

A Prisoner's Dilemma Model of the Evolution of Paternal Care

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Key Words

Paternal care · Reproductive effort · Non-reciprocal altruism · Co-operation · Prisoner's Dilemma

Abstract

The heavy energetic demands of gestation, lactation and rearing of offspring mean that studies of paternal care in primates usually focus on female reproductive effort. Here it is shown that both male and female reproductive effort must be considered in order to understand how paternal care evolved. This is done using the Prisoner's Dilemma, best known as a model of reciprocal altruism. It is found that the relative cost of reproduction for males and females is crucially important in determining co-operative and competitive strategies. In particular, when male reproductive costs are less than female reproductive costs, males co-operate with females even when females do not reciprocate. This surprising behaviour, termed non-reciprocal altruism, is comparable with male investment in a female and her offspring.

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Introduction

Recent studies of paternal investment in primates have focused largely on female costs. For example, Ross [1] argues that, in callitrichids, females can sustain high birth rates, litter weights and litter growth rates only, if males assist in infant transport. Dunbar [2] also suggests that high energetic costs associated with lactation are likely to determine whether or not males participate in infant care. However, in 1972 Trivers showed

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that breeding systems, particularly those which involve paternal care, could best be understood in terms of the relative reproductive effort of both sexes [3]. The previous year, Trivers had published a highly influential, although seemingly unrelated, paper on the evolution of co-operation between non-relatives [4]. Using a game called the Prisoner's Dilemma, he showed that even amongst selfish individuals, altruistic behaviours such as food sharing, grooming or support in fights can evolve based upon a principle of reciprocal altruism. Here the theoretical basis of both papers is combined to look at how relative reproductive effort influences co-operation between males and females. It will be shown that relative, rather than absolute, reproductive effort is crucially important in determining patterns of co-operation. In particular, when male reproductive effort is much less than female reproductive effort, males will co-operate with females even when that co-operation is not reciprocated. This behaviour, termed non-reciprocal altruism, is compared with male investment in a female and her offspring.

Reproductive effort, as defined by Trivers, measures the cost of reproduction as the extent to which a single reproductive event detracts from an individual's ability to invest in future offspring. It consists of two components, parental investment and mating costs. Parental investment measures the costs of all behaviours that directly increase an offspring's reproductive success. Since mammalian females are responsible for gestation, lactation and rearing of offspring, their costs of parental investment are very high. Typically, mean calorific intake is 66–188% higher in lactating compared to non-lactating females [5, 6]. It follows that females can best maximise their fitness by optimising their access to resources, as in the golden lion tamarin (*Leontopithecus rosalia*), where females time births to coincide with the wet season to avoid nutritional stress [7]. If males participate in the rearing of offspring, they will also incur a cost due to parental investment. However, this cost is likely to be somewhat lower than a female's parental cost [3]. If males do not involve themselves in parental care, their fitness is limited solely by the number of females they can impregnate. Hence, male reproductive effort is directly related to the costs of maintaining a large body size, competing with other males, attracting females and defending females from the advances of other males. In golden lion tamarins, male body mass decreases by 12% during June when male aggression, chasing and mate guarding is greatest [7], whilst in yellow-bellied marmots (*Marmota flaviventris*), a male's energy expenditure is related to the number and dispersion of females he defends [8]. Bercovitch and Nürnberg [9] have shown that in rhesus macaques only those males which have attained a certain level of body fat are able to sire offspring successfully. Feeding efficiency may also be compromised because of mate-guarding as happens in baboons [10], and in male red deer where feeding time is reduced by more than 85% during the rut [11].

For females, mating costs are usually low, and reproductive effort will consist almost entirely of parental care. For males, costs may involve parental care, mating effort, or both. Since this paper is concerned with the evolution of paternal care, it will be assumed that, in the first instance, male reproductive effort is determined solely by mating effort. Any paternal care that emerges will be considered as an extra cost to the male. Neither are lost mating opportunities included as costs, since these should emerge implicitly from the model. Female costs due to parental care, and male costs due to mating effort will from here on be called the costs of reproduction. Models will be developed, based on the Prisoner's Dilemma, which examine how the relative costs of reproduction for males and females affect the evolution of co-operative strategies.

		<i>Player 2</i>	
		C	D
<i>Player 1</i>	C	3 3	5 0
	D	0 5	1 1

Fig. 1. The pay-off matrix for the Prisoner's Dilemma. C indicates that a player co-operates, D that the player defects. Because the highest pay-off (5 points) is given to a player that defects when the other player co-operates, there is a high temptation to defect.

