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Evolution

Altruism: Its characteristics and evolution

(set and group selection/kin selection/human evolution)

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ABSTRACT Altruism is a group phenomenon in which some genes or individuals, which must be presumed to be selfish, benefit others at cost to themselves. The presumption of selfishness and the fact of altruism are reconciled by kin-group selection and by reciprocal altruism. Kin-group selection is clearly visible only in special cases; its role even among social insects may be overestimated; it is probably usually inhibited by competition. However, reciprocal altruism is ubiquitous. All altruism is: (*i*) potentially reciprocal; (*ii*) potentially profitable to altruists as well as to recipients; (*iii*) environmentally determined, usually by position of individuals in group or environmental situations; and (*iv*) a net-gain lottery. These generalizations are illustrated by four idealized cases; the difficulty of applying them to real cases is illustrated by alarm-calling in groups of birds. Although altruism is a group phenomenon, it evolves by individual selection, by processes equivalent to co-evolutions. Its evolution is: (*i*) opposed by competition; (*ii*) costly, complex, and slow, and tending to produce an imprecise flexible altruism rather than a precisely detailed one; and (*iii*) supplemented by group selection (differential extinction of groups). That altruism in human beings conforms to these generalizations is a good working hypothesis. However, analysis does not "take the altruism out of (human) altruism." Humans do not calculate it, but behave altruistically because they have human altruistic emotions.

This paper is one of a series of which the purpose is to look at important evolutionary problems in new ways: by treating evolution consistently as a multilevel process; by stressing *both* the simple principles that hold at all levels *and* the literally inconceivable complexity of their manifestations at living levels in the real world; by refining definitions where necessary; and by using nonmathematical rather than mathematical models, although the conclusions of mathematical evolutionists are noted.

The present paper is concerned with altruism, with its biological characteristics and evolution. This subject is indeed important both in evolutionary theory and in practical understanding of human beings. Biologists now treat it confusingly, inconsistently, and sometimes unrealistically, so that a new look at it should be useful.

Biological altruism

Altruism is defined by biologists in several different ways. I prefer now to define it broadly, as occurring in all interactions in which some individuals benefit others at cost to themselves. (It might be defined more precisely in terms of fitness transfers, but this would be too technical here.) It may be indirect or direct, involuntary or voluntary, and one-way or reciprocal, and costs may be paid by acts or in other ways. This definition excludes concepts of volition or benevolence, and includes much that is not altruism in the everyday sense of the word; the narrower, everyday concept of altruism is related to it at the end of this paper.

Altruism is a group phenomenon. It requires at least a group of two, an altruist that pays a cost and a recipient that receives a benefit. Such groups do form themselves, vary, sometimes compete, and undergo selection. Understanding their evolution requires understanding of selection-in-principle, Darwinian natural selection, group selection, kin-group selection, and altruism itself.

Selection of sets and groups

Selection-In-Principle is most simply defined as differential elimination of preformed sets, or of sets that have formed themselves by action of their members (1). This is a multilevel definition, applicable to selection among molecules (sets of atoms), genes (sets of molecules), individual organisms (sets of genes), and groups (sets) of individuals.

Darwinian Natural Selection (as distinguished from selection directed by humans) is defined in different ways by different biologists (1). I prefer to define it simply as differential elimination of individual organisms, or as set selection at the level of living individuals (sets of genes).

Two misconceptions exist about natural selection. One is that it not only eliminates but also preserves or creates. This has been implied or asserted by many evolutionists from Darwin (as noted in ref. 1) to Gilpin (ref. 2, p. 9, with references to Wright and others). However, in the absence of a guiding intelligence, which evolutionists do not detect, natural selection *cannot* make positive choices; it *cannot* directly favor, preserve, or create anything. It can only determine what kinds of genes or individuals shall *not* survive. It must allow other kinds, including novelties, to survive if evolution is to continue, but allowing survival of novelties is not the same as creating them. For further discussion of what natural selection can and cannot do and of the source of the energy of evolution, with a comparison of the force of selection to the force of an hydrolic ram, see again ref. 1.

The second misconception is that natural selection rapidly and precisely "maximizes" adaptations, including altruistic behaviors. However, evolution by selection is so costly and slow, details under selection are so numerous and diverse, and environments are so complex and change so rapidly, that most species most of the time are probably far from precisely adapted to their environments but are just a little better than their competitors, for the time being (3).

