Non-reciprocal Altruism and the Evolution of Paternal Care

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Abstract

Why do males in some species contribute to offspring care, while in others males have very little involvement with females and their offspring, beyond conception? This paper addresses this question using a combination of theoretical biology, genetic computation, game theory and data from living primates. Because of the heavy energetic demands of gestation, lactation and offspring care, studies of paternal care in mammals usually focus only 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 simulations of the Prisoner's Dilemma, best known as a model of reciprocal altruism. It is found that the relative cost of reproduction between a male and a female is crucially important in determining co-operative 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.

1. INTRODUCTION

In 1972 Trivers showed that breeding systems could best be understood in terms of the relative reproductive effort of both sexes (Trivers 1972). The previous year, Trivers had published a highly influential, although seemingly unrelated, paper on the evolution of co-operation between non-relatives (Trivers 1971). 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 the principal of reciprocal altruism. Here, the theoretical bases of both papers are 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, the costs of parental investment are very high. Typically, mean calorific intake increases by 66-188% in lactating compared to non-lactating females (Clutton-Brock 1991; Gittleman and Thompson 1988). It follows that females can best maximise their fitness by optimising their access to resources as in the golden lion tamarin where females time births to coincide with the wet season to avoid nutritional stress (Dietz *et al.* 1993). 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 (Trivers 1972). If males do not involve themselves in parental care, their fitness is limited solely by the number of females they can impregnate. Hence 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. For instance, in golden lion tamarins, male body mass decreases by 12% during June, when male aggression, chasing and mate guarding is greatest (Dietz *et al.* 1993) while in yellow bellied marmots, a male's energy expenditure is related to the number and dispersion of females he defends (Salsbury and Armitage 1995). Bercovitch and Nürnberg (1996) have shown that in rhesus macaques only those males who have attained a certain level of body fat are able to successfully sire

offspring. Feeding efficiency may also be compromised because of mate-guarding as happens in baboons (Alberts *et al.* 1996) and in male red deer in which feeding time is reduced by more than 85% during the rut (Clutton-Brock *et al.* 1988).

Usually for females mating costs are 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 cost of reproduction between males and females affects the evolution of co-operative strategies.

2. 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 saying 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), while 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 each have gained by co-operating.

Player 2

Player 1	C	D
C	**3** **3**	**5** **0**
D	**0** **5**	**1** **1**

Figure 1: The pay-off matrix for the Prisoner's Dilemma.

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 (1984; see also Axelrod and Hamilton 1981) 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.

In the standard version of the Prisoner's Dilemma, all individuals are assumed to be identical. However, in reality, characteristics such as age, sex and status are likely to affect an animal's ability to give and receive aid. For instance, Boyd (1992) has shown that subordinate and dominant animals are likely to follow very different co-operative strategies. In this paper, the affects of gender on co-operation are explored.

3. THE MODEL

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, in the first instance, that females have a higher reproductive cost. 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 who 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 'strategy strings' which dictate its strategy for playing the game. During reproduction the strategy strings of each parent are 'crossed over' and may mutate (with a chance of 1/5000). In this way each offspring inherits a combination of its parents strategy strings and strategies evolve over time. The model is a genetic algorithm (Holland 1992a,b) to determine the best strategies for playing the Prisoner's Dilemma in groups of mixed sex.

A players strategy is determined by two factors: 1) the history of interactions between the players, and 2) the sexes of the players. Ikegami (1993) 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 (1991) 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-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 gender of each player. 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 four strategy strings, one 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. Note that 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 strategies that are successful will acquire enough points to reproduce. However, strategies are in no way dependent upon accumulated payoff.

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. Also at the start of the experiment the cost of reproduction 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 fig. 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 two new offspring. The cost of reproduction (MRC or FRC) 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, the cost of reproduction is 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 investment 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 cost of reproduction 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 the author and ran on 486 PCs. Simulations would take anywhere from a few hours to a few days to complete. The program was extensively tested by fixing strategy strings to values in which there were known outcomes, and by meticulously following each stage of interaction and reproduction when strategy strings were randomly generated.

4. 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 2000. The results are assessed in terms of the average score per person 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 payoff matrix in fig. 1) while 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. 2).

A reproductive cost of 1 is practically no cost at all, and as would be expected, no particular strategy is selected at this cost. Around 25% of simulations resulted in the evolution of defection strategies, while a similar number evolved co-operative strategies. At a reproductive cost of 100, co-operation is more common, evolving in around 50% of experiments. At higher reproductive costs there is strong selection for co-operation. When the reproductive cost is greater than or equal to 200, in almost every case some kind of tit-for-tat strategy evolves. This clearly indicates that a reproductive cost 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 in male and female reproductive cost.

