

# Sexual Selection of Co-operation

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**Abstract.** Advocates of sexual selection theory have argued that various male traits, such as male co-operative behavior towards females, can evolve through female preference for mating with those males who possess that trait. This paper reports on the results of a simulation performed to test the hypothesis that female preference for mating with co-operative males can lead to an increase in the proportions of males in a population who co-operate with females. We simply model the sex differences using a single variable measuring the cost of reproduction. Our results show that even in such a simple environment there are a large number of interacting variables, which complicate the relationship between the sexual selection of co-operative males by females and the proportion of males actually co-operating with females. In fact, in most situations we modeled, sexual selection of co-operative males by females ended up causing the proportion of females that co-operate with males to increase while the proportion of males co-operating with females showed no significant increase over the random selection experiments.

## 1 Introduction and Background

Co-operation is a fundamental part of the repertoire of animal behavior. It has been extensively documented among various social animals such as primates. Co-operative behavior has been observed between members of a group who defend themselves against predators (Corning 1998), between pair-bonded males and females, between parents and children, between infants and non-parent adults (Brown 1970), between challengers to the authority of the dominant male, and between second and third ranking males and the harem females (de Waal 1982, Noe 1992). Evolutionary theorists have identified a number of mechanisms that can confer evolutionary advantages to co-operating individuals in certain situations. However, none of these mechanisms can satisfactorily explain the prevalence of co-operation among a variety of animals in a variety of situations.

Theorists study this problem by using an abstract model known as the Prisoner's Dilemma (Hamilton 1964). Prisoner's Dilemma models a world in which two agents that have to decide whether to co-operate or defect without knowing about the other agent's decision. If both agents decide to co-operate then they get a reward  $R$ , if both

decide to defect then both get the mutual defection punishment  $P$ , if one decides to co-operate while the other defects then the defector gets the defection reward  $D$  while the co-operator gets the sucker's payoff  $S$ . When  $R > \text{average}(D, S)$  (e.g., as in Table 1) a game-theoretic analysis reveals that defection is the best strategy if the two players never have to play each other again. However, if the agents repeatedly play against each other, different results emerge. Robert Axelrod (1984) held two tournaments to find out the winning strategy in a repeated Prisoner's Dilemma game. He invited others to submit strategies for playing the game and ran the submitted strategies against one another in a round robin fashion to find out which strategy can earn the largest number of points. A strategy called Tit-For-Tat (TFT) turned out to be better than all other strategies including some selfish-looking strategies. TFT strategists start out co-operating and then do what the other player did on the previous move (Axelrod 1984).

**Table 1.** Common values used for the payoff in the Prisoner's Dilemma. The matrix entries list the player's payoffs as row column.

| Decision   | Co-operate | Defect   |
|------------|------------|----------|
| Co-operate | R=3, R=3   | S=0, D=5 |
| Defect     | D=5, S=0   | D=1, D=1 |

However, this does not explain how co-operation evolves in the first place. To answer this question, Axelrod and Hamilton (1987) set up a simulation in which they randomly generated 100 strategies, allowed them to play against one another. At the end of the playing phase, the relatively more successful strategies were allowed to reproduce while the less successful ones were not. The strategies of the offsprings were generated by crossing-over the strategies of the parents and through random mutation. Axelrod and Hamilton (1987) report that after a significant number of generations, co-operative strategies such as TFT come to dominate. However, subsequent detailed analysis of repeated Prisoner's Dilemma has shown that neither TFT nor any other pure or mixed strategy is evolutionarily stable (Nowak *et al.* 1995). Which strategy emerges as winner depends on the prevalence of the competing strategies in the population. This has lead researchers to consider other factors that can enhance the evolution of co-operative behavior. Key and Aiello (2000) hypothesized that the differences in male and *reproductive cost* may be responsible for evolution of co-operation in a mixed sex environment.

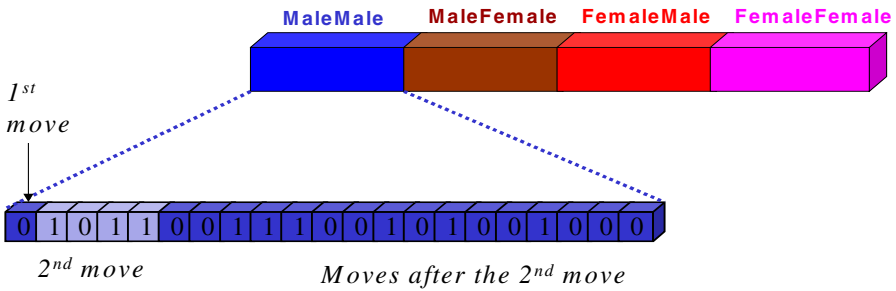
Trivers (1971) defines reproductive cost as the cost of reproduction measured to the extent that it detracts from an individual's ability to invest in future offspring. It consists of the parental investment and the mating costs. Parental investment measures the cost of parent's behavior that directly increases their offspring's reproductive success. For female mammals this includes the high cost of gestation, lactation, and rearing of the offspring. Mating costs are also significantly higher for females (because of the relatively higher costs of producing an egg, and not being able to reproduce while carrying a fetus to term). However, males spend more energy on maintaining their relatively larger bodies and on acquiring mates to reproduce with.

