Altruism

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Introduction

This brings us to the central theoretical problem of sociobiology: how can altruism, which by definition reduces personal fitness, possibly evolve by natural selection? (Wilson, 1975, p. 3)

Altruistic behaviors, which reduce the personal reproduction of an actor and benefit another individual (**Figure 1**), are found in a diverse set of organisms, ranging from microbes, through social insects, to higher vertebrates and humans (**Figure 2**). Altruism presents a conundrum for evolutionary thinking because Darwin's theory of natural selection appears to suggest that selfish and competitive strategies are favored over evolutionary time. Why would natural selection select for a behavior that reduces personal reproduction?

As we will see, altruism can evolve when the actor and recipient carry the same genes, at one or more loci – the actor can then increase copies of their genes through the recipient's reproduction. This explanation, which comes from what is called inclusive fitness (or kin selection) thinking, remains the key solution for the problem of altruism, as originally defined in the evolutionary literature. However, more than one usage of altruism has developed in behavioral ecology and with alternative definitions came other explanations, which will be discussed.

Care with definitions becomes even more important when one looks outside of biology. In common parlance,

altruism is often taken to indicate an actor's psychological 'intention' to act selflessly. The biologist's focus on 'outcome' and evolutionary fitness (**Figure 1**), therefore, can contradict the mainstream meaning of altruism in at least two ways. First, it allows the possibility of altruism in simple organisms, like microbes, that lack conscious intention. In addition, a gene for altruism will only be selected when the action increases its carrier's fitness – genes cannot be selected to produce behaviors that decrease their frequency. Evolutionary discussions of
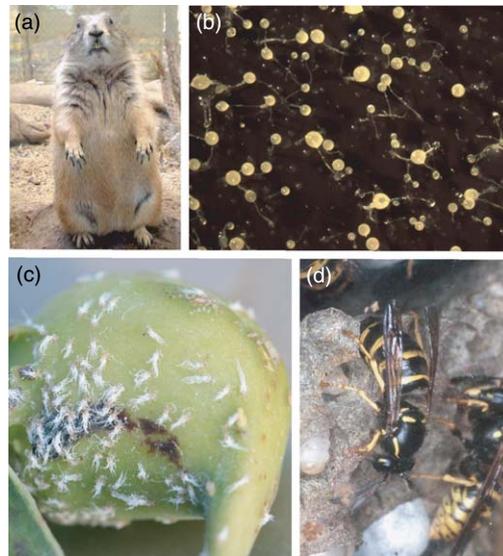
Figure 2 Species that display altruistic behaviors. (a) Prairie dogs live in family groups in communal burrows or 'towns'. When danger approaches, guard individuals will bark and warn others, at apparent cost to themselves. They also display cooperative brood care. (b) Fruiting bodies of the slime mold *Dictyostelium discoideum*. Thousands of cells aggregate together in these groups and many die altruistically to form a stalk that holds the others aloft as dispersal spores. (c) The gall-dwelling aphid *Pemphigus obesinymphae*. When disturbed, soldier aphids emerge and attack intruders. (d) The yellow-jacket eusocial wasp, *Dolichovespula saxonica*. Workers both altruistically work and lay eggs (shown) in this species. The level of worker reproduction, however, is kept low by both genetic relatedness and policing behaviors (**Figure 4**). (c) Photo used with kind permission of Patrick Abbot.

	Effect on recipient	
	+	−
+	Mutualism	Selfishness
− or 0	Altruism	Spite
	Cooperation	Competition

(Effect on actor — rows labeled + and − or 0)

Figure 1 The four types of social action based on their effect on the direct fitness (lifetime personal reproduction) of the actor and recipient. Altruism and spite can either have no or a negative fitness effect on the actor.

altruism, therefore, typically involve hidden genetic benefits, which can be troublesome for those that require altruism to be truly selfless.

The Birth of the Idea

It may be no coincidence that the concepts of altruism and natural selection were developed simultaneously in the mid-nineteenth century. Social philosophy was being much discussed and contrasting opinions abounded. On the one hand, Auguste Comte was popularizing altruism as part of his secular positivist religion, which argued for selfless acts that aid humanity and founded the new science of sociology. On the other hand, Herbert Spencer's individualism was fueling the fires of British industry. It was into this environment that Darwin proposed his individual-centered theory of evolution – natural selection.