Group Selection too can be defined in several different ways. I prefer to define it simply and literally as differential elimination of preformed groups of individual organisms, or of groups that have formed themselves by action of the individuals concerned (4, 5). As thus defined, it is set selection at the sets-of-individuals level. It occurs among simple groups of two or more individuals, special groups within populations, demes, whole species, and (in the broadest sense) groups of individuals of different species.

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Some evolutionists have thought of group selection as a creative process in which "the individual is subordinated to the group as a whole." This concept was at least adumbrated by Darwin, Haldane, and Wright; has been emphasized and amplified by Wynne-Edwards; and is still accepted, as a definition, by some evolutionists. However, the concept is unrealistic, or at best a misleading oversimplification. Like selection at other levels, group selection cannot be creative; it can make nothing new, but can act only on groups that have made themselves (by action of their member individuals); and it can act only by elimination. It is not a process in which the individual is sacrificed to the group as a whole, but one in which some individuals are sacrificed to the benefit of other individuals, which then constitute the group. It can always be translated into terms of selection of individuals in environments in which the fitnesses of some or all individuals in a group are increased by the presence of other individuals.

Genes and individuals, selfish and altruistic

Genes and the individuals carrying them must be selfish. Any kind of gene that consistently sacrificed itself to the benefit of other kinds, with no chance of any return, would eliminate itself from its gene pool. Unselfish, one-way "genes for altruism" cannot exist, although they have been invoked many times by many biologists. Dawkins (6) makes this point at book-length in *The Selfish Gene,* and other persons have said the same thing in fewer words. It follows that individuals that are unselfishly altruistic, that do not receive or "expect" any kind of return, cannot be genetically differentiated within populations of selfish nonaltruists.

This generalization is subject to exceptions. Altruistic genes might be maintained in gene pools by recurrent mutation; or pleiotropic genes with altruistic effects slightly disadvantageous to the altruists but combined with other, greater advantageous effects might be maintained by selection; or, under very limited conditions, altruistic genes might be established by deme-group selection (5, 7). However, in all these exceptional cases the altruism is presumably weak, or rare, or unstable and temporary. The cases do not seriously impair the generalization that different kinds of genes, and genetically differentiated individuals within populations, are and must be selfish.

In the preceding cases altruistic relationships are assumed to be initiated by altruists, but in other cases comparable relationships are initiated by recipients; some genes or individuals take benefits from others by actions equivalent to predation or parasitism. This is not altruism as usually defined, but it is difficult to distinguish from altruism if concepts of volition or benevolence are excluded. It can be thought of as *forced altruism,* and as such it is important, for two reasons. It is a very common form of one-way altruism (or of fitness transfer) in the real world, and it may often be the first stage in evolution of reciprocal altruism, as noted under the later heading *Evolution of altruism.* However, "forced altruists" are not unselfish; they pay the costs imposed by predation or parasitism because they must, and if they can.

Although (with exceptions that do not seriously impair the generalization) genes and the individuals carrying them must be presumed to be selfish, they often behave in ways that *as separate events* are unselfishly altruistic; they "benefit others at cost to themselves." The rest of this paper is concerned with ways in which the presumption of selfishness and the fact of altruism can be reconciled.

Kin altruism and kin-group selection

Kin or kin-group selection is a form of group selection that does reconcile the presumption of selfishness with the fact of altruism. In it, individuals make altruistic sacrifices to their kin, paying costs as individuals, but profiting genetically. Writers who have treated it recently, with historical resumés, include Wilson (8), Eberhard (9), and Dawkins (6).

Two aspects of kin-group selection—its theoretical arithmetic and its actual occurrence—should be clearly separated. The arithmetic is primarily a matter of simple fractions determined by proportions of shared genes. In ordinary, sexually reproducing, Mendelian populations, two nonidentical sibs inherit one-half of the same genes; an uncle or aunt and a nephew or niece, one-fourth; two first cousins, one-eighth; etc. These genes are identical, derived by replication of the genes of most-recent common ancestors. From these fractions it is commonly calculated that an altruist will profit genetically—will "increase the representation of its genes in the next generation"—if it sacrifices itself for more than 2 sibs, more than 4 nephews or nieces, or more than 8 first cousins; or if it makes a partial sacrifice of < one-half (any amount less than one-half) of its "personal fitness" for a sib, < one-fourth for a nephew or niece, etc.

However, these calculations ***greatly*** exaggerate the probable actual effectiveness of kin altruism and kin-group selection, for several reasons.

First, all individuals in a Mendelian population share some genes, and the selective advantage of kin (as against non-kin) altruism is reduced in proportion, or part of the advantage is spread through the whole population.