5. THE PRISONER'S DILEMMA IN A MIXED SEX ENVIRONMENT (MODEL 1)

The experiment was repeated with female cost kept constant at FRC = 1000 (very high), while male cost was varied between MRC =1 and MRC = 600. As in the control experiment, results are summarised for each sex as the average score per player per game recorded over the entire simulation. Due to space limitations, this discussion will focus on those results directly relevant to the evolution of male care giving, i.e. mixed sex interactions. Same sex interactions will be briefly summarised (see Key and Aiello (in press) for details).

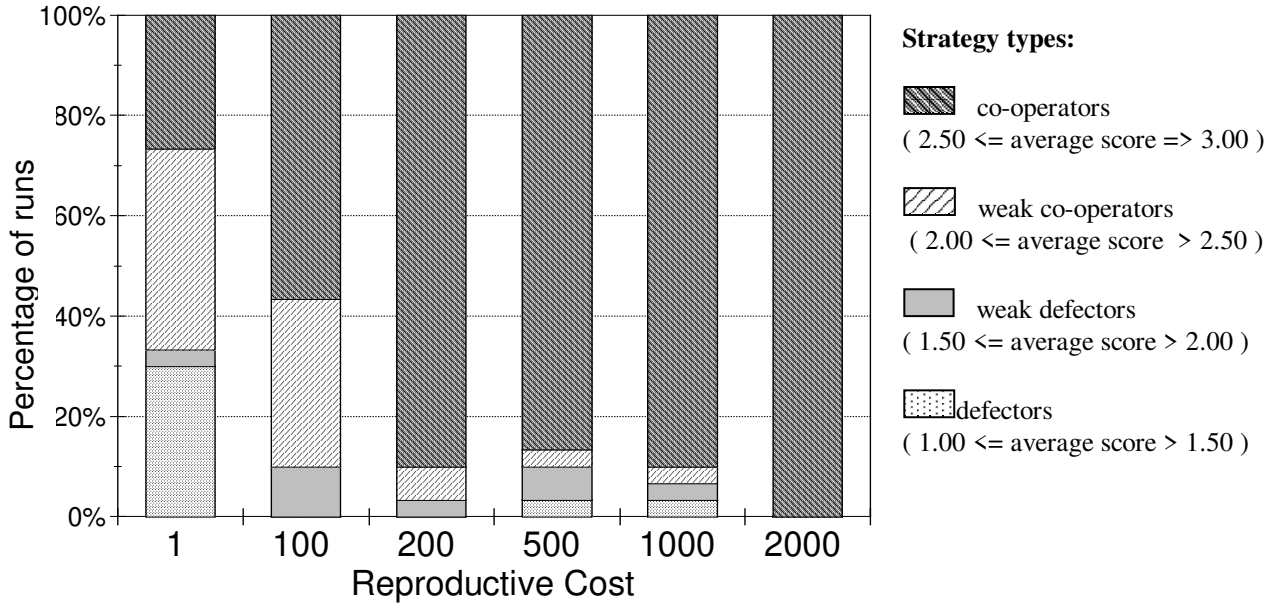

Figure 2: The control experiment. Each bar indicates the results from 30 simulations, where the shaded areas indicate the percentage of experiments where agents evolved each strategy type.

When female cost is high, females almost always adopt a strategy of tit-for-tat against other females, regardless of male cost. In contrast, interactions between males are considerably different from those expected from the control study and are indicative of considerable competition between males, even at quite high reproductive costs (e.g. MRC = 400). Only at very high reproductive costs 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 reproductive costs. Figure 3 shows the average scores gained by males and females during mixed sex interactions, for a selection of simulations. 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 (fig. 3a) both males and females participate in a reciprocally co-operative relationship in two-thirds of the experiments. The second pattern occurs when MRC is 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. For instance, at MRC = 200 (fig. 3b), co-operation is predicted to evolve in nearly every simulation (see the control experiment), however co-operative relationships are established in only a third of cases. The third and, in the context of this paper, the most interesting pattern of male-female behaviour occurs when MRC is considerably less than FRC. Under these circumstances, pay-offs become consistently biased in favour of females (fig. 3c &d). In the most extreme case, MRC = 1 (fig. 3d), in most simulations females gain more than 3 points while males score very poorly, often getting an average of less than one point per game. Similarly, when MRC = 100 (fig. 3c), 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". Since males do not gain an equivalent return for their co-operation, this type of male strategy is termed non-reciprocal altruism.