With altruism based upon selflessness, and natural selection on selfishness, their conceptual collision would appear inevitable. However, this collision was barely evident at first. While Darwin did not use the term, his writings sowed the seeds for all modern explanations for altruism: the *Origin of Species* confidently proposes a mix of family relations, colony-level benefits, and parental manipulation to explain social insect workers (**Figure 2**); and the *Descent of Man* appeals to both group-level thinking and reciprocation to explain what he called human sympathy. Furthermore, Herbert Spencer explicitly discussed altruism in biology and explained it through both family life and competition among tribes. It is also noteworthy that Spencer often took an outcome-based definition, showing that there have long been parallel traditions of thinking about altruism, one based on intention and the other on behavior (see the introduction). This said, Spencer's views differed significantly from modern definitions by taking reproduction itself to be altruistic.

In the hundred years following the *Origin*, evolutionary discussions of cooperation and altruism are spotty, and often less clear than Darwin's original writings. This includes Kropotkin's extensive discussion of cooperation, which appeals to both group selection and a, sometimes flawed, species-level argument. By the mid-twentieth century, however, it is clear that many authors understood how cooperative acts like worker sterility and human sociality could evolve through kinship, group selection, and reciprocal benefits. These include H. G. Wells (with Julian Huxley and G. P. Wells), R. A. Fisher, A. H. Sturtevant, A. E. Emerson, J. L. Lush, and Sewell Wright. However, these authors rarely used the term 'altruism' – the notable exception being J. B. S. Haldane who colorfully compared his reader altruistically rescuing some drowning relatives to sterility in insect workers – and

the concept anyway was given little space or attention. No one seemed to think that altruism was all that important:

> There will also, no doubt, be indirect effects in cases in which an animal favours or impedes the survival or reproduction of its relatives ... Nevertheless such indirect effects will in very many cases be unimportant ... (Fisher, 1930, p. 27)

Altruism via Inclusive Fitness (Kin Selection)

This all changed in the hands of a lonely London student, called Bill Hamilton, who dedicated himself to the first formal evolutionary analysis of altruism. His results are summarized with the following simple rule: altruistic behaviors will be favored by natural selection when

$$rb > c \qquad [1]$$

where b is the reproductive benefit to the recipient, c is the cost in terms of lifetime reproduction for the actor, and r is the genetic relatedness between actor and recipient (**Figure 3a**). For example, selection can favor helping a sister ($r = 0.5$) to raise her offspring when one can raise more than twice as many of her offspring (indirect fitness), than one's own (direct fitness), because this will increase the overall propagation of copies of the actor's genes. The sum of fitness effects through indirect effects and direct effects is the 'inclusive fitness effect' of a behavior (see Kin Selection).

Semantics

Hamilton's definition of altruism requires the action to carry a cost to lifetime reproduction; a position solidified by E. O. Wilson who used this altruism as a center piece for his highly influential book *Sociobiology*. Hamilton's work also emphasizes the clarity that can come with gene-level thinking, which was later popularized by Dawkin's *The Selfish Gene*.

