a man lacks confidence in his paternity

of his children, his nieces and nephews may become his closest relatives in the next generation. According to Alexander, lowered confidence in paternity may be caused by circumstances that involve husbands and wives living apart and/or long absences of husbands on hunting or military trips. Low confidence may lead to reduced paternal care by the mother's spouse, thus increasing the value of care given by the mother's brother. Mathematically, when a man can only estimate his paternity at 25% or lower, he becomes the most closely related male to the sister's offspring. Thus, in accordance with kin selection, preferential care may be given to those most genetically close to us but if the genetic components are questionable, the altruist may find the next closely related non-descendent kin to invest in. Evidence for the mother's brother's phenomenon is rare but is thought to occur in polygamous societies where confidence of paternity is relatively low.

Recent research on inclusive fitness and cooperation among kin shows that human kin selection may not only include genetic kin but also kin by marriage (in-laws) (Dyble et al. 2018). Unrelated kin and spouses may not necessarily share genes but they may have shared genetic interests in future reproduction, and therefore, may derive indirect fitness benefits through cooperating. For example, a mother may have an interest in the reproduction of her son's wife. Dyble and colleagues (2018) used a standard inclusive fitness theory to calculate a coefficient of shared reproductive interest that predicts altruism in both genetic kin and in-laws. The researchers concluded that "two-daughters-in-law or eight cousin's spouses" could be added to the inclusive fitness statement of saving two brothers and eight cousins.

### **A Recent Debate about Kin Selection**

For decades, many scientists have accepted the notion of kin selection which is based on inclusive fitness, genetic success based on personal reproduction (direct fitness), and effects on reproduction of nondescendent kin (indirect fitness). The prominent biologist E.O. Wilson was a strong proponent of kin selection, especially

in explaining the behavior of social groups of animals such as bees, ants, and termites. Recently, E.O. Wilson, Martin Nowak, a Professor of mathematics, and Benjamin Allen, a Research Associate in mathematical biology, rejected this notion and have determined that the theory is mathematically flawed (Nowak et al. 2010). They point out that a large majority of the field data does not fit with the predictions of kin selection theory. They found that cooperation was common among many species where individuals were not genetically related and many instances where cooperation was not found within species, even though the mathematics of kin selection theory would predict it. Rather than kin selection, Wilson and colleagues (Nowak et al. 2010) suggest a mathematical model for the evolution of eusociality (sociality that involves cooperative brood care, overlapping generations within a colony, and a division of labor of reproductive and non-reproductive groups). The model does not require individuals to be related to others' offspring. There continue to be many defenders of the original kin selection theory.

### Reciprocal Altruism

In *The Evolution of Reciprocal Altruism*, Trivers (1971) discusses a different type of altruism than Hamilton suggested. In this entry, he describes how it pays off for individuals to render assistance to others when the cost is low and if, in doing so, it increases the probability of receiving help of greater value in the future. Trivers (1971) describes several conditions that favor the evolution of reciprocal altruism including: (1) a long life span of individuals of a species to maximize the chance for altruistic acts to occur, (2) low dispersal rate to increase the likelihood of interactions between the same neighbors, and (3) interdependence of members of a species to keep individuals near each other. Trivers also mentions that while parental care, mutual dependence between parents and offspring, can be explained by Hamilton's model (Hamilton 1964), there is no reason that reciprocal altruism may not also operate between close kin. He also points out that these are broad conditions

that favor reciprocal altruism but how many altruistic acts occur and the symmetry of those interactions are the most important parameters.

In his original description of reciprocal altruism, Trivers (1971) interpreted cooperative interactions between members of different species as reciprocal exchanges of assistance and pointed out their similarity to the Prisoner's Dilemma game (Axelrod and Hamilton 1981). In the Prisoner's dilemma, two individuals can each either cooperate or defect. No matter what the other does, defection yields a higher payoff than cooperation. If they both defect, both do worse than if both had cooperated. If the game is played long enough, it becomes an iterated version in which strategy can be used to determine the probability of cooperation and defection as a function of history. Among a huge number of reciprocal strategies, tit for tat is one of the most simplest ones. It is based on two simple rules: to cooperate in the first trial and, in the following, to do what the other player (opponent) did in the last trial. Under certain constraints, mutual cooperation appears to be the best strategy whenever reciprocity is maintained.

