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THE EVOLUTION OF RECIPROCAL ALTRUISM

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ABSTRACT

A model is presented to account for the natural selection of what is termed reciprocally altruistic behavior. The model shows how selection can operate against the cheater (non-reciprocator) in the system. Three instances of altruistic behavior are discussed, the evolution of which the model can explain: (1) behavior involved in cleaning symbioses; (2) warning cries in birds; and (3) human reciprocal altruism.

Regarding human reciprocal altruism, it is shown that the details of the psychological system that regulates this altruism can be explained by the model. Specifically, friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, and some forms of dishonesty and hypocrisy can be explained as important adaptations to regulate the altruistic system. Each individual human is seen as possessing altruistic and cheating tendencies, the expression of which is sensitive to developmental variables that were selected to set the tendencies at a balance appropriate to the local social and ecological environment.

INTRODUCTION

ALTRUISTIC behavior can be defined as behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior, benefit and detriment being defined in terms of contribution to inclusive fitness. One human being leaping into water, at some danger to himself, to save another distantly related human from drowning may be said to display altruistic behavior. If he were to leap in to save his own child, the behavior would not necessarily be an instance of "altruism"; he may merely be contributing to the survival of his own genes invested in the child.

Models that attempt to explain altruistic behavior in terms of natural selection are models designed to take the altruism out of altruism. For example, Hamilton (1964) has demonstrated that degree of relationship is an important parameter in predicting how selection will operate, and behavior which appears altruistic may, on knowledge of the genetic relationships of the organisms involved, be explicable in terms of natural selection: those genes being selected for that contribute to their

own perpetuation, regardless of which individual the genes appear in. The term "kin selection" will be used in this paper to cover instances of this type—that is, of organisms being selected to help their relatively close kin.

The model presented here is designed to show how certain classes of behavior conveniently denoted as "altruistic" (or "reciprocally altruistic") can be selected for even when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out. The model will apply, for example, to altruistic behavior between members of different species. It will be argued that under certain conditions natural selection favors these altruistic behaviors because in the long run they benefit the organism performing them.

THE MODEL

One human being saving another, who is not closely related and is about to drown, is an instance of altruism. Assume that the chance of the drowning man dying is one-half if no one leaps in to save him, but that the chance that his potential rescuer will drown if he leaps in to save him is much smaller, say, one in

twenty. Assume that the drowning man always drowns when his rescuer does and that he is always saved when the rescuer survives the rescue attempt. Also assume that the energy costs involved in rescuing are trivial compared to the survival probabilities. Were this an isolated event, it is clear that the rescuer should not bother to save the drowning man. But if the drowning man reciprocates at some future time, and if the survival chances are then exactly reversed, it will have been to the benefit of each participant to have risked his life for the other. Each participant will have traded a one-half chance of dying for about a one-tenth chance. If we assume that the entire population is sooner or later exposed to the same risk of drowning, the two individuals who risk their lives to save each other will be selected over those who face drowning on their own. Note that the benefits of reciprocity depend on the unequal cost/benefit ratio of the altruistic act, that is, the benefit of the altruistic act to the recipient is greater than the cost of the act to the performer, cost and benefit being defined here as the increase or decrease in chances of the relevant alleles propagating themselves in the population. Note also that, as defined, the benefits and costs depend on the age of the altruist and recipient (see *Age-dependent changes* below). (The odds assigned above may not be unrealistic if the drowning man is drowning because of a cramp or if the rescue can be executed by extending a branch from shore.)

Why should the rescued individual bother to reciprocate? Selection would seem to favor being saved from drowning without endangering oneself by reciprocating. Why not cheat? ("Cheating" is used throughout this paper solely for convenience to denote failure to reciprocate; no conscious intent or moral connotation is implied.) Selection will discriminate against the cheater if cheating has later adverse effects on his life which outweigh the benefit of not reciprocating. This may happen if the altruist responds to the cheating by curtailing all future possible altruistic gestures to this individual. Assuming that the benefits of these lost altruistic acts outweigh the costs involved in reciprocating, the cheater will be selected against relative to individuals who, because neither cheats, exchange many altruistic acts.

This argument can be made precise. Assume there are both altruists and non-altruists in a population of size N and that the altruists are characterized by the fact that each performs altruistic acts when the cost to the altruist is well below the benefit to the recipient, where cost is defined as the degree to which the behavior retards the reproduction of the genes of the altruist and benefit is the degree to which the behavior increases the rate of reproduction of the genes of the recipient. Assume that the altruistic behavior of an altruist is controlled by an allele (dominant or recessive), a_2 , at a given locus and that (for simplicity) there is only one alternative allele, a_1 , at that locus and that it does not lead to altruistic behavior. Consider three possibilities: (1) the altruists dispense their altruism randomly throughout the population; (2) they dispense it nonrandomly by regarding their degree of genetic relationship with possible recipients; or (3) they dispense it nonrandomly by regarding the altruistic tendencies of possible recipients.

(1) *Random dispensation of altruism*

There are three possible genotypes: a_1a_1 , a_2a_1 , and a_2a_2 . Each allele of the heterozygote will be affected equally by whatever costs and benefits are associated with the altruism of such individuals (if a_2 is dominant) and by whatever benefits accrue to such individuals from the altruism of others, so they can be disregarded. If altruistic acts are being dispensed randomly throughout a large population, then the typical a_1a_1 individual benefits by $(1/N)\sum b_i$, where b_i is the benefit of the i th altruistic act performed by the altruist. The typical a_2a_2 individual has a net benefit of $(1/N)\sum b_i - (1/N)\sum c_j$, where c_j is the cost to the a_2a_2 altruist of his j th altruistic act. Since $-(1/N)\sum c_j$ is always less than zero, allele a_1 will everywhere replace allele a_2 .

(2) *Nonrandom dispensation by reference to kin*

This case has been treated in detail by Hamilton (1964), who concluded that if the tendency to dispense altruism to close kin is great enough, as a function of the disparity between the average cost and benefit of an altruistic act, then a_2 will replace a_1 . Tech-

nically, all that is needed for Hamilton's form of selection to operate is that an individual with an "altruistic allele" be able to distinguish between individuals with and without this allele and discriminate accordingly. No formal analysis has been attempted of the possibilities for selection favoring individuals who increase their chances of receiving altruistic acts by appearing as if they were close kin of altruists, although selection has clearly sometimes favored such parasitism (e.g., Drury and Smith, 1968).

(3) *Nonrandom dispensation by reference to the altruistic tendencies of the recipient*

What is required is that the net benefit accruing to a typical a_2a_2 altruist exceed that accruing to an a_1a_1 non-altruist, or that

$$(1/p^2)(\Sigma b_k - \Sigma c_j) > (1/q^2)\Sigma b_m,$$

where b_k is the benefit to the a_2a_2 altruist of the k th altruistic act performed toward him, where c_j is the cost of the j th altruistic act by the a_2a_2 altruist, where b_m is the benefit of the m th altruistic act to the a_1a_1 non-altruist, and where p is the frequency in the population of the a_2 allele and q that of the a_1 allele. This will tend to occur if Σb_m is kept small (which will simultaneously reduce Σc_j). And this in turn will tend to occur if an altruist responds to a "nonaltruistic act" (that is, a failure to act altruistically toward the altruist in a situation in which so doing would cost the actor less than it would benefit the recipient) by curtailing future altruistic acts to the non-altruist.

Note that the above form of altruism does not depend on all altruistic acts being controlled by the same allele at the same locus. Each altruist could be motivated by a different allele at a different locus. All altruistic alleles would tend to be favored as long as, for each allele, the net average benefit to the homozygous altruist exceeded the average benefit to the homozygous nonaltruist; this would tend to be true if altruists restrict their altruism to fellow altruists, regardless of what allele motivates the other individual's altruism. The argument will therefore apply, unlike Hamilton's (1964), to altruistic acts exchanged between members of different species. It is the *exchange* that favors such altruism, not the fact that the allele in

question sometimes or often directly benefits its duplicate in another organism.

If an "altruistic situation" is defined as any in which one individual can dispense a benefit to a second greater than the cost of the act to himself, then the chances of selecting for altruistic behavior, that is, of keeping $\Sigma c_j + \Sigma b_m$ small, are greatest (1) when there are many such altruistic situations in the lifetime of the altruists, (2) when a given altruist repeatedly interacts with the same small set of individuals, and (3) when pairs of altruists are exposed "symmetrically" to altruistic situations, that is, in such a way that the two are able to render roughly equivalent benefits to each other at roughly equivalent costs. These three conditions can be elaborated into a set of relevant biological parameters affecting the possibility that reciprocally altruistic behavior will be selected for.