Then, kin altruism yields the calculated genetic profits only if it makes the whole difference between recipients producing no offspring and producing full quotas. It is proportionately less profitable if recipients have already produced fractions of their quotas of offspring, or if they have only fractional chances of reproducing. If, for example, recipients are young kin which have only one chance in five or one in 100 of surviving later risks and reproducing, altruism to them will yield only $1/5$ or $1/100$ of the calculated genetic profit. It follows that kin altruism should be most profitable if the recipients are young adults just ready te reproduce. (Costs as well as profits are fractional in these examples; what should be emphasized is that the altruistic transactions often involve "small change" rather than substantial investment.)

A different kind of factor that must greatly diminish the effectiveness of kin altruism and kin-group selection is difficulty of kin recognition. How can young adult sibs (see above), to say nothing of more distant kin, recognize each other, unless they stay together until they are adult, which they do only in exceptional cases?

Finally, and perhaps most importantly, an individual in its behavior to another individual cannot act both as an altruist and as a competitor at the same time. Especially in situations in which close kin do not recognize each other, competition may usually be more profitable and may inhibit altruism.

I doubt if writers on kin-group selection always realize how much these factors dilute the theoretical fractions in specific cases. For example, suppose that 10 young sibs occur among 90 non-kin, that the sibs do not recognize each other, and that only 2 of the sibs will mature and reproduce (this being the expected proportion in a stable population). Then, if one sib sacrifices itself for another individual met at random, the expected indirect genetic profits are equivalent, not to $1/2$ the altruist's genes, but to $1/2 \times 1/10$ (the chance that the recipient is a sib) $\times$ $1/5$ (the chance that, if the recipient is a sib, it will survive later risks and reproduce) $= 1/100$; or if 100 young cousins occur among 900 non-kin, if the cousins do not recognize each other, and if only 8 of them will mature and reproduce, the expected indirect genetic profits of altruistic self-sacrifice of a cousin to an individual met at random are, not $\frac{1}{8}$, but $\frac{1}{8} \times \frac{1}{10} \times \frac{1}{12.5} = \frac{1}{1000}$ of the altruist's genes. These cases are imaginary and oversimplified, but seem quantitatively realistic. They suggest that small competitive advantages are likely usually to be more profitable than kin altruism.

As to actual occurrence of kin altruism and kin-group selection, altruistic behavior can be seen among close kin in some cases, but it is usually impossible to know whether it is correlated with kinship or whether it is primarily reciprocal altruism, advantageous to all individuals regardless of kinship. In general, if kin altruism and kin-group selection were important, inbreeding (which increases the proportions of genes shared by kin) and nondispersal (which keeps kin close together) should be selectively advantageous. However, most plants and animals are adapted for out- rather than inbreeding, and for effective dispersal. In the special case of human beings—the best known altruistic animals—altruistic behavior is conspicuous, but it seems to depend on contiguity and compatibility as much or more than on kinship (see *Altruism in human beings*).

Two special kinds of kin groups exist in which kin altruism and kin-group selection do occur and have been recognized (in nonquantitative terms) since Darwin. One is parent–offspring groups, in which female and sometimes male parents behave altruistically to their offspring, but profit genetically; evolutionists argue as to whether or not this should be considered a form of kin selection (see ref. 6, pp. 101–102), but the argument seems to me to be purely semantic. The other special kind of kin group occurs among ants and other social Hymenoptera, among which female sibs in a group (colony) are half-identical twins, which greatly increases the genetic profits of kin altruism (see ref. 9 for details and ref. 10 for reasons for thinking that evolution of insect societies may actually depend less on kin selection than on "extrinsic" factors, including competition).

However, in most other cases kin selection seems a difficult-to-see and unlikely factor in evolution in the real world. Mathematicians have (I think) too often taken it out of context and greatly overestimated it. Mathematical models of it are not complete and not realistic unless they include factors for the dilution of its genetic profits and for the opposing profits of out-crossing, dispersal, and especially competition.

Reciprocal altruism

The presumption of selfishness of genes and individuals and the fact of altruism are reconciled also in reciprocal altruism (11), in which two or more individuals (or other entities) benefit each other regardless of kinship, each profiting more than its altruism costs. In contrast to kin altruism, which is (I think) clearly visible only in exceptional cases, reciprocal altruism is ubiquitous in the real world. It occurs or may occur between "copies" of the same gene, between different genes in a gene pool, between genetically similar and between genetically different individuals in a population, and between individuals of different species. These cases are further considered under *Evolution of altruism*.