The Prisoner's Dilemma

The Prisoner's Dilemma is illustrated by the story of two suspects of a major crime who must each either make a confession and hence incriminate the other prisoner, or say nothing. The outcomes of confessing (defecting) or saying nothing (co-operating) can be represented by a pay-off matrix (fig. 1). The highest pay-off occurs if one individual confesses whilst the other says nothing: the confessor is set free (and gains the maximum pay-off of 5 points), whilst the co-operator is given the maximum sentence (and receives the lowest pay-off of 0 points). If both individuals defect then they both get imprisoned with a lesser sentence (a 1 point pay-off) and if they both co-operate then they are charged with a minor crime (a 3 point pay-off). In a single game of the Prisoner's Dilemma it is always best to defect no matter what you assume the other player will do. Hence, the inevitable outcome is that both players will defect, each gaining a 1-point pay-off which is much worse than the 3-point pay-off they would have gained if they had both co-operated.

Whilst in the 'one-shot' Prisoner's Dilemma it is always best to defect, the repeated (or iterated) Prisoner's Dilemma opens a doorway for co-operation to emerge. The expectation of future interactions makes co-operation an attractive option. Axelrod [12] has been the catalyst in discovering the best, most robust strategies for playing the iterated Prisoner's Dilemma. One of the simplest and most effective is called 'tit for tat' where a player reciprocates the behaviour of the other player in their previous game so that co-operation is rewarded with co-operation and defection is punished with defection.

Trivers predicted that reciprocal altruism would be prevalent in primate groups by virtue of their high sociality, large brain sizes and long life spans [4]. A balance of co-operation and competition is important in almost all aspects of group living including

access to mates, resources, allies, sleeping sites and position in hierarchy, as well as making group decisions about when to eat, what to eat and when to travel [2]. Reciprocal altruism has been reported in a number of primate species including olive baboons (*Papio anubis*) [13], vervet monkeys (*Cercopithecus aethiops*) [14, 15], howler monkeys (*Alouatta palliata*) [16], chimpanzees (*Pan troglodytes*) [17] and humans (*Homo sapiens*) [18].

Noë has argued that the Prisoner's Dilemma is a poor model of co-operation in primates because it does not allow for behaviours such as communication, bargaining, partner choice or many-player games [19–21]. However, when these aspects are incorporated into the Prisoner's Dilemma the fundamental conclusions remain the same, although strategies may become more complicated. For instance, signalling [22] provides a mechanism of partner choice, but also increases the likelihood of cheating. A more serious problem arises when reciprocal altruism is assumed to be the only outcome of the Prisoner's Dilemma [23]. For instance, Bercovitch [24] has looked at coalitions in male savannah baboons, who use alliances to attain oestrous females. He found that whilst some pairs of males clearly practised reciprocal altruism, in others differences in aid-giving potential between males created complex patterns of coalition formation. More realistic models must recognise that because individuals differ in age, sex and status, the costs and benefits of giving and receiving aid will also vary [25]. In this context, sex differences in the reproductive effort are likely to produce a wide variety of co-operative strategies within a Prisoner's Dilemma model.

The Prisoner's Dilemma and the Cost of Reproduction

In these experiments it is assumed that the only difference between a male and female is in the cost of reproduction (RC), that is the reproductive effort required to produce an offspring. It is assumed that the female has a higher RC. To pay RC, individual agents must gain points by playing the iterated Prisoner's Dilemma with other members of the population. When an agent has accumulated enough points it is able to reproduce with an agent of the opposite sex which also has enough points. This means that the players with the best strategies for playing the Prisoner's Dilemma will have the most offspring. Each agent has a set of chromosomes or 'strategy strings' which dictate its strategy for playing the game. During reproduction the strategy strings of each parent are 'crossed over' (fig. 2) and may mutate (with a chance of 1/5,000). In this way, each offspring inherits a combination of its parents' strategy strings and strategies evolve over time. The model is, in effect, a genetic algorithm [26] for determining the best strategies for playing the Prisoner's Dilemma in groups of mixed sex.

A player's strategy is determined by two factors: (1) the history of interactions between the players, and (2) the sexes of the players. Ikegami [27] has found that robust and unexploitable strategies for playing the iterated Prisoner's Dilemma ideally require a memory of the outcomes of the last two games played. Since this involves recording two moves (a play of co-operate or defect) for each player, it is called a memory length of size 4. Following Lindgren [28] the strategy string provides a response for every possible situation that could arise from a memory length of 4, i.e. 16 possible situations, where a response is encoded as '1' for co-operate and '0' for defect. For example, if the point on the strategy string labelled 'CCCC' holds a '1', this is interpreted to mean 'if both players co-operated on their last two moves, then co-operate on the next move'. The strategy string must also provide appropriate responses for when an agent first meets a new player, i.e. either 'always co-