(1) *Length of lifetime.* Long lifetime of individuals of a species maximizes the chance that any two individuals will encounter many altruistic situations, and all other things being equal one should search for instances of reciprocal altruism in long-lived species.

(2) *Dispersal rate.* Low dispersal rate during all or a significant portion of the lifetime of individuals of a species increases the chance that an individual will interact repeatedly with the same set of neighbors, and other things being equal one should search for instances of reciprocal altruism in such species. Mayr (1963) has discussed some of the factors that may affect dispersal rates.

(3) *Degree of mutual dependence.* Interdependence of members of a species (to avoid predators, for example) will tend to keep individuals near each other and thus increase the chance they will encounter altruistic situations together. If the benefit of the mutual dependence is greatest when only a small number of individuals are together, this will greatly increase the chance that an individual will repeatedly interact with the same small set of individuals. Individuals in primate troops, for example, are mutually dependent for protection from predation, yet the optimal troop size for foraging is often small (Crook, 1969). Because they also meet the other conditions outlined here, primates are almost ideal species in which to search for reciprocal altruism. Clean-

ing symbioses provide an instance of mutual dependence between members of different species, and this mutual dependence appears to have set the stage for the evolution of several altruistic behaviors discussed below.

(4) *Parental care.* A special instance of mutual dependence is that found between parents and offspring in species that show parental care. The relationship is usually so asymmetrical that few or no situations arise in which an offspring is capable of performing an altruistic act for the parents or even for another offspring, but this is not entirely true for some species (such as primates) in which the period of parental care is unusually long. Parental care, of course, is to be explained by Hamilton's (1964) model, but there is no reason why selection for reciprocal altruism cannot operate between close kin, and evidence is presented below that such selection has operated in humans.

(5) *Dominance hierarchy.* Linear dominance hierarchies consist by definition of asymmetrical relationships; a given individual is dominant over another but not vice versa. Strong dominance hierarchies reduce the extent to which altruistic situations occur in which the less dominant individual is capable of performing a benefit for the more dominant which the more dominant individual could not simply take at will. Baboons (*Papio cynocephalus*) provide an illustration of this. Hall and DeVore (1965) have described the tendency for meat caught by an individual in the troop to end up by preemption in the hands of the most dominant males. This ability to preempt removes any selective advantage that food-sharing might otherwise have as a reciprocal gesture for the most dominant males, and there is no evidence in this species of any food-sharing tendencies. By contrast, Van Lawick-Goodall (1968) has shown that in the less dominance-oriented chimpanzees more dominant individuals often do not preempt food caught by the less dominant. Instead, they besiege the less dominant individual with "begging gestures," which result in the handing over of small portions of the catch. No strong evidence is available that this is part of a reciprocally altruistic system, but the absence of a strong linear dominance hierarchy has clearly facilitated such a possibility. It is very likely that early hominid groups had a dominance system more similar

to that of the modern chimpanzee than to that of the modern baboon (see, for example, Reynolds, 1966).

(6) *Aid in combat.* No matter how dominance-oriented a species is, a dominant individual can usually be aided in aggressive encounters with other individuals by help from a less dominant individual. Hall and DeVore (1965) have described the tendency for baboon alliances to form which fight as a unit in aggressive encounters (and in encounters with predators). Similarly, vervet monkeys in aggressive encounters solicit the aid of other, often less dominant, individuals (Struhsaker, 1967). Aid in combat is then a special case in which relatively symmetrical relations are possible between individuals who differ in dominance.

The above discussion is meant only to suggest the broad conditions that favor the evolution of reciprocal altruism. The most important parameters to specify for individuals of a species are how many altruistic situations occur and how symmetrical they are, and these are the most difficult to specify in advance. Of the three instances of reciprocal altruism discussed in this paper only one, human altruism, would have been predicted from the above broad conditions.

The relationship between two individuals repeatedly exposed to symmetrical reciprocal situations is exactly analogous to what game theorists call the Prisoner's Dilemma (Luce and Raiffa, 1957; Rapoport and Chammah, 1965), a game that can be characterized by the payoff matrix

| | | |
|----------------|----------------|----------------|
| | A ₂ | C ₂ |
| A ₁ | R, R | S, T |
| C ₁ | T, S | P, P |

where $S < P < R < T$ and where A₁ and A₂ represent the altruistic choices possible for the two individuals, and C₁ and C₂, the cheating choices (the first letter in each box gives the payoff for the first individual, the second letter the payoff for the second individual). The other symbols can be given the following meanings: R stands for the reward each individual gets from an altruistic exchange if neither cheats; T stands for the temptation to cheat; S stands for the sucker's payoff that an altruist

gets when cheated; and P is the punishment that both individuals get when neither is altruistic (adapted from Rapoport and Chammah, 1965). Iterated games played between the same two individuals mimic real life in that they permit each player to respond to the behavior of the other. Rapoport and Chammah (1965) and others have conducted such experiments using human players, and some of their results are reviewed below in the discussion of human altruism.

W. D. Hamilton (pers. commun.) has shown that the above treatment of reciprocal altruism can be reformulated concisely in terms of game theory as follows. Assuming two altruists are symmetrically exposed to a series of reciprocal situations with identical costs and identical benefits, then after $2n$ reciprocal situations, each has been "paid" nR . Were one of the two a nonaltruist and the second changed to a non-altruistic policy after first being cheated, then the initial altruist would be paid $S + (n - 1)P$ (assuming he had the first opportunity to be altruistic) and the non-altruist would receive $T + (n - 1)P$. The important point here is that unless $T \gg R$, then even with small n , nR should exceed $T + (n - 1)P$. If this holds, the nonaltruistic type, when rare, cannot start to spread. But there is also a barrier to the spread of altruism when altruists are rare, for $P > S$ implies $nP > S + (n - 1)P$. As n increases, these two total payoffs tend to equality, so the barrier to the spread of altruism is weak if n is large. The barrier will be overcome if the advantages gained by exchanges between altruists outweigh the initial losses to non-altruistic types.

Reciprocal altruism can also be viewed as a symbiosis, each partner helping the other while he helps himself. The symbiosis has a time lag, however; one partner helps the other and must then wait a period of time before he is helped in turn. The return benefit may come directly, as in human food-sharing, the partner directly returning the benefit after a time lag. Or the return may come indirectly, as in warning calls in birds (discussed below), where the initial help to other birds (the warning call) sets up a causal chain through the ecological system (the predator fails to learn useful information) which redounds after a time lag to the benefit of the caller. The time lag is the crucial factor,

for it means that only under highly specialized circumstances can the altruist be reasonably guaranteed that the causal chain he initiates with his altruistic act will eventually return to him and confer, directly or indirectly, its benefit. Only under these conditions will the cheater be selected against and this type of altruistic behavior evolve.

Although the preconditions for the evolution of reciprocal altruism are specialized, many species probably meet them and display this type of altruism. This paper will limit itself, however, to three instances. The first, behavior involved in cleaning symbioses, is chosen because it permits a clear discrimination between this model and that based on kin selection (Hamilton, 1964). The second, warning calls in birds, has already been elaborately analyzed in terms of kin selection; it is discussed here to show how the model presented above leads to a very different interpretation of these familiar behaviors. Finally, human reciprocal altruism is discussed in detail because it represents the best documented case of reciprocal altruism known, because there has apparently been strong selection for a very complex system regulating altruistic behavior, and because the above model permits the functional interpretation of details of the system that otherwise remain obscure.

ALTRUISTIC BEHAVIOR IN CLEANING SYMBIOSES

The preconditions for the evolution of reciprocal altruism are similar to those for the operation of kin selection: long lifetime, low dispersal rate, and mutual dependence, for example, tend to increase the chance that one is interacting with one's close kin. This makes it difficult to discriminate the two alternative hypotheses. The case of cleaning symbiosis is important to analyze in detail because altruistic behavior is displayed that cannot be explained by kin selection, since it is performed by members of one species for the benefit of members of another. It will be shown instead that the behavior can be explained by the model presented above. No elaborate explanation is needed to understand the evolution of the mutually advantageous cleaning symbiosis itself; it is several additional behaviors displayed by the host fish to its cleaner that require a

special explanation because they meet the criteria for altruistic behavior outlined above—that is, they benefit the cleaner while apparently being detrimental to the host.