### Examples of Reciprocal Altruism

It has been suggested that altruistic acts performed between two individuals from different species may be the purest form of reciprocal altruism because there should not be any genetic enhancement from the altruistic act (Rothstein 1980). Some species interact with other species in a symbiotic relationship in which both groups have mutual dependency. For example, a large number of fish and shrimp are known to be cleaners of other larger species of fish (Feder 1966). Cleaner fish and shrimp rid host fish of ectoparasites by entering the gill or the mouth of the host fish and ingesting the parasites. Cleaner fish and shrimp are distinctly colored and behave in distinct ways (i.e., dipping and rising movements) to attract host fish to be cleaned and inhibit other fish from eating them. According to Feder (1966), there is likely a strong selection for hosts not to harm their cleaners and, as predicted, there are species that mimic

cleaners in similar colors and movements but then attempt to take a bite out of the fish approaching to be cleaned.

A host fish to be cleaned seems to perform several altruistic acts. First, it avoids eating the cleaner, even though natural selection should favor a cleaning followed by a good meal. Second, it signals to its cleaner when it is about to depart, and third, it may chase off other fish that pose a danger to the cleaner.

The behavior of the host fish may have resulted from natural selection because of the benefits of keeping the cleaner alive (Trivers 1971). To support the hypothesis that the host is repaid its initial altruism, Trivers (1971) presented several conditions favoring the evolution of reciprocal altruism. First, the host actually suffers from these parasites. Research has shown that the removal of all cleaner fish from a coral reef drastically reduces the number of larger fish within the next few days. Additionally, many of these territorial fish develop swellings, white fuzzy blotches and ulcerated sores. Secondly, finding a cleaner is difficult and dangerous. Observations show that if cleaners do not appear over one coral in about half a minute, host fish swim to another coral and wait. Thus, there may be several alternative cleaning stations to go to. In addition, it may be dangerous for some fish to be cleaned because they have to leave their protective environments. For example, moray eels do not normally leave their holes during the day time but they will in order to be cleaned. A third piece of evidence suggesting that the host is reciprocating its cleaner is that there is site specificity. Feder (1966) reviewed evidence for this, concluding that cleaner fish have regular stations to which fish wanting to be cleaned can go. This is especially evident of territorial recipients of the cleaner. Fourth, the lifespan of the cleaner seems to be easily long enough for effective selection against cheaters. And lastly, it is been shown that hosts use the same cleaner repeatedly. All of this evidence suggests that the cleaner organisms and their hosts meet the conditions for the evolution of reciprocally altruistic behavior.

Another example examined by Trivers (1971) is the warning calls in birds. Warning calls in birds do not allow for the predator to easily determine the location of the call giver. However, giving a call may occasionally result in the death of the caller, either by the observing nearby predator or a second nearby predator. Trivers (1971) suggests that the calls are selected for because they aid the bird that gives the call. It is disadvantageous for an observer bird to have a predator eat a nearby conspecific or fellow bird because the predator may then be more likely to eat the observer bird. Thus, giving a warning call prevents predators from specializing on the caller's species which includes forming a specific search for the prey species, learning the habits of the species, and perfecting its catching techniques on it. Second, the warning call prevents predators from specializing on the species locality which includes frequenting the area where the birds live and learning useful information about the area in which the bird lives. According to Trivers (1971), it does not matter if the calling bird may be helping its non-neighbors more than it is helping itself. What counts is that it outcompetes conspecifics in areas where no one is calling. The noncalling neighbors will find themselves in an area without any caller and will be selected against relative to birds in an area with callers.

There is no evidence that the birds can discriminate against cheaters but there is also no evidence that the birds stop giving calls because their neighbors are not reciprocating. It seems that just the fact that the neighbor survives repays the caller of its own altruism.

In humans, sperm donation in the USA may be an example of reciprocal altruistic behavior. European and Australian investigators contend that sperm donation is primarily altruistic and that financial motives are strictly secondary. Although in these communities, financial compensation is often withheld and yet recruitment remains successful. However, in the USA, the donor is usually paid for services rendered and without compensation, recruitment may be challenging. In a study by Rushton et al. 1981,

42 male sperm donors who were active in an insemination program were surveyed along with 50 male matched controls (note that the only difference is that they did not donate). Both donor and control groups opposed contact between offspring and donor and donors demonstrated little interest in meeting the recipients. Sixty-two percent of the donors surveyed said that money was the primary reason for participating. Thirty-six percent said that they would like to see the child and only 36% would inform their wife or partner. Two major differences in the motivation of donors versus controls were that controls were more in agreement than donors that donating sperm was altruistic. However, donors were in more agreement than controls that donating sperm was more like donating blood. In this survey, money was clearly the primary reason for donor participation. The majority of respondents would not participate if money was withheld. Furthermore, both donor and control groups favored financial compensation for participants. According to Rushton and colleagues (1981), sperm donors in the USA donate sperm based on reciprocal altruism.

