Reciprocal Altruism in Birds: A Critical Review

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Many proposed examples of reciprocal altruism are either misidentified or involve questionable assumptions concerning the costs and benefits accruing to the interactors. Waltz's (*Am. Nat.* 118: 588–592, 1981) definition of reciprocal altruism as an interaction in which "one individual aids another in anticipation that the recipient will return the favor benefiting the actor in the future" is not sufficiently restrictive: there must also be a direct fitness cost to the individual performing the original beneficent act that is less than the fitness benefit received when the act is reciprocated (again at a cost) by the second individual.

Several recurring problems in identifying potential examples of reciprocal altruism are discussed, including the assumption that restraint is an act of altruism and the misclassification of "generational mutualisms," in which individuals helping to raise young are "repaid" one generation later by the offspring they assisted in raising. No definite case of reciprocal altruism is currently known in birds, but examples in which this phenomenon may be involved include helping behavior in a few cooperative breeders and communal feeding in several taxa including gulls, jays, and juncos.

KEY WORDS: Birds; Cooperation; Mutualism; Reciprocal altruism.

INTRODUCTION

Numerous examples of reciprocal altruism (RA) have been proposed in birds in the 15 years since Trivers' (1971) seminal paper. However, authors have used various definitions of RA, and, consequently, there is considerable confusion about how widespread it is, or whether it exists at all. Here, I (1) summarize the major issues concerning the existence and extent of RA in the avian literature, (2) critically review several of the more widely cited examples in which RA has been proposed, and (3) discuss several promising recent studies in birds addressing phenomena that may involve RA.

BACKGROUND, DEFINITION, AND REVIEW

The application of RA theory to birds got off to a rather unpromising start when Trivers (1971) suggested, as an example of RA in birds, that alarm calls dissuade predators from returning to hunt in a particular area and therefore make it less likely that the caller will be killed by the predator at a later time. This hypothesis suggests that the caller benefits indirectly and at a later time, but *not* as a consequence of reciprocation on the part of another individual. Assuming that there is a cost to alarm calling, this act qualifies as a form of altruism, since nearby individuals that do not call gain more than does the caller. Because of this property, alarm calling may, at least in theory, fulfill the requirements of "weak altruism" (Wilson 1980) and may be explained by group selection models. Alternatively, several authors (e.g., Dunford 1977; Sherman 1977) have shown that alarm calling in some species occurs primarily within kin groups and can be explained by kin selection (Hamilton 1964). In any case, the example as proposed by Trivers involves no reciprocal exchange, and thus is certainly not RA.

However, this example raises the question: how should RA be defined? If defined too narrowly, we risk making it an exciting, but possibly nonexistent phenomenon; if too broadly, we include many behaviors that could reasonably be explained without the benefit of Trivers' (1971) important theoretical contribution.

As illustrated above, Trivers' (1971) usage of RA was too broad (see also West-Eberhard 1975). In order to avoid trivializing RA, it has subsequently become necessary to revise and reinterpret Trivers' (1971) article. A currently popular set of guidelines is derived from Wilson (1975). As stated by Waltz (1981), this definition involves three elements: (1) one individual aids another (2) in anticipation that the recipient will return the favor, (3) benefiting the actor at some time in the future. These requirements are necessary, but not sufficient to define a reciprocally altruistic interaction if we are to restrict the term to an intuitively valuable class of phenomena. In addition, (4) both the original and the reciprocated acts must entail a cost in direct fitness (Brown and Brown 1981) to the individuals involved. The cost is then repaid by the benefit received when the costly act is reciprocated at a later time. This additional element ensures that individuals can profitably cheat by not reciprocating, and thus completes the distinction between RA and other forms of beneficent behavior (see also Brown 1983; Conner 1986; and Rothstein and Pierotti 1988).