Feder (1966) and Maynard (1968) have recently reviewed the literature on cleaning symbioses in the ocean. Briefly, one organism (e.g., the wrasse, *Labroides dimidiatus*) cleans another organism (e.g., the grouper, *Epinephelus striatus*) of ectoparasites (e.g., caligoid copepods), sometimes entering into the gill chambers and mouth of the “host” in order to do so. Over forty-five species of fish are known to be cleaners, as well as six species of shrimp. Innumerable species of fish serve as hosts. Stomach analyses of cleaner fish demonstrate that they vary greatly in the extent to which they depend on their cleaning habits for food, some apparently subsisting nearly entirely on a diet of ectoparasites. Likewise, stomach analyses of host fish reveal that cleaners differ in the rate at which they end up in the stomachs of their hosts, some being apparently almost entirely immune to such a fate. It is a striking fact that there seems to be a strong correlation between degree of dependence on the cleaning way of life and immunity to predation by hosts.

Cleaning habits have apparently evolved independently many times (at least three times in shrimps alone), yet some remarkable convergence has taken place. Cleaners, whether shrimp or fish, are distinctively colored and behave in distinctive ways (for example, the wrasse, *L. dimidiatus*, swims up to its host with a curious dipping and rising motion that reminds one of the way a finch flies). These distinctive features seem to serve the function of attracting fish to be cleaned and of inhibiting any tendency in them to feed on their cleaners. There has apparently been strong selection to avoid eating one's cleaner. This can be illustrated by several observations. Hediger (1968) raised a grouper (*Epinephelus*) from infancy alone in a small tank for six years, by which time the fish was almost four feet in length and accustomed to snapping up anything dropped into its tank. Hediger then dropped a small live cleaner (*L. dimidiatus*) into the grouper's tank. The grouper not only failed to snap up the cleaner but opened its mouth and permitted the cleaner free entry and exit.

Soon we watched our second surprise: the grouper made a movement which in the preceding six years we had never seen him make: he spread the right gill-covering so wide that the individual gill-plates were separated from each other at great distances, wide enough to let the cleaner through (translated from Hediger, 1968 p. 93).

When Hediger added two additional *L. dimidiatus* to the tank, all three cleaned the grouper with the result that within several days the grouper appeared restless and nervous, searched out places in the tank he had formerly avoided, and shook himself often (as a signal that he did not wish to be cleaned any longer). Apparently three cleaners working over him constantly was too much for him, yet he still failed to eat any of them. When Hediger removed two of the cleaners, the grouper returned to normal. There is no indication the grouper ever possessed any edible ectoparasites, and almost two years later (in December, 1968) the same cleaner continued to “clean” the grouper (pers. observ.) although the cleaner was, in fact, fed separately by its zoo-keepers.

Eibl-Eibesfeldt (1959) has described the morphology and behavior of two species (e.g., *Aspidontus taeniatus*) that mimic cleaners (e.g., *L. dimidiatus*) and that rely on the passive behavior of fish which suppose they are about to be cleaned to dart in and bite off a chunk of their fins. I cite the evolution of these mimics, which resemble their models in appearance and initial swimming behavior, as evidence of strong selection for hosts with no intention of harming their cleaners.

Of especial interest is evidence that there has been strong selection not to eat one's cleaner even after the cleaning is over. Eibl-Eibesfeldt (1955) has made some striking observations on the goby, *Elacatinus oceanops*:

I never saw a grouper snap up a fish after it had cleaned it. On the contrary, it announced its impending departure by two definite signal movements. First it closed its mouth vigorously, although not completely, and immediately opened it wide again. Upon this intention movement, all the gobies left the mouth cavity. Then the grouper shook its body laterally a few times, and all the cleaners returned to their coral. If one frightened a grouper it never neglected these forewarning movements (translated from Eibl-Eibesfeldt, 1955, p. 208).

Randall has made similar observations on a moray eel (*Gymnothorax japonicus*) that signalled with a "sharp lateral jerk of the eel's head," after which "the wrasse fairly flew out of the mouth, and the awesome jaws snapped shut" (Randall, 1958, 1962). Likewise, Hediger's Kasper Hauser grouper shook its body when it had enough of being cleaned.

Why does a large fish not signal the end to a cleaning episode by swallowing the cleaner? Natural selection would seem to favor the double benefit of a good cleaning followed by a meal of the cleaner. Selection also operates, of course, on the cleaner and presumably favors mechanisms to avoid being eaten. The distinctive behavior and appearance of cleaners has been cited as evidence of such selection. One can also cite the distinctive behavior of the fish being cleaned. Feder (1966) has pointed out that hosts approaching a cleaner react by "stopping or slowing down, allowing themselves to assume awkward positions, seemingly in a hypnotic state." Fishes sometimes alter their color dramatically before and while being cleaned, and Feder (1966) has summarized instances of this. These forms of behavior suggest that natural selection has operated on cleaners to avoid attempting to clean fish without these behaviors, presumably to avoid wasting energy and to minimize the dangers of being eaten. (Alternatively, the behaviors, including color change, may aid the cleaners in finding ectoparasites. This is certainly possible but not, I believe, adequate to explain the phenomenon completely. See, for example, Randall, 1962.)

Once the fish to be cleaned takes the proper stance, however, the cleaner goes to work with no apparent concern for its safety: it makes no effort to avoid the dangerous mouth and may even swim inside, which as we have seen, seems particularly foolhardy, since fish being cleaned may suddenly need to depart. The apparent unconcern of the cleaner suggests that natural selection acting on the fish being cleaned does not, in fact, favor eating one's cleaner. No speculation has been advanced as to why this may be so, although some speculation has appeared about the mechanisms involved. Feder advances two possibilities, that of Eibl-Eibesfeldt (1955) that fish come to be cleaned only after their appetite has been satisfied, and one of his own, that the irritation of ecto-

parasites may be sufficient to inhibit hunger. Both possibilities are contradicted by Hediger's observation, cited above, and seem unlikely on functional grounds as well.

A fish to be cleaned seems to perform several "altruistic" acts. It desists from eating the cleaner even when it easily could do so and when it must go to special pains (sometimes at danger to itself) to avoid doing so. Furthermore, it may perform two additional behaviors which seem of no direct benefit to itself (and which consume energy and take time), namely, it signals its cleaner that it is about to depart even when the fish is not in its mouth, and it may chase off possible dangers to the cleaner:

While diving with me in the Virgin Islands, Robert Schroeder watched a Spanish hogfish grooming a bar jack in its bronze color state. When a second jack arrived in the pale color phase, the first jack immediately drove it away. But later when another jack intruded on the scene and changed its pale color to dark bronze it was not chased. The bronze color would seem to mean "no harm intended; I need service" (Randall, 1962 p. 44).

The behavior of the host fish is interpreted here to have resulted from natural selection and to be, in fact, beneficial to the host because the cleaner is worth more to it alive than dead. This is because the fish that is cleaned "plans" to return at later dates for more cleanings, and it will be benefited by being able to deal with the same individual. If it eats the cleaner, it may have difficulty finding a second when it needs to be cleaned again. It may lose valuable energy and be exposed to unnecessary predation in the search for a new cleaner. And it may in the end be "turned down" by a new cleaner or serviced very poorly. In short, the host is abundantly repaid for the cost of its altruism.

To support the hypothesis that the host is repaid its initial altruism, several pieces of evidence must be presented: that hosts suffer from ectoparasites; that finding a new cleaner may be difficult or dangerous; that if one does not eat one's cleaner, the same cleaner can be found and used a second time (e.g., that cleaners are site-specific); that cleaners live long enough to be used repeatedly by the same host; and if possible, that individual hosts do, in fact, reuse the same cleaner.

(1) *The cost of ectoparasites.* It seems almost axiomatic that the evolution of cleaners entirely dependent on ectoparasites for food implies the selective disadvantage for the cleaned of being ectoparasite-ridden. What is perhaps surprising is the effect that removing all cleaners from a coral reef has on the local "hosts" (Limbaugh, 1961). As Feder (1966) said in his review:

Within a few days the number of fishes was drastically reduced. Within two weeks almost all except territorial fishes had disappeared, and many of these had developed white fuzzy blotches, swellings, ulcerated sores, and frayed fins (p. 366).

Clearly, once a fish's primary way of dealing with ectoparasites is by being cleaned, it is quickly vulnerable to the absence of cleaners.

(2) *The difficulty and danger of finding a cleaner.* There are naturally very few data on the difficulty or danger of finding a new cleaner. This is partially because, as shown below, fish tend repeatedly to return to familiar cleaners. The only observation of fish being disappointed in their search for cleaners comes from Eibl-Eibesfeldt (1955): "If the cleaners fail to appear over one coral in about half a minute, the large fishes swim to another coral and wait there a while" (translated from p. 210). It may be that fish have several alternative cleaning stations to go to, since any particular cleaning station may be occupied or unattended at a given moment. So many fish tend to be cleaned at coral reefs (Limbaugh, 1961, observed a cleaner service 300 fish in a 6-hour period), that predators probably frequent coral reefs in search of fish being cleaned. Limbaugh (1961) suggested that good human fishing sites are found near cleaning stations. One final reason why coming to be cleaned may be dangerous is that some fish must leave their element to do so (Randall, 1962):

Most impressive were the visits of moray eels, which do not ordinarily leave their holes in the reef during daylight hours, and of the big jacks which swam up from deeper water to the reef's edge to be "serviced" before going on their way (p. 43).

