

Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'

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Trivers' model of reciprocal altruism, and its descendants based on the Prisoner's Dilemma model, have dominated thinking about cooperation and altruism between non-relatives. However, there are three alternative models of altruism directed to non-relatives. These models, which are not based on the Prisoner's Dilemma, may explain a variety of phenomena, from allogrooming among impala to helping by non-relatives in cooperatively breeding birds and mammals.

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A lion stalking a group of zebra is spotted by one individual who bolts away. The flight of one of their members alerts the rest of the group, which turn and follow suit. The evasive action of the zebra who first saw the lion was purely selfish, but the other zebra benefited nonetheless. Benefits that are a 'by-product' of 'the ordinary selfish behavior'¹ of others constitute one of two general ways in which the behavior of one animal may benefit another. The other category of beneficial behavior is 'altruism', defined as a costly act performed by one individual for the benefit of another. Had the zebra cried out in alarm before it bolted we would say it had behaved altruistically. By alarm calling, the zebra could directly inform its neighbors of the lion's approach, but only at some risk to itself. Because of the cost involved, altruistic behavior has continued to be a focus of interest in evolutionary biology since Hamilton formulated the theory of kin selection in 1964 (Ref. 2).

Trivers³ seminal paper on reciprocal altruism (see Box 1) was the first to present conditions for the evolution of altruism among non-relatives (though it can operate and probably originates among relatives⁴). Selection may favor altruism towards a non-relative if the recipient later repays the altruism such that both individuals accrue a net benefit. However, reciprocal altruism is vulnerable to individuals who cheat by failing to repay acts of altruism. Axelrod and Hamilton⁵ pre-

sented a formal model of reciprocity, based on an iterated Prisoner's Dilemma game (see Box 2). They found that if two individuals expect to interact again with some threshold probability, then cooperative strategies may out-compete non-cooperative ones. In general, individuals using successful strategies, such as 'tit-for-tat', reciprocate, retaliate if they detect cheating, but are then prepared to resume cooperating. One of the more recent champions of computer simulations, 'win-stay, lose-shift', adds the more realistic attitude of 'cheat if you can get away with it'⁶.

Models based on the Prisoner's Dilemma have dominated the literature on cooperation and altruism⁷. Kin selection and reciprocity (Prisoner's Dilemma models) are often presented as the only two models available to explain adaptive altruism (e.g. Refs 8,9). But there is more to altruism than kin selection and the Prisoner's Dilemma. Here, I present three cases in which selection may favor altruism towards non-relatives. None of these models is based on the Prisoner's Dilemma and only one might be considered a model of reciprocal altruism.

Pseudo-reciprocity: investing in by-product benefits

Colonially nesting cliff swallows (*Hirundo pyrrhonota*) use a vocalization to alert conspecifics that food, in the form of an insect swarm, has been located. Brown *et al.*¹⁰ suggest that callers increase their own foraging efficiency by attracting other birds. The insect swarms are difficult to follow and foraging time is limited by ability to track prey movements. The feeding efforts of birds attracted by the calling birds may allow the caller to track the insects and feed for a longer period.

The calling bird performs a costly act (calling) that benefits other birds who learn of the insect swarm. Unlike true reciprocal altruism, the return benefit to the caller (longer feeding time) derives not from a reciprocated costly act by the birds who hear the call, but emerges as a by-product of their selfish efforts at feeding.

Brown *et al.*¹⁰ suggested that the calling behavior of foraging cliff swallows is an example of pseudo-reciprocity¹¹. Specifically, selection will favor individual X performing an act of altruism for Y if the cost (C) to X is less than the benefit (B) that X later receives from Y, multiplied by the increase in the probability (dP) that Y will confer the benefit on X as a result of X's initial act¹¹:

$$C < (dP)B$$

Because individuals engaging in pseudo-reciprocity are investing in by-product benefits, they need not be concerned about cheating by the recipient of their altruism. The calling cliff swallow would fail to obtain return benefits only if birds hearing the call did not approach to feed on the insect swarm, which would clearly not be in their best interests.

Pseudo-reciprocity may account for a variety of altruistic phenomena¹¹. Evening bats (*Nycticeius humeralis*) provide another example. Female evening bats gather in nursing colonies containing 15–300 bats. Nearly 20% of nursing bouts observed by Wilkinson¹² involved non-descendant offspring. Females preferentially allowed non-descendant female offspring to nurse, but did not preferentially nurse matrilineal kin. Wilkinson¹² suggests that pseudo-reciprocity may play a role in the communal nursing of the evening bat. Foraging evening bats that have failed to locate food can improve their prey capture by following successful bats as they leave the colony on a foraging trip¹². With an ephemeral food supply, such by-product benefits may be important enough to warrant nursing non-descendant young to increase the number of foraging bats in the colony.