Key and Aiello (2000) modified Axelrod and Hamilton's simulation set up so that the agents were divided into two groups; males and females. The only difference between a male and a female agent was their cost of reproduction. The sex of each one of the 650 players was selected randomly and in most trials roughly half of the agents were males and the other half females. Similar to Axelrod and Hamilton's simulation, initial strategies of the players were randomly selected. A number of rounds of prisoner's dilemma games were played. In each round, two random players (regardless of their sex) were chosen to play prisoner's dilemma game a fixed number of times. However, only relatively successful players of opposite sex were allowed to mate to reproduce off springs. Key and Aiello (2000) ran their simulation by varying the male reproductive cost (MRC) from 1 to 600 and keeping the female reproductive cost (FRC) fixed at 1000. They concluded that at low costs of reproduction, males co-operate more with females than females do with them.

However, Key and Aiello's agents were not able to choose their mates. Mate selection is known to be significant factor affecting the evolution of various male traits. In a number of bird species, females are known to select males by visiting them at their special gathering places (known as leks) where males gather to show off their capabilities. Sexual selection of males by females has been used to explain various male features such as a male peacock's tail, and even speciation itself (Darwin 1900). Recently, some researchers (Miller 2000, Tallamy 2000) have argued that co-operation among males may also have evolved through sexual selection by females. This paper reports on a simulation based study we performed to test the hypothesis that female preference for mating with co-operative males can enhance the evolution of male co-operative behavior.

## 2 Experimental Setup

Our model involved building a heterosexual population of 100 agents. Each agent was modeled as a Java object with the attributes of sex, reproductive cost, and four 21-bit binary strings encoding the game playing strategy of the player. As shown in Fig.1, the first 21-bits of the 84-bit strategy string are used to encode the strategy that is to be used when a male is playing against another male. The second part when a male is playing against a female, the third when a female is playing against a male and the final part to cover the situations in which a female is playing against another female. If the first bit of the 21-bit string is 1, the player co-operates with its opponent on the first move and defects otherwise. On the second move, the player uses the knowledge of its own last move and its opponent's last move to decide what to do. Since, there are four possibilities (both co-operated, both defected, it co-operated and the opponent defected, it defected and the opponent co-operated) the second move strategy requires 4-bits to encode. Similarly, the player uses the knowledge of its own last two moves and its opponent's last two move to decide what to do on the third and the following moves. This means that 16-bits are needed to encode the strategy for the third and the following moves. As shown by Ikegami (1994), this two-step history is all that an agent needs to encode in order to learn a strategy.



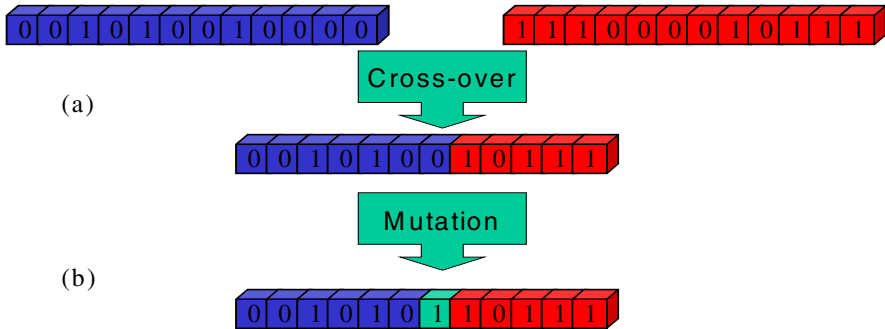
**Fig. 1.** 84-bit strategy string encoding a player's strategy for playing Prisoner's Dilemma game in a mixed sex environment.