(3) *Site specificity of cleaners.* Feder (1966) has reviewed the striking evidence for the site specificity of cleaners and concludes:

Cleaning fishes and cleaning shrimps have regular stations to which fishes wanting to be cleaned can come (p. 367).

Limbaugh, Pederson, and Chase (1961) have reviewed available data on the six species of cleaner shrimps, and say:

The known cleaner shrimps may conveniently be divided into two groups on the basis of behavior, habitat and color. The five species comprising one group are usually solitary or paired. . . . All five species are territorial and remain for weeks and, in some cases, months or possibly years within a meter or less of the same spot. They are omnivorous to a slight extent but seem to be highly dependent upon their hosts for food. This group is tropical, and the individuals are brightly marked. They display themselves to their hosts in a conspicuous manner. They probably rarely serve as prey for fishes. A single species, *Hippolydmata californica*, comprises the second group. . . . This species is a gregarious, wandering, omnivorous animal . . . and is not highly dependent upon its host for survival. So far as is known, it does not display itself to attract fishes (p. 238).

It is *H. californica* that is occasionally found in the stomachs of at least one of its hosts. The striking correlation of territoriality and solitariness with cleaning habits is what theory would predict. The same correlation can be found in cleaner fish. *Labroides*, with four species, is the genus most completely dependent on cleaning habits. No *Labroides* has ever been found in the stomach of a host fish. All species are highly site-specific and tend to be solitary. Randall (1958) reports that an individual *L. dimidiatus* may sometimes swim as much as 60 feet from its cleaning station, servicing fish on the way. But he notes,

This was especially true in an area where the highly territorial damsel fish *Pomacentris nigricans* (Lepede) was common. As one damsel fish was being tended, another nearby would assume a stationary pose with fins erect and the *Labroides* would move on to the latter with little hesitation (p. 333).

Clearly, what matters for the evolution of reciprocal altruism is that the same two individuals interact repeatedly. This will be facilitated by the site specificity of either individual. Of temperate water cleaners, the species most

specialized to cleaning is also apparently the most solitary (Hobson, 1969).

(4) *Lifespan of cleaners.* No good data exist on how long cleaners live, but several observations on both fish and shrimp suggest that they easily live long enough for effective selection against cheaters. Randall (1958) repeatedly checked several ledges and found that different feeding stations were occupied for "long periods of time," apparently by the same individuals. One such feeding station supported two individuals for over three years. Of one species of cleaner shrimp, *Stenopus hispidus*, Limbaugh, Pederson, and Chase (1961) said that pairs of individuals probably remain months, possibly years, within an area of a square meter.

(5) *Hosts using the same cleaner repeatedly.* There is surprisingly good evidence that hosts reuse the same cleaner repeatedly. Feder (1966) summarizes the evidence:

Many fishes spend as much time getting cleaned as they do foraging for food. Some fishes return again and again to the same station, and show a definite time pattern in their daily arrival. Others pass from station to station and return many times during the day; this is particularly true of an injured or infected fish (p. 368).

Limbaugh, Pederson, and Chase (1961) have presented evidence that in at least one species of cleaner shrimp (*Stenopus scutellus*), the shrimp may reservice the same individuals:

One pair was observed in the same football-sized coral boulder from May through August 1956. During that period, we changed the position and orientation of the boulder several times within a radius of approximately seven meters without disturbing the shrimp. Visiting fishes were momentarily disturbed by the changes, but they soon relocated the shrimps (p. 254).

Randall (1958) has repeatedly observed fish swimming from out of sight directly to cleaning stations, behavior suggesting to him that they had prior acquaintance with the stations. During two months of observations at several feeding stations, Eibl-Eibesfeldt (1955) became personally familiar with several individual groupers (*Epinephelus striatus*) and repeatedly observed them seeking out and being cleaned at the same feeding stations, presumably by the same cleaners.

In summary, it seems fair to say that the hosts

of cleaning organisms perform several kinds of altruistic behavior, including not eating their cleaner after a cleaning, which can be explained on the basis of the above model. A review of the relevant evidence suggests that the cleaner organisms and their hosts meet the preconditions for the evolution of reciprocally altruistic behavior. The host's altruism is to be explained as benefiting him because of the advantage of being able quickly and repeatedly to return to the same cleaner.

WARNING CALLS IN BIRDS

Marler (1955, 1957) has presented evidence that warning calls in birds tend to have characteristics that limit the information a predator gets from the call. In particular, the call characteristics do not allow the predator easily to determine the location of the call-giver. Thus, it seems that giving a warning call must result, at least occasionally, in the otherwise unnecessary death of the call-giver, either at the hands of the predator that inspired the call or at the hands of a second predator formerly unaware of the caller's presence or exact location.

Given the presumed selection against call-giving, Williams (1966) has reviewed various models to explain selection for warning cries:

(1) Warning calls are functional during the breeding season in birds in that they protect one's mate and offspring. They have no function outside the breeding season, but they are not deleted then because "in practice it is not worth burdening the germ plasm with the information necessary to realize such an adjustment" (Williams, 1966, p. 206).

(2) Warning calls are selected for by the mechanism of group selection (Wynne-Edwards, 1962).

(3) Warning calls are functional outside the breeding season because there is usually a good chance that a reasonably close kin is near enough to be helped sufficiently (Hamilton, 1964; Maynard Smith, 1964). Maynard Smith (1965) has analyzed in great detail how closely related the benefited kin must be, at what benefit to him the call must be, and at what cost to the caller, in order for selection to favor call-giving.

The first is an explanation of last resort. While it must sometimes apply in evolutionary arguments, it should probably only be invoked

when no other explanation seems plausible. The second is not consistent with the known workings of natural selection. The third is feasible and may explain the warning calls in some species and perhaps even in many. But it does depend on the somewhat regular nearby presence of closely related organisms, a matter that may often be the case but that has been demonstrated only as a possibility in a few species and that seems very unlikely in some. A fourth explanation is suggested by the above model:

(4) Warning calls are selected for because they aid the bird giving the call. It is disadvantageous for a bird to have a predator eat a nearby conspecific because the predator may then be more likely to eat him. This may happen because the predator will

- (i) be sustained by the meal,
- (ii) be more likely to form a specific search image of the prey species,
- (iii) be more likely to learn the habits of the prey species and perfect his predatory techniques on it,
- (iv) be more likely to frequent the area in which the birds live, or
- (v) be more likely to learn useful information about the area in which the birds live.

In short, in one way or another, giving a warning call tends to prevent predators from specializing on the caller's species and locality.

There is abundant evidence for the importance of learning in the lives of predatory vertebrates (see, for example, Tinbergen, 1960; Leyhausen, 1965; Brower and Brower, 1965). Rudebeck (1950, 1951) has presented important observations on the tendency of avian predators to specialize individually on prey types and hunting techniques. Owen (1963) and others have presented evidence that species of snails and insects may evolve polymorphisms as a protection against the tendency of their avian predators to learn their appearance. Similarly, Kuyton (1962; cited in Wickler, 1968) has described the adaptation of a moth that minimizes the chance of its predators forming a specific search image. Southern (1954), Murie (1944), and numerous others have documented the tendency of predators to specialize on certain localities within their range. Finally, Blest

(1963) has presented evidence that kin selection in some cryptic saturnid moths has favored rapid, post-reproductive death to minimize predation on the young. Blest's evidence thus provides an instance of a predator gaining useful information through the act of predation.

It does not matter that in giving a warning call the caller is helping its non-calling neighbors more than it is helping itself. What counts is that it outcompetes conspecifics from areas in which no one is giving warning calls. The non-calling neighbors of the caller (or their offspring) will soon find themselves in an area without any caller and will be selected against relative to birds in an area with callers. The caller, by definition, is always in an area with at least one caller. If we assume that two callers are preferable to one, and so on, then selection will favor the spread of the warning-call genes. Note that this model depends on the concept of *open* groups, whereas "group selection" (Wynne-Edwards, 1962) depends partly on the concept of closed groups.

It might be supposed that one could explain bird calls more directly as altruistic behavior that will be repaid when the other birds reciprocate, but there are numerous objections to this. It is difficult to visualize how one would discover and discriminate against the cheater, and there is certainly no evidence that birds refrain from giving calls because neighbors are not reciprocating. Furthermore, if the relevant bird groupings are very fluid, with much emigration and immigration, as they often are, then cheating would seem to be favored and no selection against it possible. Instead, according to the model above, it is the mere fact that the neighbor survives that repays the call-giver his altruism.