Box 1. Glossary

Altruism: a costly act by individual A that benefits individual B.

By-product benefit: a costly act by individual A performed for the benefit of A that incidentally benefits individual B.

By-product mutualism: an association between A and B, favored by selection on A and/or B, in which both receive by-product benefits from each other.

Pseudo-reciprocity: an altruistic act by individual A that benefits individual B and increases the probability that B will perform an act to benefit A that incidentally benefits A. Individual A is *investing* in by-product benefits.

Cooperation: behavior that requires collective action by A and B in which both benefit.

Reciprocal altruism: a costly act by individual A performed for the benefit of individual B in expectation that B will reciprocate a costly act such that A gains a net benefit.

Box 2. The Prisoner's Dilemma

Player A	Player B	
	Cooperate	Defect
Cooperate	R Reward for mutual cooperation	S Sucker's payoff
Defect	T Temptation to defect	P Punishment for mutual defection

If player B cooperates, player A gets R for cooperating and T for defecting, where $T > R$. If player B defects, player A gets the sucker's payoff, S , for cooperating and P if A defects, where $P > S$. An interaction is a Prisoner's Dilemma if the payoff values are such that $T > R > P > S$ and $R > (S + T)/2$. If two players interact only once, then the only evolutionarily stable strategy is to defect. However, if the probability that two players will interact again is sufficiently high, then successful cooperative strategies are possible. The most famous cooperative strategy is 'tit-for-tat': cooperate on the first move then copy your opponent's previous move on subsequent moves. Tit-for-tat was the champion of computer simulations in Axelrod and Hamilton's⁵ famous paper on the evolution of cooperation. Since then, other strategies such as 'Pavlov' have emerged as computer champions⁶. Pavlov is a 'win-stay, lose-shift' strategy; an individual repeats its former move if rewarded by T or R points, but switches strategies if punished with S or P points. Pavlov has two advantages over tit-for-tat. First, tit-for-tat can easily become mired in mutual defection if one individual mistakenly defects, whereas Pavlov will switch back to cooperation after experiencing mutual defection. Second, Pavlov exploits unconditional cooperators (suckers) by defecting, whereas tit-for-tat does not.

Females are nursed preferentially because females are philopatric and males disperse.

Kinship deceit: using altruism to deceive

The white-winged cough (*Corcorax melanorhamphos*) is a cooperatively breeding passerine. Helpers are critical for successful reproduction in coughs; pairs and trios fail to fledge young and groups of less than seven individuals fail to support any offspring through their first winter¹³. During or following aggressive encounters between groups, adults may herd young from another territory to their own territory. Heinsohn¹⁴ observed 14 instances of such 'kidnapping'. Adult 'kidnappers' fed unrelated fledglings that they kidnapped; three of the young survived to become unrelated helpers in their new groups.

Why do the kidnapped birds help at nests where they are unrelated to the breeder? Heinsohn¹⁴ suggested that kidnappers form 'special bonds' with kidnapped birds by feeding them. Such 'bonds' have been invoked to explain helping by non-relatives in many species (e.g. Refs 15,16). Emlen¹⁷ discusses two ways in which helpers might benefit from forming social bonds with unrelated young: (1) assisted offspring may join the helpers in the formation of same-sex coalitions that are beneficial in territory takeover or establishment; and (2) assisted offspring may later become helpers at the nests of the same birds that helped them. These hypotheses do not specify why a social bond should develop in the first place or, more importantly, why that bond should later cause the offspring to cooperate or act altruistically towards the unrelated bird that helped it.

Connor and Curry¹⁸ suggest that by feeding non-related offspring, helpers are parasitizing a kin-recognition mechanism based substantially on helping (see also Curry¹⁹). The deceived offspring perceive those who feed them as kin and later help raise their kidnapper's offspring.

Given that helpers preferentially assist kin, we expect to find 'kinship deceit' in species where: (1) help increases the reproductive success of the breeder and is costly to the helper; (2) kin are not always available to provide sufficient help; and (3) kin-recognition is based substantially on helping behavior.

If helpers preferentially assist relatives and learn to recognize kin based on who fed or nursed them, then feeding behavior should predict recipients of subsequent help better than does relatedness. Galapagos mockingbirds (*Nesomimus parvulus*) exhibit facultative helping behavior preferentially directed towards close relatives, but prior association accounts for the observed pattern of helping better than kinship does¹⁹.

The spread of kinship deceit in a population may favor more effective kin discrimination (e.g. from recognizing as kin any individual that feeds you, to only those that feed you the most), but any improvement short of self-referent phenotype matching or 'recognition alleles'²⁰ will still allow kinship deceit. Kinship deceit should be more common in unpredictable environments with high mortality. Helpers should prefer to recruit young relatives as allies because kinship deceivers will suffer the cost of having their offspring deceived in return. However, if mortality is high, helpers should hedge their bets against the loss of related young and attempt to

deceive unrelated young. Breeders without related helpers may also tolerate kinship deceivers because the cost of having one's offspring deceived may often be small compared to the benefits of having helpers.