Consider the proposal by Ligon (1983) that monogamy constitutes RA, based on Waltz's (1981) definition. The idea is that mates protect each other from predators and that males, in particular, aid their mates by behaviors such as courtship feeding. Females reciprocate, presumably by laying more eggs and raising more young. This is unquestionably cooperation; but is it RA? If so, then, as pointed out by West-Eberhard (1975), virtually any behavior having to do with sexual reproduction qualifies as RA, and the phe-

nomenon of RA becomes trivial. Whatever a female does to raise more young is clearly in her own self-interest. Similarly, whatever a male does to help his mate raise more young is in his own self-interest; courtship feeding, for example, simply represents investment in the male's current reproductive attempt, just as does competing for a territory. The exchange is reciprocal, but does not qualify as RA in an interesting sense, because the presumed altruistic act (feeding and aiding a sexual partner) involves no cost in terms of the direct fitness of the mate.

An additional definitional problem has been recognized by several recent authors who distinguish behaviors involving delayed benefits and that *incidentally* aid other individuals [such as the alarm calling example in Trivers (1971)] from behaviors in which there is a return benefit because the original recipient *chooses* to act altruistically in return (Brown 1983; Trivers 1985). The former class of behaviors, called "by-product mutualisms" by Brown (1983), "return benefit altruisms" by Trivers (1985), and "pseudo-reciprocity" by Conner (1986), are relatively common, and can be further dissected according to the nature of the associations between the individuals involved (Rothstein and Pierotti 1988). Examples of the latter class of behaviors, in which individual A chooses to act altruistically toward individual B following a reciprocal act on B's part toward A, called "score-keeping mutualisms" by Brown (1983) or simply RA, are highly prized (e.g., Wilkinson 1984) and are almost certainly not common in birds. Reciprocal altruism can, therefore, be defined as a series of interactions involving five elements: (1) one individual aids another, (2) at some fitness cost to itself, (3) in anticipation that the recipient will choose to return the favor, (4) again at some fitness cost to the actor, and (5) benefiting the actor at some time in the future.

What are some of the examples of RA that have been described in birds, and how convincing are they? A wide array of putative examples have been proposed. Unfortunately, the critical evidence is absent or ambiguous in all published cases, and the existence of RA in birds is still speculative.

STEPPARENTING

Pierotti (1980) suggested that RA is shown by gulls in an instance when a dead mate (usually a female) is replaced by a new bird who then incubates and feeds the young previously produced by the deceased parent. These stepmothers then mate the following year with the males they help. The stepparent is certainly being altruistic, and derives delayed benefits by gaining a mate and a territory in which she will most likely be able to breed subsequently. However, these return benefits are not derived at any cost to the surviving mate; after all, he of course requires another mate if he is to breed again. With no fitness cost to the survivor, this example is not recip-

rocal altruism any more than is monogamy (see also Rothstein and Pierotti 1988).

Pierotti's (1982) reply to this criticism was that the survivor is being altruistic by not chasing off the potential stepparent. There is, however, no compelling reason to believe that the survivor would benefit by doing so. As there is no cost to the survivor at any stage of this interaction, it does not constitute RA. Regardless of this flaw, Pierotti's (1982) reply raises an interesting issue: is it appropriate to consider restraint a kind of altruism, and hence encompassed by RA theory?

It is certainly possible, at least in theory, for restraint to involve altruism on the part of the participants (Axelrod and Hamilton 1971). Nonetheless, I believe that we must be very careful before invoking RA in this and similar circumstances involving restraint. If the mere absence of performing some (hypothetical) behavior is potentially RA, then we risk the possibility of categorizing all interactions between any set of individuals as RA whenever the interactors do not immediately try to kill each other. After all, the list of behaviors in which individuals do *not* engage at any one time is a long one, and limited largely by the imagination of the investigator. At the very least, the behavior in question should be one that is known to occur in circumstances similar to that in which altruism is being invoked. In addition, the behavior must be one that *would* benefit the actor if it were performed; that is, the individual's restraint must constitute an act of altruism. The following two examples serve to indicate some of the pitfalls of calling apparent restraint RA.