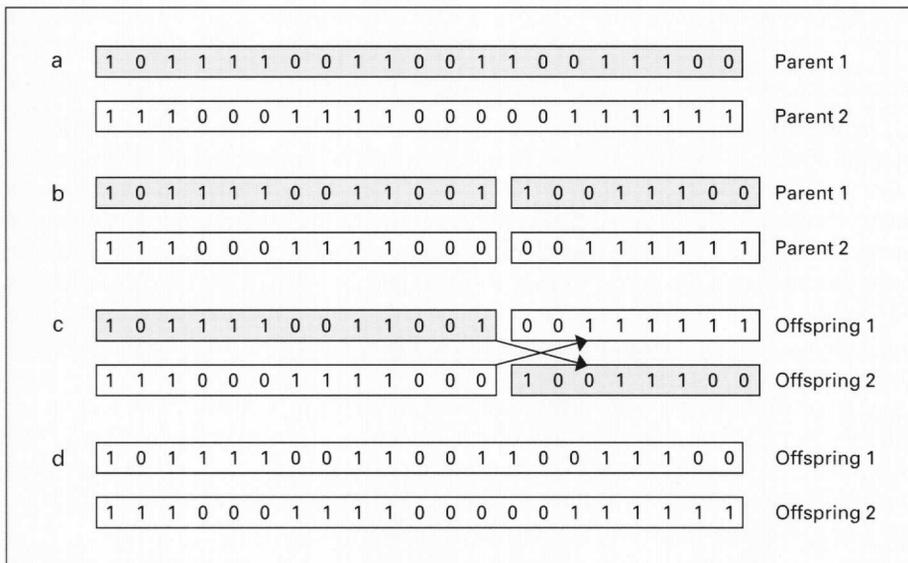


Fig. 2a-d. Reproduction involves crossover of the parents' strategy strings (a). A random point is chosen at the same point at each string, and the parent strings are cut (b). The two parts of the parent strings are swapped (c) to produce two new offspring (d).

operate' or 'always defect' (1 bit), and for the second game, i.e. what to play following CC, DD, CD or DC (4 bits). In total the strategy string must be 21 bits long ($1 + 4 + 16 = 21$) to cover all possible situations.

The other important factor is the genders of the players. It cannot be assumed that a female will behave in the same way with another female as she would with a male. Four possible situations could arise. From the point of view of the agent these are: (1) I am male, my opponent is male; (2) I am female, my opponent is female; (3) I am male, my opponent is female; (4) I am female, my opponent is male. Each player carries 4 strategy strings, 1 for each of these possible situations. Although a male, for instance, only requires strategy strings 1 and 3, his daughters will require information from strings 2 and 4. By carrying all 4 strategy strings a player contributes to the behaviour of all its children regardless of their sex.

The strategy string can potentially encode every possible strategy that remembers two turns, and is contingent upon the sex of the players. In practice, only those agents whose strategies are successful will acquire enough points to reproduce. However, strategies are in no way dependent upon accumulated pay-off.

At the start of each experiment, 650 agents are created randomly, i.e. their strategy strings are generated at random and they are assigned a sex. Each agent also has a score which at the start of the experiment is 0. Furthermore, at the start of the experiment the RC is set for males and females (MRC and FRC, respectively). Two agents are then selected at random to play 100 rounds of the Prisoner's Dilemma. They gain points according to the pay-off matrix in figure 1 and these are added to their score (this score is then carried over, so that points gained accumulate each time a player is selected to play the game). Two new agents are then selected and, if they are of opposite sex and each have enough points, they reproduce to create 2 new offspring. The RC is deducted from each player's score according to their sex and they are returned to the pool of agents. The offspring are randomly assigned a sex and put into an offspring array. Any single agent may reproduce several times, provided it has accumulated enough points during games of the Prisoner's Dilemma. The process of interaction and

reproduction continues until 650 new offspring have been created. At this point, the first generation is complete, and the offspring become the new parent population who begin a new cycle. This continues for 20,000 generations.

It is important to understand that, in this model, RC represents the minimum amount of energy required to produce an offspring. Investment below the minimum value would result in the death of the infant, and it is assumed that agents do not waste energy (points) in this way. Agents could invest more than the minimum amount of energy. Instead, it is assumed here that any excess energy is conserved and contributes to the production of the next offspring. For example, if the RC is 500 and an agent has 700 points, after reproduction its score will be reduced to 200 points and it must gain only another 300 points (through games of the Prisoner's Dilemma) in order to reproduce again.

The program used to generate this model was written in 'C' by Key [29] and ran on 486 PCs. Simulations took anywhere from a few hours to a few days to complete. The program was extensively tested by fixing strategy strings to values for which there were known outcomes, and by meticulously following each stage of interaction and reproduction when strategy strings were randomly generated.