A more recent study investigated the effect of reciprocity priming on organ donor registration intentions and behavior (O'Carroll et al. 2017). In Study 1, participants who were not currently registered organ donors took part either face-to-face or online and were randomly allocated to a reciprocity-prime or control condition. Primed participants were required to respond on a 7-point Likert scale from "*Strongly disagree*" to "*Strongly agree*," to the item "*I would accept an organ from a deceased donor in order to save my own life.*" The control item was "*Organ donation is important*," and participants responded on the same 7-point scale. Following the manipulation, they were asked to indicate, on either a paper or online questionnaire, their intention to join the organ donor register. Study 2 was similar to Study 1 but with the addition that after reporting intention, participants were then offered an organ donation information leaflet or the opportunity to click a link for further information (proxy

behavioral measure). The results of both studies showed that reciprocity-primed participants reported greater intentions to register than controls. However, in the second study, there was no evidence of donation behavior. The findings showed that using reciprocity might be an effective tool to increase individuals' intentions of organ donor registration but this increase in intention may not translate into donation behavior.

### Does Reciprocal Altruism Exist in Nonhuman Species?

While there are numerous examples of what appears to be reciprocal altruism in nonhuman species, some scientists question whether cooperation among nonhuman species truly represents reciprocal altruism or whether it is limited to strategies that generate immediate fitness benefits (e.g., Clutton-Brock 2009). Although experimental studies with captive birds and mammals have shown that the probability that individuals will assist each other can be affected by the previous behavior of partners or other group members, very few attempts have been made to measure the net fitness benefits of reciprocal altruism between non-kin. Only a few of the studies commonly cited as examples of direct reciprocity in natural populations provide evidence that definitively excludes the possibility that cooperative behavior is maintained by immediate shared benefits, manipulative tactics, or kin selection.

Not only might there be alternative possible explanations for most examples of reciprocal altruism in nonhuman species but reciprocal exchanges can be costly, resources highly valuable, there can be considerable delays between giving, and extensive opportunities for cheating. Clutton-Brock (2009) suggests that reciprocal exchanges might also require some form of language to establish expectations and intentions, to take into account the timing of exchanges, and to establish social norms to discourage cheating.

### **A Critique of Reciprocal and Genetic Altruism: Are They Really Separable?**

Reciprocal altruism and kin selection (genetic altruism) may not be clearly separable phenomena as they are currently defined. Reciprocal altruism is an exchange of favors between nonrelatives in which the giving and returning of favors occurs at different times and in which the cost of providing favors are lower than the benefits receiving them (Trivers 1971). Kin selection takes place when individuals increase their inclusive fitness by helping other individuals (usually closely related) who share the genes responsible for their aid giving behavior. Rothstein (1980) suggests that most examples of reciprocal altruism are special cases of kin selection. According to him, when conspecific reciprocal altruists exchange favors they are almost certainly doing so because they share at least some of genes responsible for their altruism. Therefore, the only type of reciprocal altruism that is distinguishable from kin selection is reciprocity between members of different species, such as the cleaner fish (Trivers 1971) described earlier. Because there are very few examples of interspecies cooperation, according to Rothstein (1980), there is generally always some genetic similarity among altruists and therefore, pure reciprocal altruism rarely exists and thus individuals who engage in reciprocal altruism are to some extent kin.

### **True Altruism and Ascetic Altruism**

#### **Conceptualizations**

There have been numerous attempts to conceptualize and explain true altruism. Simon's model (e.g., Simon 1990) suggests that, even if genes are the controlling sites of natural selection, people have the capacity to learn at the socioeconomic level which can lead to the selection of altruism. According to Simon (1990), docility is the basis for true altruism and true altruism is a by-product of docility. Docility refers to the capacity for being instructed and the tendency to accept and believe those instructions. Docile individuals are those who are adept at social

learning and who accept well the instruction society provides for them. These individuals tend to learn and believe what they perceive others in the society want them to learn and believe. Simon's model (1990) suggests that docile persons are more than compensated for their altruism by the knowledge and skills they acquire. A critical assumption of the model is that social organizations know better than individuals. That is, social organizations help structure the information that flows among individuals to improve their individual fitness. Thus, rather than function as independent individuals, there may be an accumulation of knowledge that gives each member of the group a fitness advantage.

Hoffman (1981) offers four kinds of behavioral evidence for biologically based altruism: (1) people frequently help others in society, (2) that a great deal of helping is performed by those whose needs for approval is not strong, (3) it often occurs almost immediately, and (4) that signs of relief in others appear to reinforce helping behaviors. Hoffman also suggests that natural selection requires a system that is reliable and yet also flexible and what therefore must have been acquired is a predisposition or a motive to help. And although this may be biologically based, it is nevertheless amenable to control by cognitive processes.