Four propositions

The following four propositions bring together conclusions reached thus far. They cannot be proved, but can be tested, are consistent with each other, and can be diversely exemplified. They are (I think) true of altruism in kin groups as well as in other situations, but not of "forced altruism" (see below).

(*i*) Altruism is always actually or potentially *reciprocal;* altruists always receive or "expect" (are statistically likely to receive) direct or indirect returns. Trivers, in his important paper referred to above (11), does not make this final, inclusive generalization.

(*ii*) Altruism is always actually or potentially *profitable* to all individuals concerned; all individuals at the beginning of their existence (when the eggs are fertilized or even before) "expect" to gain more than they lose, although the expected profits of different individuals need not be equal.

(*iii*) Altruists and recipients are always *environmentally,* not genetically, differentiated, usually by *position* in kin groups or environmental situations.

(*iv*) In short (in summary) altruism is a *net-gain lottery,* in which all individuals pay or risk paying costs, but receive or "expect" profits that exceed the costs.

These propositions are apparently true of all cases in which altruism is initiated by the altruists, and is evolving or stabilized by selection. Theoretical exceptions (see *Genes and individuals, selfish and altruistic*) do not seriously impair the propositions. "Forced altruism," which is not initiated by the altruists, does not conform to the propositions but probably tends to evolve in directions suggested by them.

Examples

The following somewhat arbitrary, oversimplified examples illustrate the preceding propositions.

Mendelian populations produce surplus individuals, which are essential to allow normal losses and gene substitutions, and which are altruists by definition; by dying or failing to reproduce they pay costs that may be thought of as benefiting the populations as wholes but actually benefit surviving individuals. The altruism is potentially reciprocal; any individual may be either an altruist or a recipient. It is potentially profitable to all individuals; it makes the difference between some individuals surviving and none. And altruists and recipients are environmentally determined, by position in group or environmental situations, for example, by which individuals happen to meet predators. This is a net-gain lottery in relatively simple form.

In kin groups, too, altruism is potentially reciprocal; any individual may be a sib, or an uncle (or aunt) or a nephew (or niece), or a cousin, and may pay costs or receive benefits, or both, accordingly. It is potentially profitable, directly or indirectly, to all individuals concerned. Altruists and recipients are determined by position in kin groups and in environmental situations, according to which individuals happen to be in position to give most or profit most, or to need help or give it. This is a somewhat more complex net-gain lottery.

In an idealized ant society altruism is more complexly reciprocal; female parents (queens) produce eggs and in some cases rear the first offspring altruistically, and some female offspring (workers) then reciprocate the altruism, caring for their parent at the cost of their own sterility, and workers behave altruistically to each other. The altruism is potentially profitable, directly or indirectly, to all females; all, at the beginning of their lives, have a chance of becoming queens and benefiting accordingly, and even the workers "increase the representation of their genes in the next generation" by their altruism. The "expected" profits of a female are then its chance of becoming a queen plus the indirect genetic profits of its altruism to close kin; the sum would not be easy to calculate! Altruists and recipients (the castes) are environmentally determined. This is a still more complex net-gain lottery.

The ontogeny of a multicellular organism exemplifies the propositions at another level. The somatic cells are altruists, the reproductive cells recipients; and the somatic cells interact altruistically among themselves. The altruism is potentially reciprocal; at least early in ontogeny any cell may become either a reproductive or a somatic cell or may change its role among somatic cells. All the cells presumably profit from their altruism; they all carry the same genes, and their altruism increases the chances that their genes will be represented in the next generation. Altruists and recipients—the somatic and reproductive cells—are differentiated primarily by position in the early stages of ontogeny. This too is a net-gain lottery, simple in theory but very complex in fact.

Real cases are more complex and difficult than these oversimplified examples. This fact is illustrated by a case previously considered by several writers including Trivers (ref. 11, p. 44, with additional references). If one bird in a flock calls an alarm when it sees a hawk, risking itself but warning the others, the act, seen as a single event, looks like one-way altruism. However, if, because of the alarm, the hawk catches no bird and goes away to hunt easier prey, the alarm-caller may profit from its own act; the calling then looks less altruistic. Or if later events show that any bird in the flock may either call an alarm or receive a warning, the altruism is seen to be not one-way but reciprocal. A careful observer might see all this. However, if the flock includes close kin, kin-group effects that appear only in the next generation may modify the immediately visible effects, and would be very difficult to see. [Sherman (12) has quantified a similar case, of alarm calling in groups of ground squirrels, in which altruistic warning to kin seems to be an important factor.]