The Control Experiment

The experiment was first run with male reproductive cost (MRC) equal to female reproductive cost (FRC). The simulation was run for reproductive costs between 0 and 2,000. The results are measured in terms of the average score per individual per game of Prisoner's Dilemma over the entire experiment. For example, in a co-operating population the average score is 3.00 (see the pay-off matrix in fig. 1), whilst in a population where most players defect the average score is 1.00. Intermediate scores represent intermediate behaviours. Each control experiment was run 30 times. The results are presented as a percentage bar chart (fig. 3) showing the percentage of simulations where individuals evolved to be 'defectors' (average score = 1.25), 'weak defectors' (average score = 1.75), 'weak co-operators' (average score = 2.25) and 'co-operators' (average score = 2.75) for different costs of reproduction.

An RC of 1 is practically no cost at all, and, as would be expected, no particular strategy is selected at this value. Around 25% of simulations resulted in the evolution of defection strategies, whilst a similar number evolved co-operative strategies. At an RC of 100, co-operation is more common, evolving in around 50% of experiments. At higher RCs, there is strong selection for co-operation. When the RC is greater than or equal to 200, in almost every case some kind of tit-for-tat strategy evolves, where co-operation is rewarded with co-operation and defection is punished with defection. This clearly indicates that an RC of 200 marks the threshold at or beyond which co-operation is strongly selected. This result provides a benchmark for looking at a population where there is an imbalance between male and female reproductive costs.

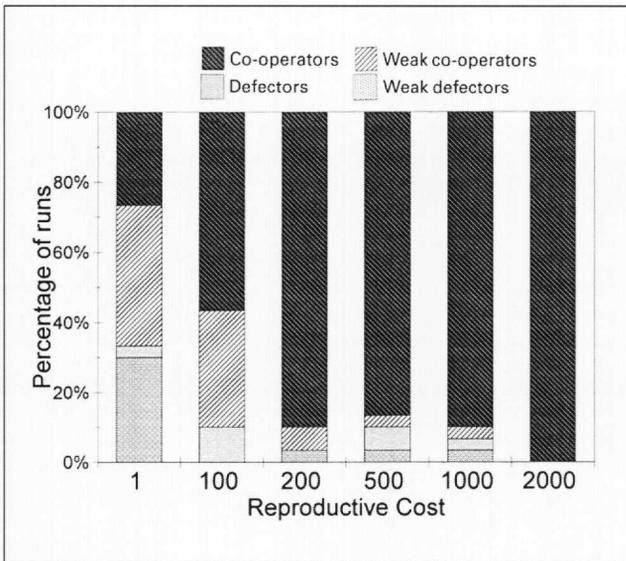


Fig. 3. The control experiment for model 1. Each bar represents the results from 30 simulations, where the shaded areas indicate the percentage of experiments in which agents evolved to be co-operators, weak co-operators, weak defectors or defectors.

The Prisoner's Dilemma in a Mixed Sex Environment (Model 1)

The experiment was repeated with FRC kept constant at 1,000 (very high), whilst MRC was varied between 1 and 600, including the benchmark figure of MRC = 200. As in the control experiment, results are summarised for each sex as the average score per player per game recorded over the entire simulation. Interactions between two females evolved exactly in the way expected from the control study at FRC = 1,000 (fig. 4). When FRC is high, females almost always adopt a strategy of tit-for-tat against other females, regardless of MRC. In contrast, interactions between males are considerably different from those expected from the control study and are indicative of considerable competition between males (fig. 5). Whilst co-operation between male players is expected when MRC \geq 200, in the mixed sex environment when MRC = 200 reciprocal altruism was the dominant strategy in just 27% of the experiments. Even at MRC = 400 males co-operated in fewer than half of the runs. Only at very high RC do males tend to co-operate, e.g. at MRC = 600. The males are behaving much less co-operatively in the presence of females than they would in a single sex population.

Interactions between males and females are far more complex than those of single sex interactions and are crucially dependent on the ratio of male and female RC. Depending on the ratio of FRC to MRC, three different patterns of behaviour emerge. Reciprocal altruism evolves when MRC approaches FRC, for example when MRC = 600 both males and females participate in a reciprocally co-operative relationship (fig. 6a) in two-thirds of the experiments. The second pattern occurs when MRC is

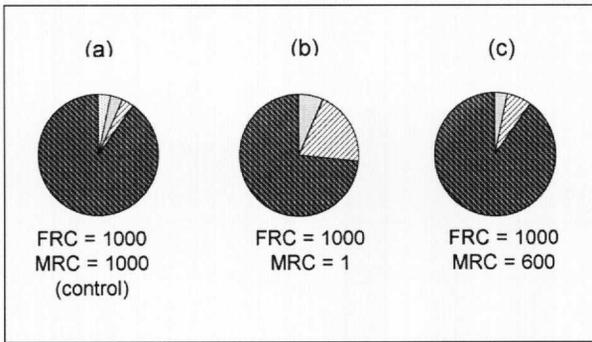


Fig. 4. Average scores for female-female interactions over 30 simulations for model 1. The key is the same as for figure 3.