Non-reciprocal altruism is a puzzling result, in view of the fact that individual males do not gain any reproductive advantage from co-operating with the females (a male is unlikely to reproduce with a female that he co-operates with). There is a group benefit: 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. None-the-less, intuition would suggest that it is better for any individual male to cheat and gain the extra points, while his male companions continue to provision the females. However, such males can be forced by females to be non-reciprocal altruists. Usually, in simulations in which non-reciprocal altruism evolves, females alternately co-operate and defect, while the male always co-operates. This leads to an average payoff 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-

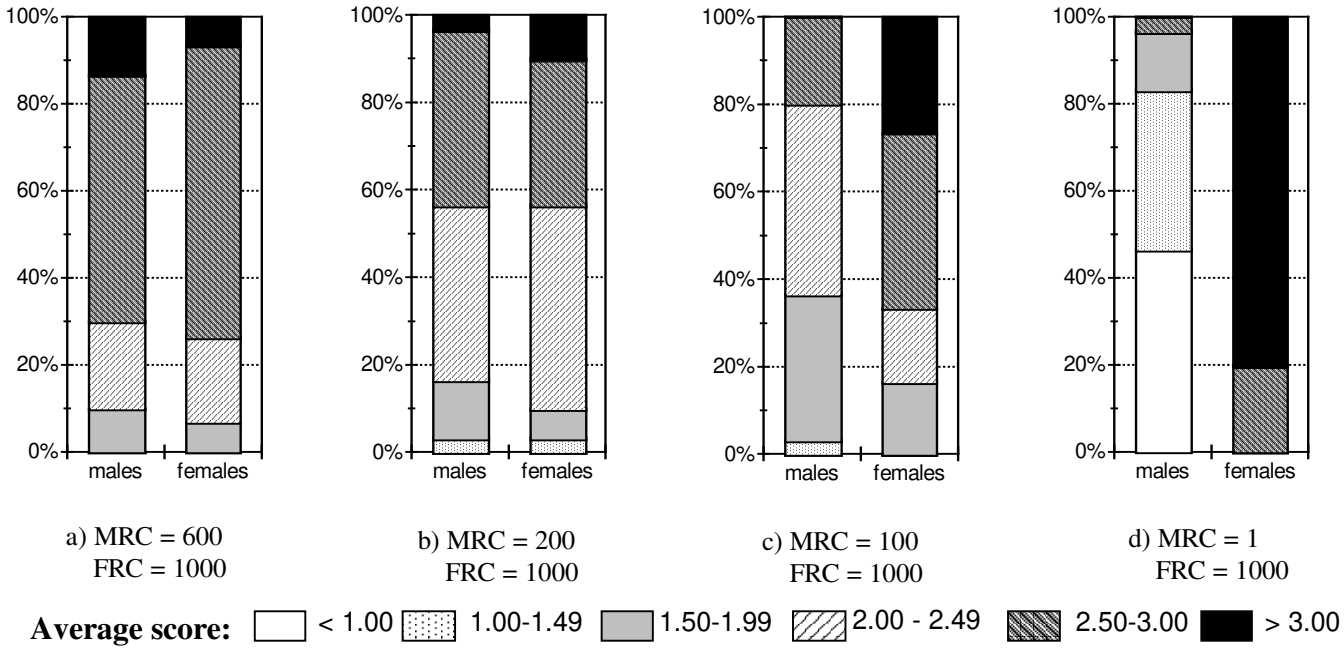

Figure 3: Average scores obtained during male-female interaction for males versus females.

off of 1.00, which is worse than the pay-off of 1.50 he would receive from non-reciprocal altruism.

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 a complex system and understanding why different strategies evolve within certain thresholds is by no means simple. 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 (Key 1998). Because of the complexity of the processes underlying the model, the simulations were repeated using different values for the key variables to test the robustness of the results. The experiments were repeated for FRC = 2000 at different values of MRC. The results mirrored those described for FRC = 1000 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 <= 0.1xFRC. 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 were found to affect the results in any way.