RECOGNITION OF NEIGHBORING SONGS

Falls and Brooks (1975) showed that male white-throated sparrows (*Zonotrichia albicollis*) react much less aggressively to songs of neighbors than to songs of strangers when playbacks are made from an established territorial boundary, but that there is no difference in response when playbacks are performed within the male's territory. Trivers (1985) interpreted this apparent restraint as an example of RA, suggesting that male A reacts aggressively to neighbor B only when, by virtue of the playback, male B appears to be cheating on the system.

In contrast, the phenomenon is readily explainable on the basis that a male bird stands to gain nothing by attacking a neighbor in the latter's established space, whereas the male stands to lose valuable territory by failing to attack neighbors intruding on their boundary or strangers (with whom a boundary has not been established) singing anywhere. With no benefit to be derived by attacking a neighbor singing at his boundary, a male shows no altruism by his apparent restraint, and the example does not constitute RA.

RESTRAINT AND TREE SWALLOW HELPERS

Another putative example of RA in birds based on restraint is that of Lombardo (1985) who claimed to have experimentally demonstrated the existence of tit-for-tat (TFT) (Axelrod and Hamilton 1981) in the interactions between helper and breeder tree swallows (*Tachycineta bicolor*).

Helpers in this species occur sporadically and are not related to those they help. Nonetheless, they are tolerated by breeders. Lombardo (1985) placed a stuffed swallow outside acive nests and then either replaced two nestlings with dead babies or handled the babies but left them intact in the nest. When the parents returned, they exhibited significantly more aggression toward a model "helper" positioned near the nest than to the controls when the dead babies had been placed in the nest. Lombardo (1985) suggests that as long as the helper cooperates (presumably by helping and not hurting the young) the parents reciprocate by tolerating him (that is, by restraining their aggression). Replacing the young with dead babies simulates "defection" by the helpers, following which, the breeders immediately defect and aggressively try to chase the helper away. Following the model of Axelrod and Hamilton (1981), my vision of the presumed payoff matrices for this interaction is given in Table 1 (two are necessary because of the asymmetry of the interaction; see below).

I believe that neither TFT, nor RA of any kind, has been demonstrated in this example. Several critical requirements for RA have not been shown;

Table 1. A Possible Set of Payoff Matrices for Tree Swallow Breeder–Helper Interactions Following the Prisoner's Dilemma Paradigm, based on Lombardo 1985[a]

			Parent (2) Restraint	Parent (2) Defect
Helper (1)	Restraint	R	Helps and gains experience (Tolerates helper)	S Helps and gains experience (Chases helper away)
	Defect	T	Kills nestlings (Tolerates helper)	P Kills nestlings (Chases helper away)

			Helper (2) Restraint	Helper (2) Defect
Parent (1)	Restraint	R	Tolerates helper (Helps)	S Tolerates helper (Kills nestlings)
	Defect	T	Chases helper away (Helps)	P Chases helper away (Kills nestlings)

[a] Requirements for the prisoner's dilemma are $T > R > P > S$ and $R > (S + T)/2$. Tables are derived from the point of view of individual (1); behavior of individual (2) is given second, in parentheses. None of the values of the variables are known (see text).

for example, in order to qualify as RA, it must be demonstrated that the parents benefit by having the helper feed their young or defend against predators, and that these behaviors involve significant fitness costs to the helper. For the TFT paradigm, it must be shown that there is a strong potential advantage to the helper if he can "defect" and disrupt the nesting attempt of the breeders (that is, that $T > R$ and $P > S$ in the top half of Table 1). Lombardo (1985) suggests that by disrupting a nesting attempt, helpers may usurp the nest, but no evidence is presented for this proposal, and the references he lists in support of this hypothesis are not relevant. In contrast, by assisting, the helper might at least gain some experience useful in his own future breeding attempts, suggesting that $R > T$ and $S > P$. Other necessary conditions in Table 1 are equally unlikely.

Additionally, even if the payoff matrices fit the prisoner's dilemma game, the contest is grossly asymmetric. For example, in the event that "both defect" in Table 1, the cost to the helper of being chased away (P in the top half) is certainly much less than the cost to the breeder of having its young killed (P in the bottom half). This in itself presents a serious and possibly fatal complication for applying this paradigm to the interaction.