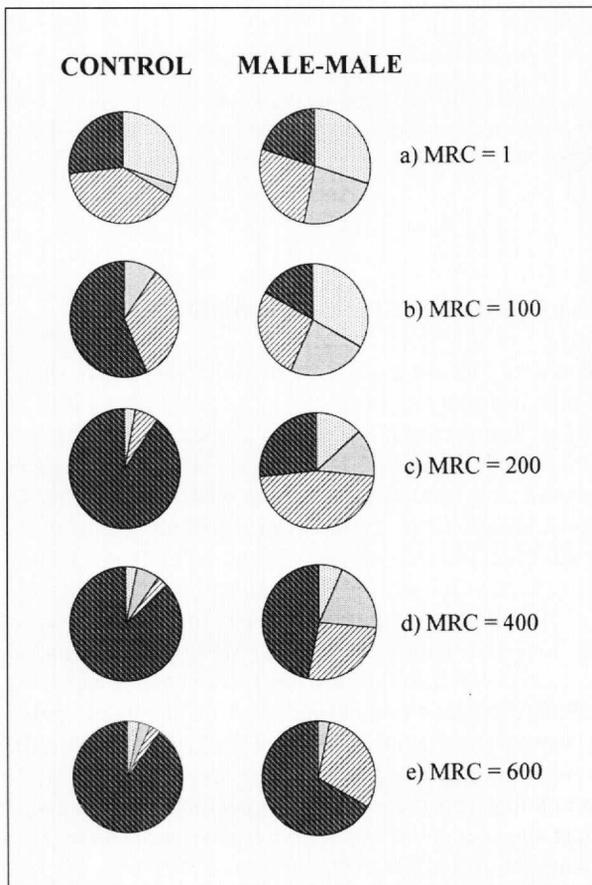


Fig. 5. Average scores for male-male interactions over 30 simulations for model 1. The key is the same as for figure 3.

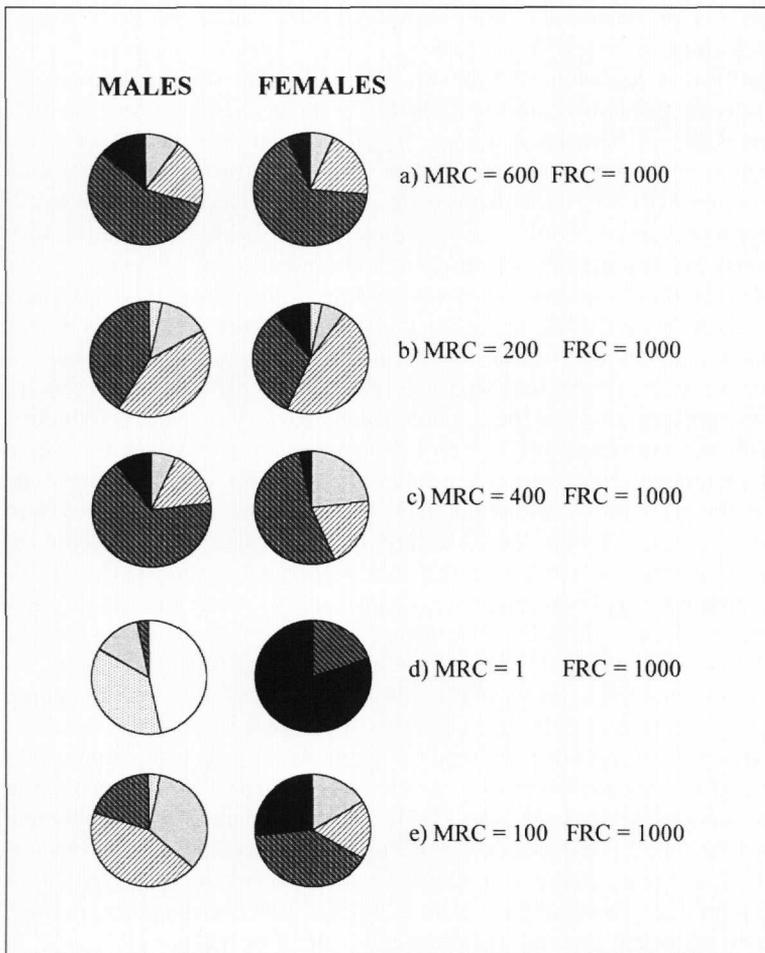


Fig. 6. Average scores for male-female interactions for males versus females for model 1. An average score greater than 3.00 (■) indicates a strategy of exploitation, whilst an average score of less than 1.00 (□) shows that a player is being exploited. Other strategies are represented as in figure 3.

greater than 100, but less than 600. There is considerable variation between these experiments indicating a wide variety of behaviour patterns and, in many cases, high levels of competition (fig. 6b, c). At this level, males are not co-operating with each other (fig. 5) and male-female interactions seem to provide males with an opportunity to gain much needed points. Since females must also acquire as many points as possible there is an increase in competition and, as a result, both males and females suffer low pay-offs. For instance, at $MRC = 200$ (fig. 6b), co-operative relationships are established in only a third of cases. Furthermore, at $MRC = 400$ (fig. 6c), although the overall level of co-operation is higher, males consistently attain higher scores than females in mixed sex

interactions. This may be because at a lower reproductive cost, males are more able to take the risk of defecting.