Parceling: keeping a partner out of a Prisoner's Dilemma

Impala (*Aepyceros melampus*) groom each other on the head and neck by making upward sweeping motions with their tongue or lower incisors, behavior that apparently serves to reduce their unusually high tick load²¹. To initiate a grooming bout, one individual approaches another and delivers a bout of grooming. Grooming bouts are exchanged in a highly reciprocal manner until each individual has delivered 3–6 bouts of grooming to its partner²¹.

What appears to be an obvious candidate for 'tit-for-tat' may in fact be an example of 'parceling'²². The key difference between the two models is that individuals engaged in tit-for-tat are in a Prisoner's Dilemma, but parcelers are not. In parceling, individuals make decisions sequentially and have the option to desert their partner to seek a new one – another impala standing nearby in our present example. Upon receiving a bout of grooming an impala can make any of three moves: (1) do nothing; (2) reciprocate a bout of grooming; or (3) leave and seek grooming from another impala. The parceling model assumes that 'doing nothing' is not a viable option; the benefit of receiving an occasional free bout of grooming would be outweighed by the cost of an increasing parasite load. Individuals *need* grooming. The choice then is reduced to the relative benefits and costs of reciprocating versus defecting. The cost of staying (C_s) is the bout of grooms that must be given to the partner, the benefit of staying (B_s) is the grooming that will be received from the partner devalued by the probability that the partner will defect. The benefit of leaving (B_l) is the grooming that will be received from a new partner, the cost of leaving (C_l) is the cost of finding and initiating an interaction with a different individual. Impala will stay and reciprocate if $B_s - C_s > B_l - C_l$. However, impala in a herd are standing practically shoulder to shoulder, so the cost of leaving would seem to be quite small. As it turns out, the individual that initiates a bout of grooming always grooms first; Hart and Hart²³ never observed soliciting at the initiation of a grooming interaction, but such behavior was common once grooming commenced. Thus, whether it stays or leaves, an impala that needs grooming is going to have to deliver a bout of grooming to get another, and the choice is to remain with



Fig. 1. Simultaneous hermaphroditism is common among the shallow water seabasses of the family Serranidae. Here, two mating hamlets (*Hypoplectrus* sp.) take turns offering each other parcels of eggs for fertilization in a phenomenon known as egg-trading. Photograph by Steve Hoffman.

an individual that has demonstrated need (by initiating the interaction) or approaching one that has not.

By parcelling into bouts the amount of grooming their partner needs, impala are eliminating any opportunity for their partner to obtain a short-term benefit by defecting. If an impala did not parcel, but satisfied its partner's needs with one long bout of grooming, the partner would not reciprocate because it would need no further grooming.

Parcelling may also explain egg-trading in simultaneous hermaphrodites^{24,25}. Black hamlets (*Hypoplectrus nigricans*) are strictly diurnal seabasses that spend the day alone defending a feeding territory^{26,27}. All reproduction occurs during two hours before sunset when individuals move from their feeding territories to a spawning area where they pair for mating. Paired hamlets typically alternate courtship displays, with the last to display being the first to release eggs for the other to fertilize (Fig. 1). Each individual's clutch of eggs is offered in four or five parcels, and parcels are exchanged reciprocally. Black hamlet eggs are more expensive than sperm^{28,29} and must be released the day they are produced or they become inviable. Thus, hamlets are vulnerable to individuals who fertilize their eggs and then, instead of offering eggs in return, leave to fertilize the eggs of another individual. However, leaving may be costly, in terms of searching and courtship costs, and possibly the risk of predation. By parcelling, hamlets can manipulate their partner's optimal strategy in favor of staying and paying a parcel of eggs in expectation of receiving another. The benefit of staying declines as the number of eggs remaining to be spawned declines, but, because of the synchronous nature of hamlet reproduction, the benefits of leaving also decline. The chance of finding an unpaired individual with eggs will decline rapidly during the spawning period.

One permanently monogamous species, the harlequin bass (*Serranus tigrinus*) does

not parcel but has a very narrow window for reproduction; all spawning occurs from 22 minutes before, to 10 minutes after, sunset³⁰. Pressley suggested that 'by delaying spawning until just prior to taking nighttime shelter, each pair member increases its probability of receiving eggs by limiting its partner's ability to search out other mates'. Thus, harlequin bass keep their partners out of a Prisoner's Dilemma by synchrony alone, whereas black hamlets employ synchrony and parcelling.