Beyond these problems, the only reciprocation involved in the natural situation is the presumed restraint exhibited by breeders toward the helpers. As pointed out earlier, this claim opens up a Pandora's box of problems and thus deserves more than normal caution.

HELPING AT THE NEST

The most common application of RA in birds has been to explain the evolution of cooperative breeding. Cooperative breeding occurs when more than one individual of the same sex shares breeding status within a social unit (mate sharing), or when groups contain nonbreeding helpers at the nest. Several authors have suggested that RA might be involved in the latter phenomenon.

The most widely cited of these works is Ligon and Ligon's (1978, 1983) fine study on the green woodhoopoe (*Phoeniculus purpureus*) in Africa. Helpers in this species are usually related to those they help. Even when they are unrelated, however, they appear to compete for opportunities to feed the young. Ligon and Ligon (1978, 1983) suggest that this altruistic act may later be reciprocated when the nestlings grow up, at which time the younger birds may (1) disperse with the original helper and (2) help the original helper gain a territory and raise his own young.

This system certainly involves a mutualistic exchange between birds dispersing together. However, in order to qualify as RA, the younger bird must incur some cost as a consequence of his presumed act of reciprocation. For example, dispersing with a dominant may provide the bird's best chance to breed at some time, in which case he should disperse with, and even be

a helper to, the older bird, whether the latter had helped raise him or not. Indeed, Ligon and Ligon (1983) present data indicating that, among pairs of males immigrating together, the subordinate male frequently outlives the dominant and has equivalent lifetime reproductive success. If the younger bird is acting purely in its own self-interest and does not incur any cost, the phenomenon reduces to an example of pseudoreciprocity (following the classification of Rothstein and Pierotti 1988) rather than RA.

As suggested by Conner (1986), one unambiguous way to address the question of whether RA is involved is to determine whether or not the system is vulnerable to cheating. According to this line of reasoning, unless a subordinate would be better off by *not* dispersing with the dominant (after having received its help as a nestling) helping in the green woodhoopoe is not likely to involve RA.

Although helping at the nest involves a reciprocal exchange of aid in some species, it is, in general, quite different from the usual conceptualizations of RA, in that the act of reciprocity is one generation removed from the original altruistic act. This is a critical point because it makes the punishment of cheaters impossible. Because each generation depends on the subsequent one for help in raising young, Brown (1983) has called this class of phenomena "generational mutualisms."

In a few species, however, such as the white-fronted bee eater *Merops bullockoides* (Emlen 1981) and the bell miner (*Manorina melanophrys*) currently being studied by Clarke (1984), reciprocal helping at the nest may occur within the same season. In bell miners, for example, individuals may simultaneously breed and help at the nests of several neighbors, only some of which are relatives. Clarke (in preparation) compared the aid given by an unrelated helper with the amount reciprocated by each of the three recipients (male parent, female parent, and offspring) during the subsequent breeding attempts by the helper. He found that only male parents reciprocated to any substantial degree, and that overall there was no correlation between the amount of original aid and the amount of aid reciprocated by any of the three classes of recipients. However, some degree of reciprocation occurred in 58% of the cases in which both parties were still alive.

Clarke (in preparation) suggests that the level of nonreciprocation reflects the relative unimportance of reciprocity. Although this is true for breeding females and the offspring, the relatively high reciprocation rate (more than 50% of times when reciprocation could have taken place) for breeding males seems quite compatible with that expected from RA theory. Furthermore, the rate of reciprocation might increase even more with additional years of data on these long-lived birds. On the other hand, the effects of the help are more difficult to assess: how much cost does helping incur and how much do breeders need it? Also troublesome is the absence of a correlation between initial help and degree of reciprocation, as this implies no discrimination against cheaters (reciprocation might, however, involve

some indirect payoff to inclusive fitness, thereby decreasing the observed correlation of help given between interactors [Rothstein and Pierotti 1988]).