The third pattern of male-female behaviour, in which pay-offs become consistently skewed in favour of females, occurs when MRC is considerably less than FRC (fig. 6d, e). When MRC = 1, females attain a score greater than 3.00 in 80% of cases, whilst the majority of males are receiving very low scores in return (1.00, or less than 1.00). Similarly, when MRC = 100, females are consistently achieving higher scores than males. These scores reflect a situation where males are always co-operating with females even though the females are not returning the same level of co-operation, i.e. females are exploiting male 'suckers'. In effect, males are exhibiting non-reciprocal altruism. This result seems contradictory if you consider that individual males do not gain any reproductive advantage from co-operating with the females (a male will not necessarily reproduce with a female that he co-operates with). There is a group benefit, in that if the males are provisioning the females, the females will reach reproductive status more quickly (i.e. enough points to meet FRC) and so the population as a whole will reproduce more quickly. Nonetheless, it would seem better for any individual male to cheat and gain the extra points whilst his male companions continue to provision the females. However, such males can be forced by females to be non-reciprocal altruists.

The most common form of non-reciprocal altruism occurs where the female alternately co-operates and defects whilst the male always co-operates, leading to an average pay-off of 1.50 to the male and 4.00 to the female (see the pay-off matrix in fig. 1). Females that have evolved this strategy of alternating co-operation and defection are usually completely intolerant of defection from the male. That is, they will defect in reply to all male strategies except unconditional co-operation. Any male that attempts to defect will receive an average pay-off of 1.00, which is worse than the pay-off of 1.50 he would receive from non-reciprocal altruism. Furthermore, if a male defects the female also receives just 1.00, which is a quarter of what she would expect from a non-reciprocal altruism male. This means that it will take 4 times longer for the female to attain enough points to reproduce, by which time most males will have enough points to meet MRC and defecting males lose their advantage over co-operating males.

Three behaviours have been predicted to evolve between males and females: reciprocal altruism, competition and non-reciprocal altruism. Since the model involves both non-linear and stochastic processes, this is a complex system, and understanding why different strategies evolve within certain threshold ranges is by no means simple [29]. For instance, there is much more variation in the reproductive success of males than females and the success of a non-reciprocal altruist is partly dependent upon the number of games a male must play in order to acquire enough points to reproduce (further details are available from the authors, or see reference [29]). Because of the complexity of the processes underlying the model, the simulations were repeated using different values for the key variables to test the robusticity of the results. The experiments were repeated for FRC = 2,000 at different values of MRC. The results mirrored those described for FRC = 1,000 and indicate that it is the ratio of FRC to MRC that is important rather than the absolute values. Male non-reciprocal altruism in favour of females is only seen when $MRC \leq 0.1 \times FRC$. Likewise, intense competition both between males and between males and females, resulting in low pay-offs, occurs when MRC is approximately half FRC. Male-male and male-female interactions display reciprocal altruism only when MRC approaches the value of FRC. The experiment was

also repeated for different population sizes, numbers of interactions (i.e. the number of rounds of the Prisoner's Dilemma that a pair play) and mutation rates. None of these factors was found to affect the results in any way.

The Further Evolution of Non-Reciprocal Altruism (Model 2)

In the model that has been developed, RC represents Trivers' concept of reproductive effort, and the points gained by playing the Prisoner's Dilemma are equivalent to energy or fitness. Only when a certain level of energy intake or fitness has been achieved can an agent reproduce. The model shows that when the reproductive effort required by a male to produce an offspring is low in comparison to female reproductive effort, males behave as non-reciprocal altruists, investing in the females of the group and enabling females to reproduce more quickly. Males are sacrificing their own fitness and, as a consequence of this, potential mating opportunities for the benefit of the female and her offspring. This is akin to paternal investment in a female and her offspring. Model 1 suggests that the evolution of paternal investment could be triggered by a heavy imbalance in the level of reproductive effort between the sexes. However, since there is no link between the interaction and reproduction phases of the model it is more than likely that males are investing in the mothers of another male's future offspring. If males must invest in the females, they would be better off ensuring that they are investing in the mother of their own infant. Once this link between co-operation and reproduction is made, the males may invest even more heavily in the females and their offspring.