It is almost impossible to gather the sort of evidence that would discriminate between this explanation and that of Hamilton (1964). It is difficult to imagine how one would estimate the immediate cost of giving a warning call or its benefit to those within earshot, and precise data on the genetic relationships of bird groupings throughout the year are not only lacking but would be most difficult to gather. Several lines of evidence suggest, however, that Hamilton's (1964) explanation should be assumed with caution:

- (1) There exist no data showing a decrease in warning tendencies with decrease in the genetic relationship of those within earshot. Indeed, a striking feature of warning calls is that they are given in and out of the breeding season, both before and after migration or dispersal.
- (2) There do exist data suggesting that close kin in a number of species migrate or disperse great distances from each other (Ashmole, 1962; Perdeck, 1958; Berndt and Sternberg, 1968; Dhont and Hublé, 1968).
- (3) One can advance the theoretical argument that kin selection under some circumstances should favor kin dispersal in order to avoid competition (Hamilton, 1964, 1969). This would lead one to expect fewer closely related kin near any given bird, outside the breeding season.

The arguments advanced in this section may also apply, of course, to species other than birds.

HUMAN RECIPROCAL ALTRUISM

Reciprocal altruism in the human species takes place in a number of contexts and in all known cultures (see, for example, Gouldner, 1960). Any complete list of human altruism would contain the following types of altruistic behavior:

- (1) helping in times of danger (e.g. accidents, predation, intraspecific aggression);
- (2) sharing food;
- (3) helping the sick, the wounded, or the very young and old;
- (4) sharing implements; and
- (5) sharing knowledge.

All these forms of behavior often meet the criterion of small cost to the giver and great benefit to the taker.

During the Pleistocene, and probably before, a hominid species would have met the preconditions for the evolution of reciprocal altruism: long lifespan; low dispersal rate; life in small, mutually dependent, stable, social groups (Lee and DeVore, 1968; Campbell, 1966); and a long period of parental care. It is very likely that dominance relations were of the relaxed, less linear form characteristic of the living chimpan-

zee (Van Lawick-Goodall, 1968) and not of the more rigidly linear form characteristic of the baboon (Hall and DeVore, 1965). Aid in intra-specific combat, particularly by kin, almost certainly reduced the stability and linearity of the dominance order in early humans. Lee (1969) has shown that in almost all Bushman fights which are initially between two individuals, others have joined in. Mortality, for example, often strikes the secondaries rather than the principals. Tool use has also probably had an equalizing effect on human dominance relations, and the Bushmen have a saying that illustrates this nicely. As a dispute reaches the stage where deadly weapons may be employed, an individual will often declare: "We are none of us big, and others small; we are all men and we can fight; I'm going to get my arrows," (Lee, 1969). It is interesting that Van Lawick-Goodall (1968) has recorded an instance of strong dominance reversal in chimpanzees as a function of tool use. An individual moved from low in dominance to the top of the dominance hierarchy when he discovered the intimidating effects of throwing a metal tin around. It is likely that a diversity of talents is usually present in a band of hunter-gatherers such that the best maker of a certain type of tool is not often the best maker of a different sort or the best user of the tool. This contributes to the symmetry of relationships, since altruistic acts can be traded with reference to the special talents of the individuals involved.

To analyze the details of the human reciprocal-altruistic system, several distinctions are important and are discussed here.

(1) *Kin selection.* The human species also met the preconditions for the operation of kin selection. Early hominid hunter-gatherer bands almost certainly (like today's hunter-gatherers) consisted of many close kin, and kin selection must often have operated to favor the evolution of some types of altruistic behavior (Haldane, 1955; Hamilton, 1964, 1969). In general, in attempting to discriminate between the effects of kin selection and what might be called reciprocal-altruistic selection, one can analyze the form of the altruistic behaviors themselves. For example, the existence of discrimination against non-reciprocal individuals cannot be explained on the basis of kin selection, in which the advantage accruing to close kin is what makes the

altruistic behavior selectively advantageous, not its chance of being reciprocated. The strongest argument for the operation of reciprocal-altruistic selection in man is the psychological system controlling some forms of human altruism. Details of this system are reviewed below.

(2) *Reciprocal altruism among close kin.* If both forms of selection have operated, one would expect some interesting interactions. One might expect, for example, a lowered demand for reciprocity from kin than from nonkin, and there is evidence to support this (e.g., Marshall, 1961; Balıkcı, 1964). The demand that kin show some reciprocity (e.g., Marshall, 1961; Balıkcı, 1964) suggests, however, that reciprocal-altruistic selection has acted even on relations between close kin. Although interactions between the two forms of selection have probably been important in human evolution, this paper will limit itself to a preliminary description of the human reciprocally altruistic system, a system whose attributes are seen to result only from reciprocal-altruistic selection.

(3) *Age-dependent changes.* Cost and benefit were defined above without reference to the ages, and hence reproductive values (Fisher, 1958), of the individuals involved in an altruistic exchange. Since the reproductive value of a sexually mature organism declines with age, the benefit to him of a typical altruistic act also decreases, as does the cost to him of a typical act he performs. If the interval separating the two acts in an altruistic exchange is short relative to the lifespans of the individuals, then the error is slight. For longer intervals, in order to be repaid precisely, the initial altruist must receive more in return than he himself gave. It would be interesting to see whether humans in fact routinely expect "interest" to be added to a long overdue altruistic debt, interest commensurate with the intervening decline in reproductive value. In humans reproductive value declines most steeply shortly after sexual maturity is reached (Hamilton, 1966), and one would predict the interest rate on altruistic debts to be highest then. Selection might also favor keeping the interval between act and reciprocation short, but this should also be favored to protect against complete non-reciprocation. W. D. Hamilton (pers. commun.) has suggested that a detailed analysis of age-dependent changes in kin altruism and reciprocal altruism

should show interesting differences, but the analysis is complicated by the possibility of reciprocity to the kin of a deceased altruist (see *Multi-party interactions* below).

(4) *Gross and subtle cheating.* Two forms of cheating can be distinguished, here denoted as gross and subtle. In *gross cheating* the cheater fails to reciprocate at all, and the altruist suffers the costs of whatever altruism he has dispensed without any compensating benefits. More broadly, gross cheating may be defined as reciprocating so little, if at all, that the altruist receives less benefit from the gross cheater than the cost of the altruist's acts of altruism to the cheater. That is, $\sum_i c_{ai} > \sum_j b_{aj}$, where c_{ai} is the cost of the i th altruistic act performed by the altruist and where b_{aj} is the benefit to the altruist of the j th altruistic act performed by the gross cheater; altruistic situations are assumed to have occurred symmetrically. Clearly, selection will strongly favor prompt discrimination against the gross cheater. *Subtle cheating*, by contrast, involves reciprocating, but always attempting to give less than one was given, or more precisely, to give less than the partner would give if the situation were reversed. In this situation, the altruist still benefits from the relationship but not as much as he would if the relationship were completely equitable. The subtle cheater benefits more than he would if the relationship were equitable. In other words,

$$\sum_{i,j} (b_{qi} - c_{qj}) > \sum_i (b_{qi} - c_{ai}) > \sum_{i,j} (b_{aj} - c_{ai})$$

where the i th altruistic act performed by the altruist has a cost to him of c_{ai} and a benefit to the subtle cheater of b_{qi} and where the j th altruistic act performed by the subtle cheater has a cost to him of c_{qj} and a benefit to the altruist of b_{aj} . Because human altruism may span huge periods of time, a lifetime even, and because thousands of exchanges may take place, involving many different "goods" and with many different cost/benefit ratios, the problem of computing the relevant totals, detecting imbalances, and deciding whether they are due to chance or to small-scale cheating is an extremely difficult one. Even then, the altruist is in an awkward position, symbolized by the folk saying, "half a loaf is better than none," for if attempts to make the relationship equitable lead to the rupture of the relationship, the al-

truist, assuming other things to be equal, will suffer the loss of the substandard altruism of the subtle cheater. It is the subtlety of the discrimination necessary to detect this form of cheating and the awkward situation that ensues that permit some subtle cheating to be adaptive. This sets up a dynamic tension in the system that has important repercussions, as discussed below.