Another attempt at explaining true altruism has been to involve the construct of empathy. Aronfreed (1972) accounted for both the origin of empathy and the capacity of emphatic reactions to produce altruistic behavior. He observed that small children learn to feel bad when others feel bad and they learn to feel good when others feel good early in their lives because these conditions serve as conditioned stimuli, which through associations come to evoke similar affective responses. The motivation behind empathy is to relieve distress, which we supposedly feel when we see someone else suffering. Relieving one's own distress may appear to be a selfish act but Hoffman (1981) argues that although the consequence of helping reduces the helper's distress, there is evidence that the conscious intention of helpers is to reduce the distress of another. In addition, he suggests that since

motives are always accompanied by feelings of satisfaction, a feeling of satisfaction cannot be used to distinguish between egoist and altruistic motives.

Mary Maxwell discusses her conceptualization of true altruism in her book *Morality Among Nations: An Evolutionary View* (Maxwell 1990). In it, she proposes that reciprocal altruism led to the development of moral emotions (which she credits as Triver's idea). Moral emotions cause the development of notions of right and wrong. Notions of right and wrong result in the institutionalization of morality in human society. She believes it is faulty logic to state that natural selection requires altruism to be selfish and therefore all altruism is selfish. Rather, she contends that humans have entered into a "new human-created environment" in which mortality has different ways of controlling behavior and motives.

Joseph Lopreato defines true or ascetic altruism as behavior, conscious or unconscious which, guided by innate predispositions, potentially reduces the inclusive fitness of the benefactor while increasing that of the beneficiary (Lopreato 1981). In his article on *Genuine Altruism in Homo sapiens*, he attempts to search for and explain altruism as behavior that reduces the inclusive fitness of the giver while increasing that of the recipient. He refers to altruism as "ascetic altruism" because of the ambiguity with use of the term "altruism" and to include the concept of self-denial that is included in the concept of asceticism.

According to Lopreato (1984), true altruism evolved as a result of an increase in complexity of society or groups. Social pressures and demands of society (to help when needed) increased as the complexity of groups increased. However, as the selfish gene theory (Dawkins 1976) professes, we are internally driven to maximize our own genetic fitness. The drive to fulfill our social demands conflicts with our drive for genetic fitness. This opposition causes dissonance that ultimately causes shame. In order to rid ourselves of this dissonance and shame, we gain souls or moralistic behavior. The soul allows us to be truly altruistic. As groups become more complex and increasingly demanding, the

hierarchy of altruism would consist of true altruism at the top existing in groups with high socialization and complex interactions. At the bottom of the hierarchy would be genetic altruism existing in groups with very little social interaction and dependency. And reciprocal altruism should fall in the middle.

The evolution of the soul is a by-product of self-deception whose main effect was and may still be the maximization of inclusive fitness (Lopreato 1984). Self-deception may have evolved from increasing complexity of the reciprocal system and as a means of coping with flagrant cheating of an evolving dominance order. As long as self-deception and the idea of soul exist, a certain percentage of individuals are likely to fall victims to them.

### Does True Altruism Exist?

The ultimate question about true altruism is whether it exists such that people do things for each other without expecting something in return.

Several studies report physical and psychological benefits associated with altruistic behavior. For example, volunteerism is positively correlated with self-reported happiness, health, and well-being (see Filkowski et al. 2016 for review). People who regularly volunteer report greater satisfaction in life and exhibit reduced rates of depression and anxiety compared to those who do not volunteer. Similarly, engaging in acts of kindness has also been associated with increased well-being. These findings indicate that being aware of the kindness of others and of one's own acts of kindness is related to increased self-reported levels of well-being. In a study by Otake et al. (2006), participants were asked to count the number of acts of kindness they performed for 1 week. A control condition did not partake in the "counting kindness" task. Results indicated that counting acts of kindness significantly increased self-report levels of happiness. Together, these studies suggest that altruistic behaviors not only benefit others but also have profound positive effects on the current and future physical and psychological well-being of the person performing the behavior.

Lopreato (1981) describes a discussion involving the sociobiologist E.O. Wilson, about whether Mother Theresa is an example of ascetic or true altruism. Mother Theresa was a member of the Missionaries of Charity and therefore nonreproductive. In Calcutta and elsewhere, she cared for poor, the forsaken, the sick, and the foundlings. She received international honor and recognition, including the 1979 Nobel Peace Prize. E.O. Wilson notes that even Mother Theresa is selfish, “for she seeks to save her soul” (cited in Lopreato 1981). Lopreato (1981) suggests that the sociobiology of altruism concerns the salvation of genes and not souls and therefore Mother Theresa is a true altruist and there may be others like her. She sacrificed her reproductive fitness in the service of countless individuals who are unrelated to her.