Examples

The social insects are among the best and most discussed examples of Hamilton's altruism in behavioral ecology (**Figure 2d**). Not only are they social, they are eusocial, with their division of work and reproduction among colony members. Comparable altruism occurs in other insects including some gall-forming aphids and thrips, which have a defensive soldier caste (**Figure 2c**). In social vertebrates, sibling care is common that is no doubt often formally altruistic (**Figure 2a**). However, individuals can
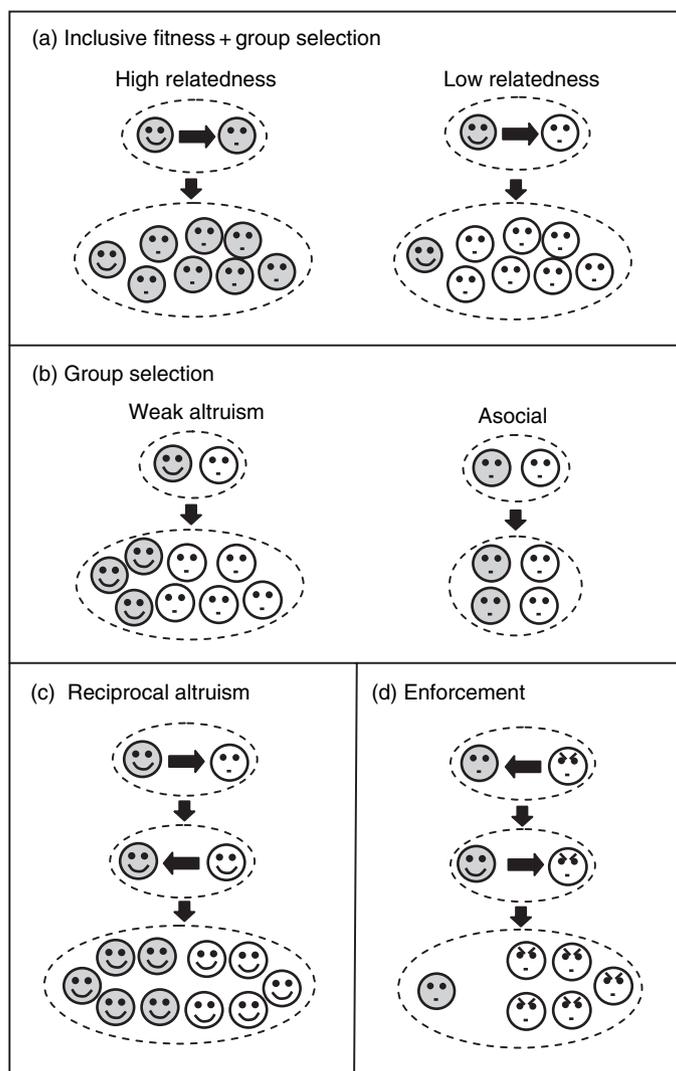
Figure 3 Four nonmutually exclusive processes that generate altruism or altruism-like behaviors. Altruists are smiling and same-color individuals are genetically related. (a) Strong altruism can be selected when individuals are genetically related (left-hand side) but not when they are unrelated (right-hand side). (b) Weak altruism (gray, left-hand side) can be selected when helping the group feeds back on the actor, even though this increases the fitness of other group members more (white, left-hand side), because it increases reproduction relative to the population as a whole (right-hand side). (c) Reciprocal altruism can increase personal reproduction. (d) Enforcement: one individual forces altruism-like behavior from another individual that may or may not obtain a fitness benefit from their action. Note that the behaviors in (b) and (c) increase the personal reproduction of the actor, and are therefore not altruism in the original strict sense of Hamilton, which required a decrease in the personal reproductive fitness of the actor. Also, actions that arise purely through enforcement (d) are better viewed as adaptations of the enforcer, rather than altruistic adaptations of the helping individual.

usually reproduce later on, making it difficult to distinguish between true altruism, and behaviors with a delayed reproductive benefit. An interesting potential exception, however, is human menopause, which appears to reduce personal reproduction in order to help raise grand-offspring and under some definitions would constitute altruism. Altruism is also found in microbes (**Figure 2b**). For example, individual cells often pay a growth cost to release a shared product, like digestive enzymes, which benefit other cells. There are good data to support the idea that relatedness drives altruism in the

social insects (**Figure 4**) and vertebrates (see Kin Selection), and the altruistic release of shared products in microbes has been shown to require genetic relatedness among cells.

Altruism via Group Selection

Another way to phrase the above explanation for altruism is in terms of group selection: when groups contain genetically related individuals (there is between-group genetic