(5) *Number of reciprocal relationships.* It has so far been assumed that it is to the advantage of each individual to form the maximum number of reciprocal relationships and that the individual suffers a decrease in fitness upon the rupture of any relationship in which the cost to him of acts dispensed to the partner is less than the benefit of acts dispensed toward him by the partner. But it is possible that relationships are partly exclusive, in the sense that expanding the number of reciprocal exchanges with one of the partners may necessarily decrease the number of exchanges with another. For example, if a group of organisms were to split into subgroups for much of the day (such as breaking up into hunting pairs), then altruistic exchanges will be more likely between members of each subgroup than between members of different subgroups. In that sense, relationships may be partly exclusive, membership in a given subgroup necessarily decreasing exchanges with others in the group. The importance of this factor is that it adds further complexity to the problem of dealing with the cheater and it increases competition within a group to be members of a favorable subgroup. An individual in a subgroup who feels that another member is subtly cheating on their relationship has the option of attempting to restore the relationship to a completely reciprocal one or of attempting to join another subgroup, thereby decreasing to a minimum the possible exchanges between himself and the subtle cheater and replacing these with exchanges between a new partner or partners. In short, he can switch friends. There is evidence in hunter-gatherers that much movement of individuals from one band to another occurs in response to such social factors as have just been outlined (Lee and DeVore, 1968).

(6) *Indirect benefits or reciprocal altruism?* Given mutual dependence in a group it is possible to argue that the benefits (non-altruistic)

of this mutual dependence are a positive function of group size and that altruistic behaviors may be selected for because they permit additional individuals to survive and thereby confer additional indirect (non-altruistic) benefits. Such an argument can only be advanced seriously for slowly reproducing species with little dispersal. Saving an individual's life in a hunter-gatherer group, for example, may permit non-altruistic actions such as cooperative hunting to continue with more individuals. But if there is an optimum group size, one would expect adaptations to stay near that size, with individuals joining groups when the groups are below this size, and groups splitting up when they are above this size. One would only be selected to keep an individual alive when the group is below optimum and not when the group is above optimum. Although an abundant literature on hunter-gatherers (and also nonhuman primates) suggests that adaptations exist to regulate group size near an optimum, there is no evidence that altruistic gestures are curtailed when groups are above the optimum in size. Instead, the benefits of human altruism are to be seen as coming directly from reciprocity—not indirectly through non-altruistic group benefits. This distinction is important because social scientists and philosophers have tended to deal with human altruism in terms of the benefits of living in a group, without differentiating between non-altruistic benefits and reciprocal benefits (e.g., Rousseau, 1954; Baier, 1958).

THE PSYCHOLOGICAL SYSTEM UNDERLYING HUMAN RECIPROCAL ALTRUISM

Anthropologists have recognized the importance of reciprocity in human behavior, but when they have ascribed functions to such behavior they have done so in terms of group benefits, reciprocity cementing group relations and encouraging group survival. The individual sacrifices so that the group may benefit. Recently psychologists have studied altruistic behavior in order to show what factors induce or inhibit such behavior. No attempt has been made to show what function such behavior may serve, nor to describe and interrelate the components of the psychological system affecting altruistic behavior. The purpose of this section

is to show that the above model for the natural selection of reciprocally altruistic behavior can readily explain the function of human altruistic behavior and the details of the psychological system underlying such behavior. The psychological data can be organized into functional categories, and it can be shown that the components of the system complement each other in regulating the expression of altruistic and cheating impulses to the selective advantage of individuals. No concept of group advantage is necessary to explain the function of human altruistic behavior.

There is no direct evidence regarding the degree of reciprocal altruism practiced during human evolution nor its genetic basis today, but given the universal and nearly daily practice of reciprocal altruism among humans today, it is reasonable to assume that it has been an important factor in recent human evolution and that the underlying emotional dispositions affecting altruistic behavior have important genetic components. To assume as much allows a number of predictions.

(1) *A complex, regulating system.* The human altruistic system is a sensitive, unstable one. Often it will pay to cheat: namely, when the partner will not find out, when he will not discontinue his altruism even if he does find out, or when he is unlikely to survive long enough to reciprocate adequately. And the perception of subtle cheating may be very difficult. Given this unstable character of the system, where a degree of cheating is adaptive, natural selection will rapidly favor a complex psychological system in each individual regulating both his own altruistic and cheating tendencies and his responses to these tendencies in others. As selection favors subtler forms of cheating, it will favor more acute abilities to detect cheating. The system that results should simultaneously allow the individual to reap the benefits of altruistic exchanges, to protect himself from gross and subtle forms of cheating, and to practice those forms of cheating that local conditions make adaptive. Individuals will differ not in being altruists or cheaters but in the degree of altruism they show and in the conditions under which they will cheat.

The best evidence supporting these assertions can be found in Krebs's (1970) review of the relevant psychological literature. Although he

organizes it differently, much of the material supporting the assertions below is taken from his paper. All references to Krebs below are to this review. Also, Hartshorne and May (1928–1930) have shown that children in experimental situations do not divide bimodally into altruists and “cheaters” but are distributed normally; almost all the children cheated, but they differed in how much and under what circumstances. (“Cheating” was defined in their work in a slightly different but analogous way).

(2) *Friendship and the emotions of liking and disliking.* The tendency to like others, not necessarily closely related, to form friendships and to act altruistically toward friends and toward those one likes will be selected for as the immediate emotional rewards motivating altruistic behavior and the formation of altruistic partnerships. (Selection may also favor helping strangers or disliked individuals when they are in particularly dire circumstances). Selection will favor a system whereby these tendencies are sensitive to such parameters as the altruistic tendencies of the liked individual. In other words, selection will favor liking those who are themselves altruistic.

Sawyer (1966) has shown that all groups in all experimental situations tested showed more altruistic behavior toward friends than toward neutral individuals. Likewise, Friedrichs (1960) has shown that attractiveness as a friend was most highly correlated among undergraduates with altruistic behavior. Krebs has reviewed other studies that suggest that the relationship between altruism and liking is a two-way street: one is more altruistic toward those one likes and one tends to like those who are most altruistic (e.g., Berkowitz and Friedman, 1967; Lerner and Lichtman, 1968).

Others (Darwin, 1871; Williams, 1966; and Hamilton, 1969) have recognized the role friendship might play in engendering altruistic behavior, but all have viewed friendship (and intelligence) as prerequisites for the appearance of such altruism. Williams (1966), who cites Darwin (1871) on the matter, speaks of this behavior as evolving

in animals that live in stable social groups and have the intelligence and other mental qualities necessary to form a system of personal friendships and animosities that transcend the limits of family relationships (p. 93).

This emphasis on friendship and intelligence as prerequisites leads Williams to limit his search for altruism to the Mammalia and to a "minority of this group." But according to the model presented above, emotions of friendship (and hatred) are not prerequisites for reciprocal altruism but may evolve *after* a system of mutual altruism has appeared, as important ways of regulating the system.

(4) *Moralistic aggression*. Once strong positive emotions have evolved to motivate altruistic behavior, the altruist is in a vulnerable position because cheaters will be selected to take advantage of the altruist's positive emotions. This in turn sets up a selection pressure for a protective mechanism. Moralistic aggression and indignation in humans was selected for in order

(a) to counteract the tendency of the altruist, in the absence of any reciprocity, to continue to perform altruistic acts for his own emotional rewards;

(b) to educate the unreciprocating individual by frightening him with immediate harm or with the future harm of no more aid; and

(c) in extreme cases, perhaps, to select directly against the unreciprocating individual by injuring, killing, or exiling him.

Much of human aggression has moral overtones. Injustice, unfairness, and lack of reciprocity often motivate human aggression and indignation. Lee (1969) has shown that verbal disputes in Bushmen usually revolve around problems of gift-giving, stinginess, and laziness. DeVore (pers. commun.) reports that a great deal of aggression in hunter-gatherers revolves around real or imagined injustices—inequities, for example, in food-sharing (see, for example, Thomas, 1958; Balikci, 1964; Marshall, 1961). A common feature of this aggression is that it often seems out of all proportion to the offenses committed. Friends are even killed over apparently trivial disputes. But since small inequities repeated many times over a lifetime may exact a heavy toll in relative fitness, selection may favor a strong show of aggression when the cheating tendency is discovered. Recent discussions of human and animal aggression have failed to distinguish between moralistic and other forms of aggression (e.g., Scott, 1958; Lorenz, 1966; Montague, 1968; Tinber-

gen, 1968; Gilula and Daniels, 1969). The grounds for expecting, on functional grounds, a highly plastic developmental system affecting moralistic aggression is discussed below.