Nonetheless, this is one of the better possible examples of RA in birds. Because there is considerable variation in the degree to which helpers are related to those they help (Clarke 1984), this system (and that of Emlen's [1981] white-fronted bee eaters) would be particularly amenable to statistical analyses designed to separate the relative effects of kinship and reciprocity as has been done for vampire bats by Wilkinson (1984, 1988).

MATE SHARING

A second phenomenon encompassed by cooperative breeding is mate sharing (or cooperative polygamy). Mate sharing typically involves many forms of apparently altruistic behaviors among birds, who are at least in some cases unrelated.

One interesting study of such a species is that of Craig (1984), who proposed that the pukeko (*Porphyrio porphyrio*), a New Zealand rail, was "caught" in the prisoner's dilemma. In this species, coalitions of males are able to defend larger territories than singletons, but singletons produce more than three times as many young per male on a yearly basis than do males sharing a female (2.0 versus 0.6 young per adult). Craig (1984) suggested that males remaining as singletons are "cooperating" with each other (by *not* forming coalitions) so as to gain greater reproductive success. However, there is considerable competition for space, and Craig proposes that forming coalitions with another male leads to a short-term advantage because of the larger amount of space such coalitions can command over singletons, and of the possibility that they might even evict a singleton. Such "defection" (by forming coalitions) ultimately leads to the observed system of mate sharing: that is, the majority of birds are left with the "punishment for mutual defection" (*P*) represented by the lower reproductive success of males sharing mates. My interpretation of the presumed payoff matrix for this interaction is presented in Table 2.

There are several problems in interpreting this situation in terms of the two-person prisoner's dilemma. First, it is an unorthodox way of explaining the evolution of mate sharing (i.e., as the result of mutual defection and the *failure* of cooperation rather than the reverse). Second, there must be at least three individuals involved, since otherwise there is no way that one male could defect and form a male–male coalition while the second male breeds as a singleton. Third, it is unlikely that the necessary conditions for the payoff matrix are fulfilled. For example, males sharing mates in the absence of competition from other such coalitions must reproduce much better not only than normal mate-sharing groups ($T > P$; Table 2) but also better than singleton males in the population ($T > R$), which, as mentioned above, produce three times as many young per male as coalitions in the

Table 2.   A Possible Payoff Matrix for Male Pukeko Breeder–Breeder Interactions Following the Prisoner's Dilemma Paradigm, based on Craig 1985[a]

		Male B	
		Cooperate	Defect
Male A	Cooperate	R Breed as a singleton	S Breed as a singleton (Form a ♂–♂ coalition)
	Defect	T Form a ♂–♂ coalition (Breed as a singleton)	P Form a ♂–♂ coalition

[a] Requirements for the prisoner's dilemma are $T > R > P > S$ and $R > (S + T)/2$. Table is presented from the viewpoint of male A; behavior of male B is in parentheses. Measured in surviving young per season, R = 2.0, P = 0.6; S and T are unknown (see text).

natural situation. It is also necessary that singleton males breeding in competition with male–male coalitions do worse than males breeding as coalitions in competition with other such coalitions ($S < P$), again regardless of the three-fold advantage enjoyed by singleton males in the natural situation. Because of the manner in which coalitions are able to usurp space from singletons (Craig 1984) this latter condition may be met in some cases, but is unlikely to be true generally and at the very least is highly speculative.

Mate sharing similar to that described for the pukeko, although relatively rare, occurs in several well-known species of birds and mammals. For example, male lions (*Panthera leo*) form coalitions to take control of prides of females even though their individual reproductive success is lower than it would be if each male assumed control of a pride by himself (Bygott et al. 1979). An alternative to Craig's (1984) hypothesis that this type of interaction involves the prisoner's dilemma is that it behooves a singleton male *without access to a pride* to make the best of a bad job and enlist the help of another male, related or not, to fight for a pride (Koenig 1981). Such coalitions are clearly of immediate, mutual benefit to all participants, and thus do not constitute RA.