Evolution of altruism

Altruism is a group phenomenon and evolves by group selection, which (as noted earlier in this paper) can always be translated into terms of individual selection. If it is asked how groups that consist of two or more individuals playing different roles can evolve by individual selection, the answer is by co-evolution or its equivalent.

One gene or one kind of individual may (in effect) co-evolve with itself if "copies" of it play different roles in different positions in kin groups or environmental situations; it is the roles that (in effect) co-evolve. A gene that induces altruism among close kin might do this, and co-evolution without genetic differentiation of altruists and recipients may occur also in responsive altruism (ref. 5, p. 3749). This might begin with appearance of a mutant gene which causes the individual carrying it to offer responsive altruism to other individuals. If the gene does not appear in other individuals, the offers will be refused and the gene will probably be eliminated. However, if, by the chances of Mendelian heredity, the F_1 or F_2 includes more than one individual carrying the gene, offers of altruism may elicit altruistic acts in response; responsive altruism may become selectively advantageous; and a behavioral group may be formed and may evolve. This does not require spatial isolation, and, although it is most likely to begin among close kin, it does not depend on kin selection. Groups like this are conspicuous in humans.

Co-evolution of roles involving more than one gene but not genetic differentiation of altruists and recipients is exemplified by the evolution of an idealized ant society. A hypothetical, oversimplified, "tri-determinant" model of it (4) postulates three genes: (*i*) a gene that increases parent–offspring and reciprocal altruism among all females within family groups; (*ii*) a gene that makes all females susceptible to becoming either queens or workers, in response to nongenetic environmental factors; and (*iii*) a gene, also present in all females, that induces special behaviors in response to special situations.

Co-evolution of genetically differentiated individuals within a population is exemplified by evolution of reciprocally altruistic males and females in Mendelian populations.

Co-evolutions of reciprocally altruistic species range from sets of two, as the fungus and alga in a lichen, to sets of many species, as in complexly organized communities.

Co-evolution of reciprocal altruists may be inhibited by "cheaters," which accept benefits from altruists but make no return (ref. 11, p. 44), but reciprocal altruism is in fact so common that cheating must often be avoided, countered, tolerated, or used. In kin groups, effective cheating might require mimicking kinship, which might be difficult. In responsive altruism, the required response might be an actual altruistic act, which could not be mimicked. Or in an intelligent animal, perhaps only in human beings, cheating may be recognized and countered. However, these are special cases. A more general case might begin with a move, not by an altruist, but by a recipient, which might initiate a simple host-parasite (or prey-predator) relationship, the host being a "forced altruist." Host and parasite might then co-evolve in ways advantageous to themselves, the host toward tolerance for the parasite, the parasite toward moderation in its demand on the host (because outright elimination of the host would eliminate the parasite too). Finally, the host might "use" the parasite, perhaps as a source of vitamins, or as a means of eliminating weak or overage individuals, or directly in defense against other parasites, or indirectly as a "weapon of competition" (ref. 13, p. 3151). The relationship would then have evolved into reciprocal altruism. I think that this kind of co-evolution, endlessly diverse in detail, may be a multilevel process, occurring among genes and individuals in single populations as well as among different species.

Three general comments about evolution of altruism suggest themselves.

First, evolution of altruism is always opposed by competition; an individual cannot at the same time both altruistically increase and competitively decrease another's chances of surviving and reproducing. Altruism will not evolve unless it is more profitable than competition.

Second, the kinds and amounts of altruism that are selectively advantageous depend on complex interactions in groups that usually include both kin and non-kin individuals, and the proportions of kin and non-kin, and opportunities for interactions, change with dispersal rates and population densities, which themselves change with amounts and distributions of resources. Change in one resource may greatly change the kind and amount of altruism that is profitable in a particular case and may also change the kind and amount of opposing competition. This is only one of many possible examples of how environmental change may change patterns of altruism. The patterns are presumably unstable; and costly, slow natural selection should not be expected to produce complexly precise behaviors to fit them. A generalized, flexible altruism may be both simpler in its evolution and more advantageous.

Third, group selection presumably supplements individual selection in evolution of altruism. Groups in which altruism is relatively ineffective are presumably eliminated, not by a mysterious groups-as-wholes effect, but by differential elimination of individuals that do not receive the reciprocal advantages of altruism. An example is suggested under *Altruism in human beings*.