(a) Enforcement + inclusive fitness: colonies with a queen

(b) Inclusive fitness: colonies without a queen
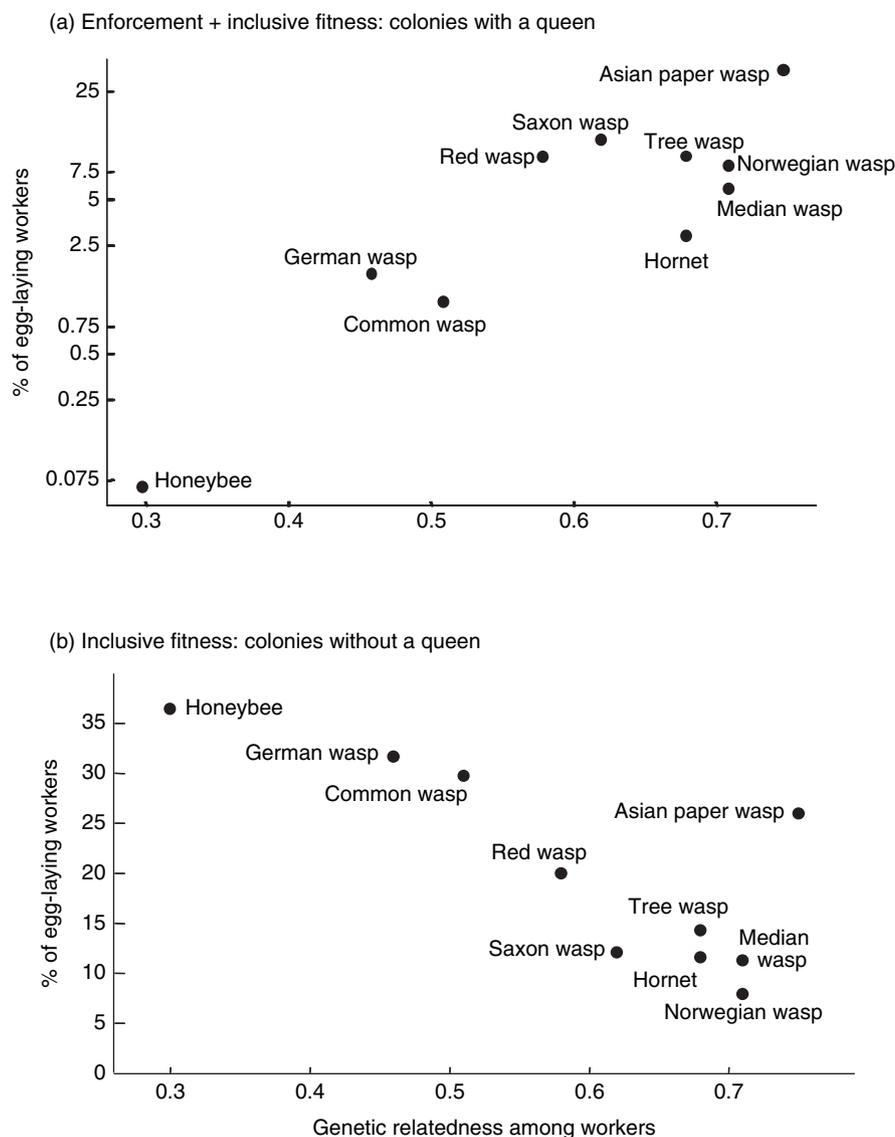
Figure 4 Worker altruism is driven by a combination of inclusive-fitness effects and enforcement in social insect colonies. (a) Altruistic self-restraint due to enforcement. In colonies where the mother queen is alive, the workers can raise either the queen's or other workers' eggs. In species where relatedness among workers is high, they tend to raise the workers' eggs because they are highly related to them, but in species where relatedness among workers is low, like the honeybee, workers 'police' each others' eggs and remove them. This reduces the benefits to worker reproduction which, alongside indirect fitness benefits, promotes reproductive self-restraint. (b) Altruistic self-restraint due to inclusive-fitness effects. If the queen dies the workers compete to lay eggs. However, when relatedness is high, many show altruistic self-restraint and do not attempt to reproduce. Reproduced from Wenseleers T and Ratnieks FL (2006) Enforced altruism in insect societies. *Nature* 444: 50.

variance), selection can favor altruistic actions that invest in the group and increase its productivity. Importantly, and despite occasional misguided claims to the contrary, this logic is fully compatible with and complementary to inclusive-fitness theory: one can explain worker sterility by focusing on benefits to relatives (inclusive fitness), or the benefits at the colony level (group selection), but in the end both genetic relatedness and benefits are required for Hamilton's altruism (**Figure 3a**). Like inclusive fitness, group-selection thinking can be traced back to Darwin (and also Spencer), and there were brief but explicit

mathematical models by Haldane and Wright in the mid-twentieth century. However, it then got a bad name when Wynne-Edwards applied it uncritically to groups of unrelated individuals, such as large vertebrate populations, where individual-level selection will dominate and suppress altruism. It was correctly reformulated in the 1970s with the work of George Price, D. S. Wilson, and, once more, Hamilton. Price's work, specifically the Price equation, has since been central to the development of many branches of social evolution theory. This includes the development of cultural models of cooperation, where

imitation within groups increases between-group variance and promotes the spread of cooperative traits through 'cultural group selection'. But there remains a point of departure between group selection and inclusive fitness when it comes to definitions.

Semantics

In the group-selection framework, altruism has been defined as cooperative acts that lower reproductive share in the group. However, this can include actions that increase personal reproduction (**Figure 3b**), which is not altruism by Hamilton's definition. Consider, for example, a prairie dog (**Figure 2a**) that contributes to the tunnels in its town and suffers a 10% decrease in its reproduction relative to another group member. This can evolve through selfish benefits alone if the tunnels allow all town members to double their reproduction. This is illustrated by a simple extension of Hamilton's rule:

$$\overbrace{\frac{b}{n}(n-1)r}^{\text{Indirect/kin benefit}} + \underbrace{\left(\frac{b}{n}\right).1}_{\text{Direct/individual benefit}} > c \qquad [2]$$

where n is group size, b is the group benefit of which each individual gets a share b/n, and c is the individual cost. The individual-benefit term contains relatedness of the actor to itself, $r_{\text{self}} = 1$, and even with no relatives in the group ($r = 0$), tunneling can still evolve if there are feedback benefits to the actor. This type of behavior has been termed 'weak' altruism (**Figure 3b**) because it carries a personal (direct fitness) benefit, which distinguishes it from Hamilton's (strong) altruism, like that of sterile insect workers (**Figure 3a**).