Fischer²⁶ and Enquist and Leimar³¹ suggested that egg-trading is a defensive strategy to reduce the costs of interacting with a cheater. If a fish offered a parcel of eggs to its partner but received none in return, at least it still had most of its eggs left to trade with a new partner. In the parcelling model, egg-trading is an offensive rather than a defensive strategy; parcelling does not simply reduce the costs of being cheated; it manipulates a partner's optimum strategy from defection to cooperation.

Beyond the Prisoner's Dilemma

Of the three models presented here, only one – parcelling – may be considered a model of reciprocal altruism, and it is not based on the Prisoner's Dilemma^{22–24}. In fact, all three models were developed directly in response to claims for 'tit-for-tat' in which the behavior described did not appear to meet the assumptions of Axelrod and Hamilton's⁵ model. For example, tit-for-tat was a successful strategy only in an iterated Prisoner's Dilemma; in a single-move Prisoner's Dilemma the only evolutionarily stable strategy is to defect⁵. The interaction between helper and unrelated offspring is a single-move game, one bird helps raise another in expectation of being helped later on. If their behavior is based on the Prisoner's Dilemma, we should not see altruism towards unrelated offspring. In the tit-for-tat model, the probability of a further interaction is independent of either player's decision to cooperate or defect. This is clearly not the case in egg-trading or impala allogrooming, where one or two consecutive defections ends an interaction. Further, in tit-for-tat, players do not have the option to change partners as do the parcelling seabass and impala.

If these behaviors are found to meet the assumptions of the Prisoner's Dilemma, or if the results of previous analyses are robust against violations of the assumptions, then empiricists will face the task of distinguishing these models from Prisoner's Dilemma models. Some tests are available. For example, the kinship-deceit hypothesis predicts that deceived offspring will perceive their helpers as relatives, which may manifest itself in other contexts such as inbreeding avoidance¹⁸.

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References

- West-Eberhard, M.J. (1975) *Q. Rev. Biol.* 50, 1–33
- Hamilton, W.D. (1964) *J. Theor. Biol.* 7, 1–52
- Trivers, R.L. (1971) *Q. Rev. Biol.* 46, 35–57
- Alexander, R.D. (1979) *Darwinism and Human Affairs*, University of Washington Press
- Axelrod, R. and Hamilton, W.D. (1981) *Science* 211, 1390–1396
- Nowak, M. and Sigmund, K. (1993) *Nature* 364, 56–58
- Dugatkin, L.A., Mesterton-Gibbons, M. and Houston, A.I. (1992) *Trends Ecol. Evol.* 7, 202–205
- Gadagkar, R. (1993) *Trends Ecol. Evol.* 8, 232–234
- Krebs, J.R. and Davies, N.B. (1993) *An Introduction to Behavioral Ecology*, Blackwell
- Brown, C.R. (1991) *Anim. Behav.* 42, 551–564
- Connor, R.C. (1986) *Anim. Behav.* 34, 1562–1566
- Wilkinson, G.S. (1992) *Behav. Ecol. Sociobiol.* 31, 225–235
- Heinsohn, R.G. (1991) *Acta XX Congr. Int. Ornithol.* 1309–1316
- Heinsohn, R.G. (1991) *Anim. Behav.* 41, 1097–1100
- Ligon, D.L. (1983) *Am. Nat.* 121, 366–384
- Emlen, S.T. et al. (1991) *Am. Nat.* 138, 259–270
- Emlen, S.T. (1991) in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 301–335, Blackwell
- Connor, R.C. and Curry, R.L. *Anim. Behav.* (in press)
- Curry, R.L. (1988) *Behav. Ecol. Sociobiol.* 22, 141–152
- Sherman, P.W. and Holmes, W.G. (1985) in *Experimental Behavioural Ecology and Sociobiology* (Hölldobler, B. and Lindauer, M., eds), pp. 437–460, Sinauer
- Hart, B.L., Hart, L.A., Mooring, M.S. and Olubayo, R. (1992) *Anim. Behav.* 44, 615–631
- Connor, R.C. *Anim. Behav.* (in press)
- Hart, B.L. and Hart, L.A. (1992) *Anim. Behav.* 44, 1073–1083
- Connor, R.C. (1992) *J. Evol. Biol.* 5, 523–528
- Friedman, J.W. and Hammerstein, P. (1991) in *Game Equilibrium Models I* (Selten, R., ed.), pp. 257–275, Springer-Verlag
- Fischer, E.A. (1980) *Anim. Behav.* 28, 620–633
- Fischer, E.A. (1988) *Ethol. Sociobiol.* 9, 119–136
- Fischer, E.A. (1987) *Environ. Biol. Fish.* 18, 143–148
- Fischer, E.A. and Hardison, P.D. (1987) *Environ. Biol. Fish.* 20, 301–310
- Pressley, P.H. (1981) *Z. Tierpsychol.* 56, 33–46
- Enquist, M. and Leimar, O. (1993) *Anim. Behav.* 45, 747–757