To investigate this hypothesis, the experiment was repeated with the difference that after a male and female have finished interacting (playing the Prisoner's Dilemma) they can reproduce, with the proviso that they each have enough points. This does not guarantee reproductive access for the male, but makes it much more likely than in the first model. The simulation was run 30 times for each set of variables. As in model 1, the control experiment was run with male RC equal to female RC. The results for model 2 (fig. 7) are almost identical to those for model 1 (fig. 3). Most importantly, once again reciprocal altruism dominates as a strategy whenever RC is greater than, or equal to 200.

The main experiment was run with FRC = 1,000 and the value of MRC was varied. The results have been summarised in figure 8 which shows how the average score for each interaction type (male-male, female-female, male-female and female-male) varied with the ratio of MRC to FRC. The results for female-female interactions are exactly the same as in model 1, that is females nearly always co-operate with each other, regardless of MRC. The results for male-male interactions differ from model 1 in that male-male competition does not evolve. As predicted by the control model, males are highly co-operative with each other at MRC = 200, in fact they are no less co-operative than they are at MRC = 800.

The results for the inter-sex interactions strongly predict the evolution of non-reciprocal altruism. The greater the difference in MRC and FRC the greater the divergence in their average scores. For instance, when MRC = 200 females gained, on average, 4.74 points from their games against males whilst males received just 0.38 points in return. In 73% of these simulations, males always co-operated whilst females always defected, giving females 5.00 points and males the suckers' pay-off of 0. To differentiate this from the behaviour that evolves in model 1, it will be called strong non-reciprocal

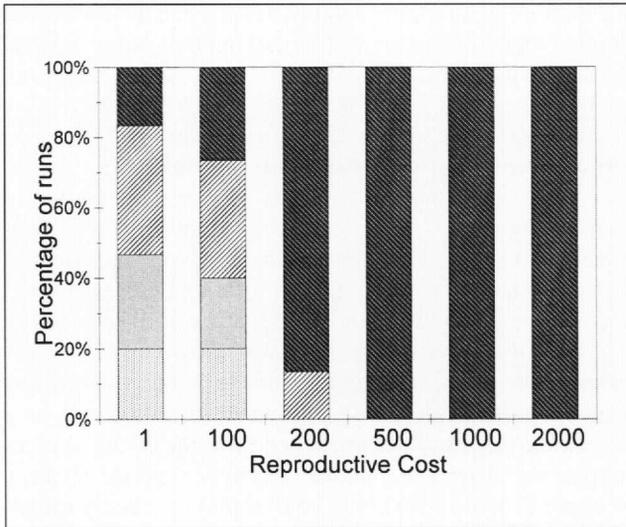


Fig. 7. The control experiment for model 2, indicating the average scores per player over 30 simulations for varying values of RC. The key is as in figure 3.

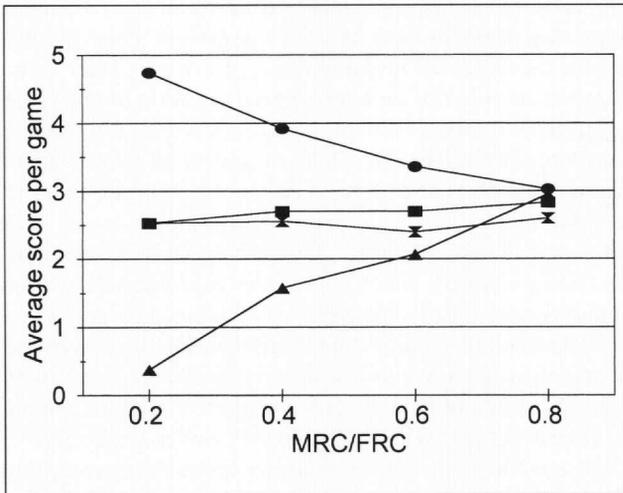


Fig. 8. Summary of results for model 2. Each point represents the average score per player per game of Prisoner's Dilemma over 30 simulations. Scores are shown separately for different interaction types: male vs. male (▼), female vs. female (■), male vs. female (▲) and female vs. male (●).

altruism. In the other 27% of experiments, non-reciprocal altruism of the type described in model 1 evolved. That is, males always co-operated whilst females alternately co-operated and defected. In not one experiment did any strategy other than non-reciprocal altruism evolve. At $MRC = 400$, non-reciprocal altruism was the dominant strategy in all but one simulation, although strong non-reciprocal altruism did not evolve. Even at $MRC = 600$ males behaved as non-reciprocal altruists in 40% of experiments. Only at $MRC = 800$ do the scores even out, where both sexes played a strategy of reciprocal altruism.