Examples

Because of the conceptual overlap, group-selected altruism includes all of the inclusive fitness examples above. Furthermore, feedback benefits of the sort that generate weak altruism must be common in many societies but are difficult to distinguish from inclusive fitness benefits. One example of weak altruism, however, is cooperative next founding by unrelated social insect queens. Here, co-investing in the colony can provide feedback fitness benefits when queens are later able to contribute to sexual offspring.

Altruism via Direct Fitness

In addition to weak altruism, several other processes that increase the personal reproduction of the actor (direct fitness) have been proposed to explain altruism-like behaviors. In the 1970s, Robert Trivers showed that helping can be selected when it increases the chance of return help, which he termed reciprocal altruism (tit for tat; **Figure 3c**). A closely related idea is that of indirect reciprocity, whereby helping others improves reputation, which then increases the chance of being helped. More generally, feedback benefits to personal reproduction (direct fitness) are central to all manner of cooperative behaviors, including cooperation among genes and species, for example, plants provide nectar and insects pollinate in return:

> individual flowers which had the largest glands or nectaries, and which excreted most nectar, would oftenest be visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. (Darwin, 1859)

Semantics

A focus on direct fitness has led to a third general approach to modeling social evolution, called direct fitness or neighbor-modulated fitness theory, which again complements the inclusive-fitness and group-selection approaches. However, an action that evolves purely through direct-fitness feedbacks means increased personal reproduction and departs from Hamilton's altruism. Curiously, however, Hamilton started his original papers with a neighbor-modulated model (the fitness effect of others on the focal individual), before making a switch to inclusive fitness (the fitness effect of the focal individual on others) on which he based his rule.

Examples

Reciprocal altruism and indirect reciprocity are extremely important in human cooperation, but the requirement for recognition and memory of others means that they occur in relatively few other species. Potential examples include other primates and vampire bat blood-sharing, but inclusive fitness and group benefits also occur in these systems. More generally, however, cooperation that is selected due to direct-fitness feedback benefits is fundamental to social evolution, including between-species cooperation.

Altruism via Enforcement

Most recently, explanations for altruistic-like behaviors have focused upon a somewhat sinister mechanism: enforcement. This idea can be traced not only to the 1970s and Richard Alexander who proposed parental manipulation to explain insect workers (**Figure 3d**), but also to Darwin,

whose writings suggest something similar. While policing and punishment can explain apparent acts of altruism, however, one still needs an explanation for how policing, which carries a personal cost, can evolve the so-called 'second-order problem'. For this, one must appeal again to some or all of the above theories: inclusive fitness, group selection, and direct benefits.

Semantics

If a helping behavior has arisen completely through enforcement, the primary evolutionary adaptation is in the enforcer, rather than the helping individual. The helping behavior, therefore, should probably not be considered an altruistic adaptation. This objection can be overturned, however, when an altruistic action evolves through a combination of enforcement and inclusive-fitness effects, as occurs in the social insects (below).

Examples

Enforcement, punishment, and policing are central to cementing the altruism in many social groups. This includes queen and worker policing in many species of social insects, whereby the queen and workers suppress the reproduction of other workers. The suppression means that natural selection favors workers that invest more in the indirect fitness from helping than direct fitness from their own reproduction, which increases altruistic self-restraint (**Figure 4**). In addition, dominant males in macaque societies police and punish noncooperative individuals, and dominance hierarchies help to resolve breeding conflicts in many insect and vertebrate groups.

A Synthetic View of Altruism and Cooperation

Altruistic behaviors are a central component of many social systems. Any judgment on the extent of altruism in the natural world, however, will always depend upon definition. A requirement for conscious intention restricts altruism to creatures with sophisticated cognition, such as humans. However, the fitness-based definition of behavioral ecology reveals a wealth of additional examples, which typically arise through a combination of mechanisms. Centrally though, actions that decrease lifetime reproduction can readily evolve when there are indirect benefits that increase overall inclusive fitness. This is nowhere more obvious than in the social insects, where workers spend their entire life building, guarding, and foraging to raise a myriad of their relatives' offspring.

See also: Cooperation; Kin Selection.

Further Reading

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