6. THE FURTHER EVOLUTION OF NON-RECIPROCAL ALTRUISM (MODEL 2)

In the model that has been developed, the cost of reproduction 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 the female and her offspring. Model 1 would suggest 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. Linking interactions and reproduction made no difference to the results in the control condition, when male and female reproductive costs are equal. However, when male and female reproductive costs differ the results are quite different to

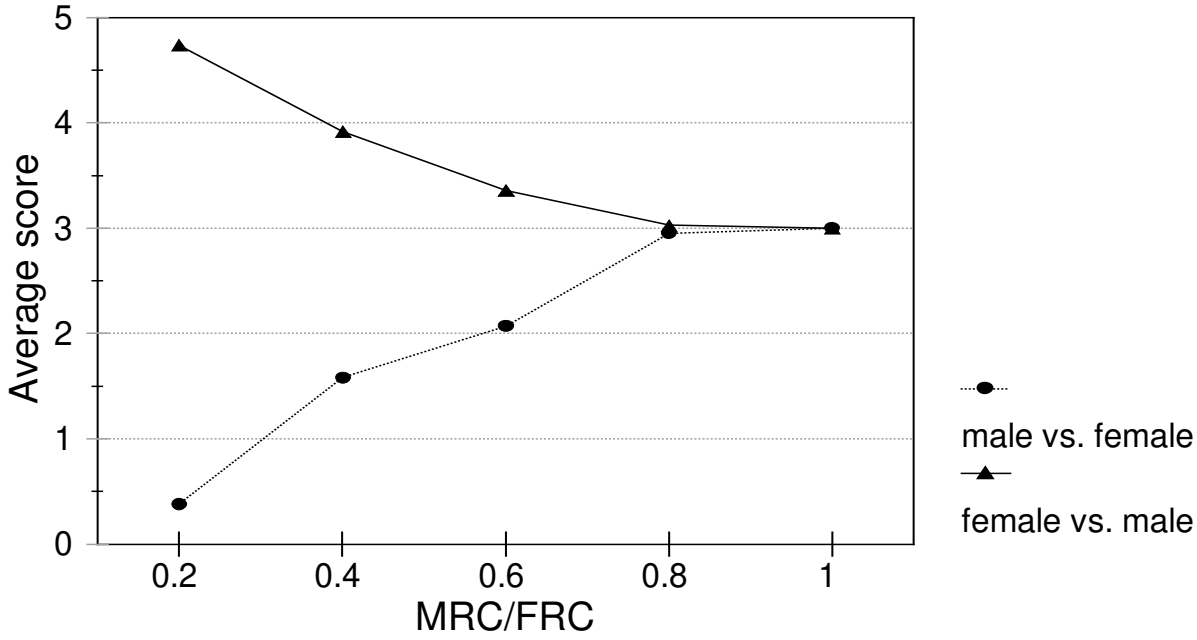

Figure 4: Summary of results for model 2. Each point represents the average score per player per game of Prisoner's Dilemma over 30 simulations.

those for model 1. As before, this results section will focus only on mixed sex interactions, for more information on same sex interactions see Key (1998) or Key and Aiello (in press).

Figure 4 shows how the average score for mixed sex interactions varies with the ratio of MRC to FRC. The greater the difference in male and female costs the greater the divergence in their average scores. For instance, when FRC = 1000 and MRC = 200 (MRC/FRC = 0.2) females gain, on average, 4.74 points from their games against males whilst males receive just 0.38 points in return. In 73% of these simulations males always co-operated whilst females always defected, giving females 5 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 altruism. In the other 27% of experiments non-reciprocal altruism of the type described in Model 1 evolves. 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 and FRC = 1000, 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 behave as non-reciprocal altruists in 40% of experiments. Only at MRC = 800 do the scores even out, where both sexes play a strategy of reciprocal altruism.

Model 1 suggested that non-reciprocal altruism could evolve, even when interactions and reproduction are not linked, if male reproductive costs are very low compared with female costs. Model 2 shows that when the interaction and reproduction phases of the model are linked, there is strong selection for non-reciprocal altruism, even when male reproductive costs are quite high (60% of female reproductive costs). The important issue here is paternity certainty. In the first model, there was little chance that males, by playing non-reciprocal altruism, were investing in their own offspring: i.e. paternity certainty was low. In the second model paternity certainty is much higher: the chances that males will reproduce with the females they interact with is just over 50% (Key 1998). Thus the combination of higher paternity certainty (around 50%) and high female reproductive costs, in comparison to males, strongly selects for the evolution of non-reciprocal altruism, or male care.