(4) *Gratitude, sympathy, and the cost/benefit ratio of an altruistic act*. If the cost/benefit ratio is an important parameter in determining the adaptiveness of reciprocal altruism, then humans should be selected to be sensitive to the cost and benefit of an altruistic act, both in deciding whether to perform one and in deciding whether, or how much, to reciprocate. I suggest that the emotion of gratitude has been selected to regulate human response to altruistic acts and that the emotion is sensitive to the cost/benefit ratio of such acts. I suggest further that the emotion of sympathy has been selected to motivate altruistic behavior as a function of the plight of the recipient of such behavior; crudely put, the greater the potential benefit to the recipient, the greater the sympathy and the more likely the altruistic gesture, even to strange or disliked individuals. If the recipient's gratitude is indeed a function of the cost/benefit ratio, then a sympathetic response to the plight of a disliked individual may result in considerable reciprocity.

There is good evidence supporting the psychological importance of the cost/benefit ratio of altruistic acts. Gouldner (1960) has reviewed the sociological literature suggesting that the greater the need state of the recipient of an altruistic act, the greater his tendency to reciprocate; and the scarcer the resources of the donor of the act, the greater the tendency of the recipient to reciprocate. Heider (1958) has analyzed lay attitudes on altruism and finds that gratitude is greatest when the altruistic act does good. Tesser, Gatewood, and Driver (1968) have shown that American undergraduates thought they would feel more gratitude when the altruistic act was valuable and cost the benefactor a great deal. Pruitt (1968) has provided evidence that humans reciprocate more when the original act was expensive for the benefactor. He shows that under experimental conditions more altruism is induced by a gift of 80 per cent of \$1.00 than 20 per cent of \$4.00. Aronfreed (1968) has reviewed the considerable evidence that sympathy motivates altruistic be-

havior as a function of the plight of the individual arousing the sympathy.

(5) *Guilt and reparative altruism.* If an organism has cheated on a reciprocal relationship and this fact has been found out, or has a good chance of being found out, by the partner and if the partner responds by cutting off all future acts of aid, then the cheater will have paid dearly for his misdeed. It will be to the cheater's advantage to avoid this, and, providing that the cheater makes up for his misdeed and does not cheat in the future, it will be to his partner's benefit to avoid this, since in cutting off future acts of aid he sacrifices the benefits of future reciprocal help. The cheater should be selected to make up for his misdeed and to show convincing evidence that he does not plan to continue his cheating sometime in the future. In short, he should be selected to make a reparative gesture. It seems plausible, furthermore, that the emotion of guilt has been selected for in humans partly in order to motivate the cheater to compensate his misdeed and to behave reciprocally in the future, and thus to prevent the rupture of reciprocal relationships.

Krebs has reviewed the evidence that harming another individual publicly leads to altruistic behavior and concludes:

Many studies have supported the notion that public transgression whether intentional or unintentional, whether immoral or only situationally unfortunate, leads to reparative altruism (p. 267).

Wallace and Sadalla (1966), for example, showed experimentally that individuals who broke an expensive machine were more likely to volunteer for a painful experiment than those who did not, but only if their transgression had been discovered. Investigators disagree on the extent to which guilt feelings are the motivation behind reparative altruism. Epstein and Hornstein (1969) supply some evidence that guilt is involved, but on the assumption that one feels guilt even when one behaves badly in private, Wallace and Sadalla's (1966) result contradicts the view that guilt is the only motivating factor. That private transgressions are not as likely as public ones to lead to reparative altruism is precisely what the model would predict, and it is possible that the common psychological assumption that one feels guilt even when one behaves badly in private

is based on the fact that many transgressions performed in private are *likely* to become public knowledge. It should often be advantageous to confess sins that are likely to be discovered before they actually are, as evidence of sincerity (see below on detection of mimics).

(6) *Subtle cheating: the evolution of mimics.* Once friendship, moralistic aggression, guilt, sympathy, and gratitude have evolved to regulate the altruistic system, selection will favor mimicking these traits in order to influence the behavior of others to one's own advantage. Apparent acts of generosity and friendship may induce genuine friendship and altruism in return. Sham moralistic aggression when no real cheating has occurred may nevertheless induce reparative altruism. Sham guilt may convince a wronged friend that one has reformed one's ways even when the cheating is about to be resumed. Likewise, selection will favor the hypocrisy of pretending one is in dire circumstances in order to induce sympathy-motivated altruistic behavior. Finally, mimicking sympathy may give the appearance of helping in order to induce reciprocity, and mimicking gratitude may mislead an individual into expecting he will be reciprocated. It is worth emphasizing that a mimic need not necessarily be conscious of the deception; selection may favor feeling genuine moralistic aggression even when one has not been wronged if so doing leads another to reparative altruism.

Instances of the above forms of subtle cheating are not difficult to find. For typical instances from the literature on hunter-gatherers see Rasmussen (1931), Balikci (1964), and Lee and DeVore (1968). The importance of these forms of cheating can partly be inferred from the adaptations to detect such cheating discussed below and from the importance and prevalence of moralistic aggression once such cheating is detected.

(7) *Detection of the subtle cheater: trustworthiness, trust, and suspicion.* Selection should favor the ability to detect and discriminate against subtle cheaters. Selection will clearly favor detecting and countering sham moralistic aggression. The argument for the others is more complex. Selection may favor distrusting those who perform altruistic acts without the emotional basis of generosity or

guilt because the altruistic tendencies of such individuals may be less reliable in the future. One can imagine, for example, compensating for a misdeed without any emotional basis but with a calculating, self-serving motive. Such an individual should be distrusted because the calculating spirit that leads this subtle cheater now to compensate may in the future lead him to cheat when circumstances seem more advantageous (because of unlikelihood of detection, for example, or because the cheated individual is unlikely to survive). Guilty motivation, in so far as it evidences a more enduring commitment to altruism, either because guilt teaches or because the cheater is unlikely not to feel the same guilt in the future, seems more reliable. A similar argument can be made about the trustworthiness of individuals who initiate altruistic acts out of a calculating rather than a generous-hearted disposition or who show either false sympathy or false gratitude. Detection on the basis of the underlying psychological dynamics is only one form of detection. In many cases, unreliability may more easily be detected through experiencing the cheater's inconsistent behavior. And in some cases, third party interactions (as discussed below) may make an individual's behavior predictable despite underlying cheating motivations.

The anthropological literature also abounds with instances of the detection of subtle cheaters (see above references for hunter-gatherers). Although I know of no psychological studies on the detection of sham moralistic aggression and sham guilt, there is ample evidence to support the notion that humans respond to altruistic acts according to their perception of the motives of the altruist. They tend to respond more altruistically when they perceive the other as acting "genuinely" altruistic, that is, voluntarily dispatching an altruistic act as an end in itself, without being directed toward gain (Leeds, 1963; Heider, 1958). Krebs (1970) has reviewed the literature on this point and notes that help is more likely to be reciprocated when it is perceived as voluntary and intentional (e.g., Goranson and Berkowitz, 1966; Lerner and Lichtman, 1968) and when the help is appropriate, that is, when the intentions of the altruist are not in doubt (e.g., Brehm and Cole,

1966; Schopler and Thompson, 1968). Krebs concludes that, "When the legitimacy of apparent altruism is questioned, reciprocity is less likely to prevail." Lerner and Lichtman (1968) have shown experimentally that those who act altruistically for ulterior benefit are rated as unattractive and are treated selfishly, whereas those who apparently are genuinely altruistic are rated as attractive and are treated altruistically. Berscheid and Walster (1967) have shown that church women tend to make reparations for harm they have committed by choosing the reparation that approximates the harm (that is, is neither too slight nor too great), presumably to avoid the appearance of inappropriateness.

Rapoport and Dale (1967) have shown that when two strangers play iterated games of Prisoner's Dilemma in which the matrix determines profits from the games played there is a significant tendency for the level of cooperation to drop at the end of the series, reflecting the fact that the partner will not be able to punish for "cheating" responses when the series is over. If a long series is broken up into subseries with a pause between subseries for totaling up gains and losses, then the tendency to cheat on each other increases at the end of each subseries. These results, as well as some others reported by Rapoport and Chammah (1965), are suggestive of the instability that exists when two strangers are consciously trying to maximize gain by trading altruistic gestures, an instability that is presumably less marked when the underlying motivation involves the emotions of friendship, of liking others, and of feeling guilt over harming a friend. Deutsch (1958), for example, has shown that two individuals playing iterated games of Prisoner's Dilemma will be more cooperative if a third individual, disliked by both, is present. The perceived mutual dislike is presumed to create a bond between the two players.

It is worth mentioning that a classic problem in social science and philosophy has been whether to define altruism in terms of motives (e.g., real vs. "calculated" altruism) or in terms of behavior, regardless of motive (Krebs, 1970). This problem reflects the fact that, wherever studied, humans seem to make distinctions about altruism partly on the basis of motive,

and this tendency is consistent with the hypothesis that such discrimination is relevant to protecting oneself from cheaters.