Discussion

The experiments presented in this paper predict a wide variety of co-operative strategies, although a few broad patterns emerge. The models are complex, and their applicability to real life situations remains to be tested, although primates are ideal for such an endeavour due to the variability in their cooperative relationships. Some suggestions will be made here as to possible ways in which these models may be applied to the study of primate behaviour.

Females are predicted to be highly co-operative with each other, and this is certainly the predominant trend in group-living primates. Females co-operate with each other over a whole spectrum of behaviours from grooming and support in fights to food-sharing and infant care. Whilst a substantial portion of this co-operation is probably due to kin selection, co-operation also occurs between unrelated females. For instance, Seyfarth and Cheney [14] used playback experiments to show that vervet females will respond to calls of help from unrelated individuals who have recently groomed them (in contrast they would respond to the calls of relatives regardless of prior grooming activity). De Waal [30] describes how chimpanzee females band together to protect themselves from overly aggressive males, and in bonobos (*Pan paniscus*), unrelated females partake in food-sharing and genito-genital rubbing [31].

In model 1, intra-male interactions are very competitive, much more so than we would expect from the control scenario. It is interesting that when MRC is around half the FRC male-female interactions are also very competitive. It is as if males are using their interactions with females to compensate for their poor scores from male-male interactions. It would be expected, then, that male-female competition will be highest in those species in which male-male competition is also high.

The most surprising result from these models is that when MRC is equal to, or less than 10% of FRC , males will behave as non-reciprocal altruists. That is, they will invest in females and their offspring at a cost to themselves in terms of time, energy and (implicitly) lost mating opportunities. Importantly, non-reciprocal altruism is predicted regardless of whether or not the male mates with the female. This hypothesis requires rigorous testing in the field. However de Waal [pers. comm.] has suggested that this model may help to explain observations of male cooperation in capuchins. De Waal et al. [32] looked at voluntary food-sharing in brown capuchins (*Cebus apella*), and found food transfers (from a possessor in one cage, to a receiver in an adjacent cage) were most frequent between partners of opposite sex. A later study on the same monkeys found that adult males 'share more generously and less discriminately than females, and that their sharing is not necessarily mutual' [33]. In contrast, food-sharing by females was influenced by the agonistic and social relationships they had with their partner, and

females were much more likely to practise reciprocal sharing. At the very least these two results indicate that male and female capuchins are using different co-operative strategies. Furthermore, the male behaviour seems very similar to non-reciprocal altruism.

Non-reciprocal altruism is predicted to be a male response to a relative increase in female reproductive effort. If FRCs remain high and males are investing in females, then it is to a male's advantage to invest in those females who are likely to become mothers of their own offspring. This link between male co-operation with females and reproduction occurs in a number of primate species which are not usually monogamous or polyandrous. Stanford et al. [34] have shown that the presence of oestrus females is the best predictor of hunting behaviour in male chimpanzees, and bonobo males have been reported to give food to females immediately after, or even in the midst of intercourse [35, 36]. Smuts [37] reports that subordinate male baboons (*Papio anubis*) in a harem group often form special friendships with females, helping them in the care and protection of offspring in the expectation of future matings. Model 2 predicts that once interactions and reproduction become linked, males will behave as non-reciprocal altruists even when their own costs are comparatively high, and that they are likely to co-operate even more (strong non-reciprocal altruism). This investment may imply an increased cost for the male, in terms of parental effort, but as long as total male reproductive effort does not exceed 60% of the female reproductive effort the behaviour is likely to persist.

In both models, when non-reciprocal altruism occurs females must, by definition, defect more often than males. There have been many studies of the iterated Prisoner's Dilemma in humans, where individuals literally play the game against each other. In over a hundred studies it has been found that females are more likely to defect than males [18]. Given that paternal care is an important aspect of human social groups, these results support the idea that non-reciprocal altruism could be an important psychological mechanism underlying the evolution of male care in humans.

This study has reached a number of conclusions with regard to the evolution of cooperation both within and between sexes. Inter-female cooperation is predicted to occur whenever female energetic costs are high, whilst interactions between males are likely to be competitive even when male costs are relatively great. Most importantly, it has been shown that it is the relative energetic costs to males and females, rather than the absolute costs to either sex, which determine when paternal care may occur. It is predicted that males will care for females and their offspring when male reproductive effort is much less than female reproductive effort. It follows that paternal care could be a response either to an elevation of FRC or to a decrease in MRC. This model is concerned with the origins of co-operation, and a transitory state is predicted whereby males will care for females and their offspring regardless of paternity. Given this situation, males should attempt to co-operate only with future mates and male care will become an integral part of the social system. These hypotheses remain to be tested on field data, and primates are ideal candidates since they display a wide variety of different co-operative behaviours. Nonetheless, it is likely that the model is generally applicable to any species in which there is, or has been at some point in its evolutionary history, an imbalance in the ratio of male and female energetic costs.

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