## Cross-References

- ▶ Alarm calls
- ▶ Cheating
- ▶ Deception
- ▶ Decision-Making
- ▶ Ensociality
- ▶ E.O. Wilson
- ▶ Genes
- ▶ Helping Behavior
- ▶ Hymenoptera
- ▶ Kin Selection
- ▶ Kinship
- ▶ Prisoner’s Dilemma
- ▶ Reciprocity
- ▶ Reproductive Fitness
- ▶ Richard Dawkin’s
- ▶ Robert Trivers
- ▶ Origin of Species

## References

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325–383.

Aronfreed, J. (1972). The socialization of altruistic and sympathetic behavior: Some theoretical and experimental analyses. In J. Macauley &

L. Berkowitz (Eds.), *Altruism and helping behaviors*. Orlando: Academic Press.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211, 1390–1396.

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, 462, 51–57.

Comte, A. (1858). *The catechism of positive religion*/translated from the French of Auguste Comte by Richard Congreve. London: J. Chapman. (page images at Hathi Trust Digital Library).

Darwin, C. (1859). *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*. London: John Murray.

Darwin, C. (1871). *The descent of man*. London: John Murray.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dyble, M., Gardner, A., Vinicius, L., & Migliano, A. B. (2018). Inclusive fitness for in-laws. *Biology Letters*, 14, 20180515.

Feder, H. M. (1966). Cleaning symbioses in the marine environment. In S. M. Henry (Ed.), *Symbioses*. New York: Academic Press.

Filkowski, M. M., Cochran, R. N., & Haas, B. W. (2016). Altruistic behavior: Mapping responses in the brain. *Neuroscience and Neuroeconomics*, 5, 65–75.

Haldane, J. B. S. (1932). *The causes of evolution*. London: Longman.

Hamilton, W. D. (1964). The genetical evolution of social behavior II. *Journal of Theoretical Biology*, 7, 17–52.

Hoffman, M. L. (1981). Is altruism part of human nature? *Journal of Personality and Social Psychology*, 40, 121–137.

Lopreato, J. (1981). Toward a theory of genuine altruism in *Homo sapiens*. *Ethology and Sociobiology*, 2(3), 113–126.

Lopreato, J. (1984). Sociality, II: Ascetic altruism. In J. Lopreato (Ed.), *Human nature and biocultural evolution*. Boston: Allen and Unwin.

Maxwell, M. (1990). *Morality among nations: An evolutionary view*. New York: State University of New York Press.

Nowak, M., Tarnita, C., & Wilson, E. O. (2010). The evolution of eusociality. *Nature*, 466(7310), 1057–1062.

O’Carroll, R. E., Haddow, L., Foley, L., & Quigley, J. (2017). If you needed an organ transplant would you have one? The effect of reciprocity priming and mode of delivery on organ donor registration intentions and behaviour. *British Journal of Health Psychology*, 22(3), 577–588.

Otake, K., Shimai, S., Tanaka-Matsumi, J., Otsui, K., & Fredrickson, B. L. (2006). Happy people become happier through kindness: A counting kindnesses intervention. *Journal of Happiness Studies*, 7(3), 361–375.

Rothstein, S. I. (1980). Reciprocal altruism and kin selection are not clearly separable phenomena. *Journal of Theoretical Biology*, 87, 255–261.

- Rushton, J. P., & Sorrentino, R. M. (1981). Altruism and helping behaviors: A historical perspective. In J. P. Rushton & R. M. Sorrentino (Eds.), *Altruism and helping behavior*. Hillsdale: Lawrence Erlbaum Associate.
- Rushton, J. P., Chrisjohn, R. D., & Fekken, G. C. (1981). The altruistic personality and the self-report altruism scale. *Personality and Individual Differences*, *1*, 292–302.
- Sherman, P. W. (1985). Alarm calls in Belding's ground squirrels to aerial predators: Nepotism or self-preservation? *Behavioral Ecology and Sociobiology*, *17*, 313–323.
- Simon, H. A. (1990). A mechanism for social selection and successful altruism. *Science*, *250*, 1665–1668.
- Smith, M. (1964). Group selection and kin selection. *Nature*, *201*(4924), 1145–1147.
- Trivers, R. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35–57.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.
- Wilson, E. O. (1975). *On human nature*. London: Harvard University Press.
- Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behavior*. London: Oliver & Boyd.