(8) *Setting up altruistic partnerships.* Selection will favor a mechanism for establishing reciprocal relationships. Since humans respond to acts of altruism with feelings of friendship that lead to reciprocity, one such mechanism might be the performing of altruistic acts toward strangers, or even enemies, in order to induce friendship. In short, do unto others as you would have them do unto you.

The mechanism hypothesized above leads to results inconsistent with the assumption that humans always act more altruistically toward friends than toward others. Particularly toward strangers, humans may initially act more altruistically than toward friends. Wright (1942) has shown, for example, that third grade children are more likely to give a more valuable toy to a stranger than to a friend. Later, some of these children verbally acknowledged that they were trying to make friends. Floyd (1964) has shown that, after receiving many trinkets from a friend, humans tend to *decrease* their gifts in return, but after receiving many trinkets from a neutral or disliked individual, they tend to *increase* their gifts in return. Likewise, after receiving few trinkets from a friend, humans tend to increase their gifts in return, whereas receiving few trinkets from a neutral or disliked individual results in a decrease in giving. This was interpreted to mean that generous friends are taken for granted (as are stingy non-friends). Generosity from a non-friend is taken to be an overture to friendship, and stinginess from a friend as evidence of a deteriorating relationship in need of repair. (Epstein and Hornstein, 1969, provide new data supporting this interpretation of Floyd, 1964.)

(9) *Multiparty interactions.* In the close-knit social groups that humans usually live in, selection should favor more complex interactions than the two-party interactions so far discussed. Specifically, selection may favor learning from the altruistic and cheating experiences of others, helping others coerce cheaters, forming multiparty exchange systems, and formulating rules for regulated exchanges in such multiparty systems.

(i) *Learning from others.* Selection should

favor learning about the altruistic and cheating tendencies of others indirectly, both through observing interactions of others and, once linguistic abilities have evolved, by hearing about such interactions or hearing characterizations of individuals (e.g., "dirty, hypocritical, dishonest, untrustworthy, cheating louse"). One important result of this learning is that an individual may be as concerned about the attitude of onlookers in an altruistic situation as about the attitude of the individual being dealt with.

(ii) *Help in dealing with cheaters.* In dealing with cheaters selection may favor individuals helping others, kin or non-kin, by direct coercion against the cheater or by everyone refusing him reciprocal altruism. One effect of this is that an individual, through his close kin, may be compensated for an altruistic act even after his death. An individual who dies saving a friend, for example, may have altruistic acts performed by the friend to the benefit of his offspring. Selection will discriminate against the cheater in this situation, if kin of the martyr, or others, are willing to punish lack of reciprocity.

(iii) *Generalized altruism.* Given learning from others and multiparty action against cheaters, selection may favor a multiparty altruistic system in which altruistic acts are dispensed freely among more than two individuals, an individual being perceived to cheat if in an altruistic situation he dispenses less benefit for the same cost than would the others, punishment coming not only from the other individual in that particular exchange but from the others in the system.

(iv) *Rules of exchange.* Multiparty altruistic systems increase by several-fold the cognitive difficulties in detecting imbalances and deciding whether they are due to cheating or to random factors. One simplifying possibility that language facilitates is the formulation of rules of conduct, cheating being detected as infraction of such a rule. In short, selection may favor the elaboration of norms of reciprocal conduct.

There is abundant evidence for all of the above multiparty interactions (see the above references on hunter-gatherers). Thomas (1958), for example, has shown that debts of reciprocity do not disappear with the death of the

“creditor” but are extended to his kin. Krebs has reviewed the psychological literature on generalized altruism. Several studies (e.g., Darlington and Macker, 1966) have shown that humans may direct their altruism to individuals other than those who were hurt and may respond to an altruistic act that benefits themselves by acting altruistically toward a third individual uninvolved in the initial interaction. Berkowitz and Daniels (1964) have shown experimentally, for example, that help from a confederate leads the subject to direct more help to a third individual, a highly dependent supervisor. Freedman, Wallington, and Bless (1967) have demonstrated the surprising result that, in two different experimental situations, humans engaged in reparative altruism only if it could be directed to someone other than the individual harmed, or to the original individual only if they did not expect to meet again. In a system of strong multiparty interactions it is possible that in some situations individuals are selected to demonstrate generalized altruistic tendencies and that their main concern when they have harmed another is to show that they are genuinely altruistic, which they best do by acting altruistic without any apparent ulterior motive, e.g., in the experiments, by acting altruistic toward an uninvolved third party. Alternatively, A. Rapoport (pers. commun.) has suggested that the reluctance to direct reparative altruism toward the harmed individual may be due to unwillingness to show thereby a recognition of the harm done him. The redirection serves to allay guilt feelings without triggering the greater reparation that recognition of the harm might lead to.

(10) *Developmental plasticity.* The conditions under which detection of cheating is possible, the range of available altruistic trades, the cost/benefit ratios of these trades, the relative stability of social groupings, and other relevant parameters should differ from one ecological and social situation to another and should differ through time in the same small human population. Under these conditions one would expect selection to favor developmental plasticity of those traits regulating altruistic and cheating tendencies and responses to these tendencies in others. For example, developmental plasticity may allow the growing orga-

nism's sense of guilt to be educated, perhaps partly by kin, so as to permit those forms of cheating that local conditions make adaptive and to discourage those with more dangerous consequences. One would not expect any simple system regulating the development of altruistic behavior. To be adaptive, altruistic behavior must be dispensed with regard to many characteristics of the recipient (including his degree of relationship, emotional makeup, past behavior, friendships, and kin relations), of other members of the group, of the situation in which the altruistic behavior takes place, and of many other parameters, and no simple developmental system is likely to meet these requirements.

Kohlberg (1963), Bandura and Walters (1963), and Krebs have reviewed the developmental literature on human altruism. All of them conclude that none of the proposed developmental theories (all of which rely on simple mechanisms) can account for the known diverse developmental data. Whiting and Whiting (in prep.) have studied altruistic behavior directed towards kin by children in six different cultures and find consistent differences among the cultures that correlate with differences in child-rearing and other facets of the cultures. They argue that the differences adapt the children to different adult roles available in the cultures. Although the behavior analyzed takes place between kin and hence Hamilton's model (1964) may apply rather than this model, the Whittings' data provide an instance of the adaptive value of developmental plasticity in altruistic behavior. No careful work has been done analyzing the influence of environmental factors on the development of altruistic behavior, but some data exist. Krebs has reviewed the evidence that altruistic tendencies can be increased by the effects of warm, nurturant models, but little is known on how long such effects endure. Rosenhan (1967) and Rettig (1956) have shown a correlation between altruism in parents and altruism in their college-age children, but these studies do not separate genetic and environmental influences. Class differences in altruistic behavior (e.g., Berkowitz, 1968; Ugurel-Semin, 1952; Almond and Verba, 1963) may primarily reflect environmental influences. Finally Lutzker (1960) and

Deutsch (1958) have shown that one can predict the degree of altruistic behavior displayed in iterated games of Prisoner's Dilemma from personality typing based on a questionnaire. Such personality differences are probably partly environmental in origin.

It is worth emphasizing that some of the psychological traits analyzed above have applications outside the particular reciprocal altruistic system being discussed. One may be suspicious, for example, not only of individuals likely to cheat on the altruistic system, but of any individual likely to harm oneself; one may be suspicious of the known tendencies toward adultery of another male or even of these tendencies in one's own mate. Likewise, a guilt-motivated show of reparation may avert the revenge of someone one has harmed, whether that individual was harmed by cheating on the altruistic system or in some other way. And the system of reciprocal altruism may be employed to avert possible revenge. The Bushmen of the Kalahari, for example, have a saying (Marshall, 1959) to the effect that, if you wish to sleep with someone else's wife, you get him to sleep with yours, then neither of you goes after the other with poisoned arrows. Likewise, there is a large literature on the use of reciprocity to cement friendships between neighboring groups, now engaged in a common enterprise (e.g., Lee and DeVore, 1968).

The above review of the evidence has only begun to outline the complexities of the human

altruistic system. The inherent instability of the Prisoner's Dilemma, combined with its importance in human evolution, has led to the evolution of a very complex system. For example, once moralistic aggression has been selected for to protect against cheating, selection favors sham moralistic aggression as a new form of cheating. This should lead to selection for the ability to discriminate the two and to guard against the latter. The guarding can, in turn, be used to counter real moralistic aggression: one can, in effect, *impute* cheating motives to another person in order to protect one's own cheating. And so on. Given the psychological and cognitive complexity the system rapidly acquires, one may wonder to what extent the importance of altruism in human evolution set up a selection pressure for psychological and cognitive powers which partly contributed to the large increase in hominid brain size during the Pleistocene.

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