7. DISCUSSION

Individual differences, for instance in age, sex or rank, are likely to affect the types of co-operative strategies that individual's employ. This paper has focused on how sex differences in the energetic cost of producing offspring can influence co-operation. Varying the costs of reproduction for males and females promotes the evolution of a wide range of different strategies, some of which have been discussed here. Perhaps the most interesting of these is non-reciprocal altruism, in which males invest in females and their offspring at a cost to themselves in terms of time, energy and (implicitly) lost mating opportunities. This strategy is analogous to male care giving. Non-reciprocal altruism only evolves when male reproductive costs are less than female reproductive costs. The exact nature of this relationship is determined by paternity certainty. When paternity certainty is low

(model 1) males will only behave as non-reciprocal altruists when MRC is less than or equal to 10% of FRC. As paternity certainty increases (i.e. the probability that a male will mate with the female with whom he is co-operating increases), then non-reciprocal altruism becomes a more robust strategy. In model 2, in which paternity certainty is around 50%, non-reciprocal altruism evolves even when MRC is 60% of FRC. Model 2, in which interactions are reproduction are linked, may be especially useful in studying co-operation in primates, who have long life-spans and usually live in social groups in which males and females spend long periods in close association. The primate literature suggests that, even in species which are not usually monogamous or polyandrous, males may use co-operation with females to secure mating opportunities. Stanford *et al.* (1994) have shown that the presence of oestrus females is the best predictor of hunting behaviour in male chimpanzees, who then share any meat caught with the females. In addition, bonobo males are known to give food to females immediately after, or even in the midst of intercourse (Kuroda 1984; de Waal 1987). Baboon males are known to form special friendships with females, helping them in the care and protection of offspring in the expectation of future matings (Smutts 1985).

Most field studies on co-operation have focused on either reciprocal altruism or kin selection (for a review, see Dugatkin 1997). The possibility that other types of co-operative strategies are possible, such as non-reciprocal altruism, has not been properly recognised. However, de Waal (pers. comm.) has suggested that this model may help to explain observations of male co-operation in capuchins. De Waal and his co-workers (1993) 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 discriminatingly than females, and that their sharing is not necessarily mutual" (de Waal 1997 p.376). 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 practice 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.

The models developed here suggest that the key to understanding the evolution of male care, is the difference in reproductive costs for males and females. Under what circumstances is the male cost of reproduction less than the female cost of reproduction? This is a difficult question to answer, not least because it is by no means clear what the real costs of reproduction are, and how they should be measured. Key (1998) looked at sex differences in the *energetic* cost of producing offspring. The energetic cost of reproduction is defined as the sum of the energetic costs of all activities which contribute to the production of a single surviving offspring. For females these costs are likely to be high, due to the energetic costs of gestation and lactation. Energetic costs for males may also be high, due to the demands of mate-guarding, courtship and male-male competition. In many cases, high levels of male-male competition are manifest in the much larger body size of males, and maintaining this large body is energetically expensive.

Key and Ross (submitted) assessed the energetic cost of reproduction for male and female primates using a variety of data: body mass, activity patterns, gestation length, lactation length and inter-birth interval. We found that sex differences in body mass are the best predictor of sex differences in energetic costs. In species such as the gorilla, in which males are 60% larger than females, the energetic costs of reproduction are almost identical for males and females. That is, the energetic costs of gestation and lactation for females are matched by the energetic costs to the male of maintaining a large body size. However, in species in which males and females are of similar size, female energetic costs exceed those of males. This is because females must meet the direct energetic demands of reproduction over and above the energetic costs of body maintenance which will be similar for each sex. Therefore, if the models presented here are correct, male care giving is expected in those species in which male and female body size are similar. This is exactly what happened in primates: low sexual dimorphism in body mass is strongly correlated with male care giving (Key 1998: chi-squared test, $p < 0.05$, $n = 40$). Of course, a correlation does not necessarily indicate a causal relationship, and the interactions between body size dimorphism and breeding systems are likely to be complex. Changes in body size dimorphism may arise due to changes in male and/or female body size (Martin *et al.* 1994) for instance due to changes in male-male competition, age at maturity, age a first reproduction or for thermoregulatory reasons. Whatever the cause, these results point to the possibility that changes in body size can shift the balance of energetic costs between the sexes, and thus provoke changes in reproductive strategy.

This paper has combined data and ideas anthropology, genetic computation, game theory and theoretical biology in order to take a new look at the evolution of male care giving. It has been shown that male care giving is most likely to evolve when female energetic costs are high relative to male energetic costs. Preliminary analyses using primate data suggest that female energetic costs exceed those of males in species in which males and females are of similar body mass. Since there is also a close relationship between low sexual dimorphism and the incidence of male care, this offers some tentative support to the idea that sex differences in energy expenditure do have an affect on the breeding system. Further research into sex differences in energy

expenditure in living populations, and the relationship with behaviour, are required to more rigorously test these models.

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