Altruism in human beings

Analysis of altruism in human beings can raise unscientific emotions even among biologists. I shall try to ask questions and offer tentative answers rather than to pontificate about it.

First, does analysis in terms of genes and selection and costs and profits "take the altruism out of (human) altruism"? I think not. Humans do not calculate the profits of altruism, but pay the costs or run the risks of it because they have human altruistic emotions.

Does altruism in humans conform to the "four propositions" offered on a preceding page? I think it does; at least this is a good working hypothesis. Human altruism does seem to be potentially reciprocal and profitable; some individuals do happen to lose by it, but all "expect" (are statistically likely to receive) profits that exceed their costs, although the expectation is usually not conscious, and although the profits are (and are expected to be) unequal. Altruists and recipients are environmentally determined, by position in groups or environmental situations; no persons are condemned by their genes to be altruists with no chance of being recipients. Altruism is therefore a net-gain lottery for humans as well as for other organisms.

Is altruism in human beings genetically determined? I think it is and is not. A man is a man and behaves as one because of his genes. However, no specific "genes for altruism" have been found in humans; "sociobiologists" are sometimes accused of postulating them, but rarely do. (However, behavior is a function of the whole organism, and many genes are known that change structures, physiologies, or endocrine systems in ways that change behaviors.)

What part do kin altruism and kin-group selection play in humans? Parent–offspring altruism is conspicuous and its importance unquestioned. Altruism is conspicuous also among human sibs and less-close kin, but it is not precisely proportional to kinship; it is greatly modified, either reinforced or cancelled, by individual likes and dislikes. Among young adults, among whom kin altruism should be most profitable genetically, it is overridden by attractions and reciprocal altruism between *non-kin* males and females. In general, altruism in humans seems correlated with congruity and compatibility more than with kinship, and this suggests that human altruism is responsive more than kin-related. Sahlins (14) makes the same point—that human altruism is not closely correlated with genetic kinship—in greater detail; readers of his book should read also Simpson's (15) review of it.

How has altruism evolved in human beings? Altruistic behaviors do not fossilize, and evidence derived from observation of surviving hunter-gatherers and nonhuman primates is indirect and incomplete, so the answer must be largely inference and outright guessing. We can guess that among our remote prehuman ancestors altruistic behaviors may have been determined in some detail by specific genes and may have evolved by genetic variation and selection, but now, although our altruism still has a broad genetic base, the details of it and its evolution seem to be determined socially more than genetically. This has involved a shift to evolution at a new, social level. Variation and selection occur at the new level, but with new characteristics: the variation is amplified by something like inheritance of acquired characters, which greatly increases the rates and amounts of diversification that occur before selection; and, although selection is still primarily by elimination, it can be supplemented by intelligent choice. Diversification and evolution at the new level are increasingly rapid and complex, but still (I think) result in co-evolutions of reciprocal altruists.

Does altruism in humans conform to the three "general comments" made under *Evolution of altruism?* I think so. Human altruism is opposed and sometimes inhibited by competition. It is imprecise in detail; some biologists seem to suggest that evolution by selection has produced altruistic behaviors in humans precisely adapted to degrees of kinship, the costs and profits of kin and non-kin altruism, and the profits of selfish cheating and the counter-profits of detecting and preventing it. But we have only to look around us to see that human altruism is not so precisely detailed. It is also not precisely limited; our altruistic emotions often extend beyond the limits of human beings to cats and whales and even plants. (However, reason may justify man's altruism to these and other organisms.) Group selection does supplement individual selection in evolution of altruism in humans; this is illustrated by control of "cheating."

"Cheating," or acceptance of altruism without reciprocation, does occur in human populations. Milder forms of it, including minor failures of responses or cooperation, are recognized and countered or tolerated by individuals. More serious forms are controlled by laws or other group actions. However, control is not perfect. Human populations usually carry loads of nonaltruists, and if the loads become too great, whole populations may be eliminated; this results in a kind of group selection which has presumably continually supplemented individual selection in evolution of altruism in humans, and may still operate. "Forced altruism," including outright slavery, also occurs in human beings, and does sometimes (I think) evolve into reciprocal altruism.

My tentative and I hope not dogmatic conclusion is that altruism as we see it in ourselves—the narrower everyday concept of it—fits remarkably well into the broader biological concept.

Note. This paper is intended only as a new introduction to an important but confusing subject, and has deliberately been kept simple, with only enough references to give interested readers an entry to more extensive literature.

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