COMMUNAL FEEDING

Although not conclusive, a class of phenomena that may in some cases involve RA is adoption, crèching, and communal feeding. Consider adoption in gulls, discussed by Pierotti (1980). Imagine that, over a period of several days or from one season to another, some parents do badly and have little to feed their young while others do well and have a great deal. It would then cost parents doing well very little to feed additional young, whereas the young themselves (as well as their parents) would benefit substantially by adoption, given that they would die otherwise. At a later time, these roles could be reversed, thereby fulfilling this important requirement of RA.

There are difficulties with the hypothesis that this phenomenon is RA: first, reversal of roles, as required by RA, has yet to be demonstrated in any species. Indeed, in a typical colonial situation it would be highly unlikely that two unrelated starving offspring in different years would be reciprocally adopted by each other's parents. Because altruistic acts would rarely if ever be reciprocated by the original recipients, there is little likelihood that cheaters could be punished. Regardless of these problems, it seems possible that some such cases of adoption could involve RA.

Communal feeding, which occurs in some cooperative breeders and in a few crèching species, is another promising area in which RA could occur in birds. Caraco and Brown (1986) have shown that, under some circumstances, communal feeding of young by more than one set of parents decreases the variance in interfeeding intervals. This might be advantageous if it reduces the probability that an offspring will go so long without being fed that it either starves or makes so much noise that it is discovered by a predator. Such communal feeding could be RA if parents preferentially feed the same nondescendant young, and if communal feeding is based at least in part on a reciprocal exchange with other parents. Also necessary is that the cost to a parent of feeding the offspring not its own is less than the benefit the parent receives in terms of the decreased probability that its own offspring will be eaten by predators attracted to the unrelated offspring's begging. If this condition is not met, the interaction is better considered one of mutualistic cooperation rather than RA (Rothstein and Pierotti 1988).

One possible example is the cooperatively-breeding Mexican jay (*Aphelocoma ultramarina*), in which pairs within groups indiscriminately feed each other's young following fledging (Brown and Brown 1980). Assuming that parents can recognize their own young following fledging, this may involve RA and could confer the benefits of reduced variance in feeding interval modeled by Caraco and Brown (1986).

Another possible, although still speculative, example occurs in yellow-eyed juncos (*Junco phaeonotus*) in the Chiricahua mountains of southeastern Arizona (K. Sullivan, unpublished data). Sullivan found that in a year of low food supply (1984) pairs of territorial family groups with fledglings frequently merged, sharing territories and indiscriminantly feeding each other's fledglings, although offspring from other territories continued to be chased off. This did not happen in either 1985 or 1986, which were much better food years (E. Greene, unpublished data). Thus, there is the possibility that (1) reciprocation only occurs when food conditions are so poor that the decrease in variance allowed by communal feeding significantly benefits pooling offspring, and (2) discrimination can and does occur (communal territoriality and feeding during a nesting attempt was always observed only between the same pairs of collaborating family groups). Interestingly enough, such reciprocity only occurred between pairs containing fledglings of similar age, and thus the interactions were symmetric.

Sullivan's study was not designed to study RA; therefore, critical data

on costs and benefits are absent. Hence it is possible that the observed pattern of feeding was simply an unusual instance of a breakdown in offspring recognition. Further, for this example to constitute RA it would again be necessary to show that the costs incurred by a parent as a result of feeding the unrelated offspring be greater than the benefits it receives from the same act due to the decreased probability that the begging offspring will attract a predator to the parent's own young (thereby necessitating the reciprocal act by the second set of parents to yield a net fitness benefit). Nonetheless, fragmentary as it is, this example comes as close as any current published avian example to meeting the standards for RA that have now been set by Wilkinson (1984).

CONCLUSION

Reciprocal altruism theory has not fared well in the avian literature because of definitional problems and because it has been applied to many examples in which is only debatably appropriate. Nevertheless, it is possible that RA may occur in several contexts in birds. This presents a considerable challenge to ornithologists, as there are currently no unambiguous examples of RA in this taxon.

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