The sex of an agent was randomly chosen to be male or female. Game playing strategies of the first generation of agents were also randomly generated. Next, two players were randomly selected to play 100 rounds of Prisoner's Dilemma game. After 150 game playing rounds, relatively successful players of the opposite sex were allowed to mate and reproduce children. Strategies of the off springs were produced by crossing over the strategies of their parents and through random mutation as shown in Fig. 2. The chances of a strategy gene randomly mutating from 0 to 1 or vice versa were 1 in 5000. Similar to Key and Aiello's experiments, the only difference between a male and female agent was the cost of reproduction. We ran the experiment by varying MRC from 1 to 1000 and keeping FRC fixed at 1000. The metrics we measured were the proportion of males and females receiving co-operation and defection from players of the same and opposite sex.

Similar to Key and Aiello (2000), interactions of a the players of a sex  $G$  with a player  $A$  were deemed co-operative if the average number of points per game gained by player  $A$  from players of sex  $G$  (i.e., sum of the points obtained by  $A$  from players of sex  $G$  divided by the number of Prisoner's Dilemma games  $A$  played with players of sex  $G$ ) exceeded 2.25. If  $A$  obtained less than 2.75 points per game from players of sex  $G$ , the players of sex  $G$  were considered to have been weakly co-operative to  $A$ . If  $A$  on the other hand, fared less than 1.75 points per game with players of sex  $G$ , its interactions with players of sex  $G$ , were considered to have been dominated by defections. Those managing between 1.75 and 2.25 points per game from players of sex  $G$  were considered to have received weak defections from players of that sex. During each experiment, we computed the proportion of males and females who received co-operation/weak-co-operation/defection/weak-defection from players of the same and the opposite sex. The experiment was run 20 times and the average proportions calculated.

We performed this experiment with two mate selection strategies; random selection and selection of most co-operative male by females. In the first experiment, females randomly selected a male agent to mate with. In the second experiment, a female preferred to mate with the male player who had been the most co-operative to her during their game playing round. If the most co-operative player was not able to mate (because of not having accumulated enough points to mate), the next most co-

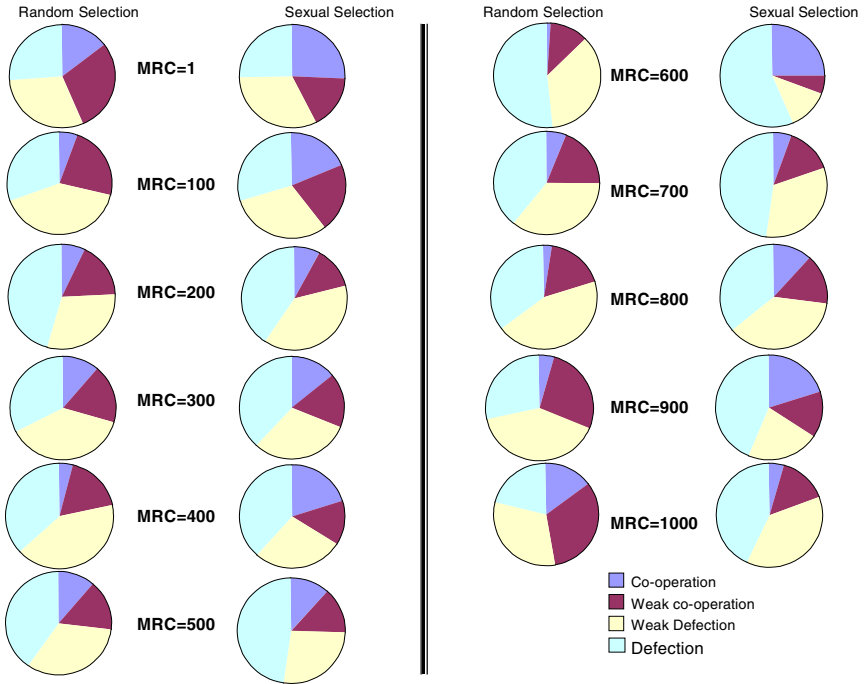
operative player was chosen. The purpose of conducting these two experiments was to test the hypothesis that males co-operate significantly more with females when females sexually select males for co-operation. We performed t-tests to see if the differences between the mean proportions obtained from the two experiments indicated two different distributions and if the mean proportion of the females receiving co-operation from males in the sexual selection experiment was significantly (with 0.05 being the level of significance) larger than the mean proportion of females receiving co-operation from males in the random selection experiment.



**Fig. 2.** (a) A random partition point  $P$  between 1 and the length of the strategy string  $N$  is selected and the first  $P$  bits are copied from the first string while the remaining  $N-P$  bits are copied from the second bit-string to create the cross-over bit-string. (b) A random bit location  $L$  is selected. Another random number  $R$  between 1 and 5000 is generated. If  $R$  equals 2500 the value of the  $L$ th bit is flipped from 1 to 0 or vice versa.

### 3 Results and Analysis

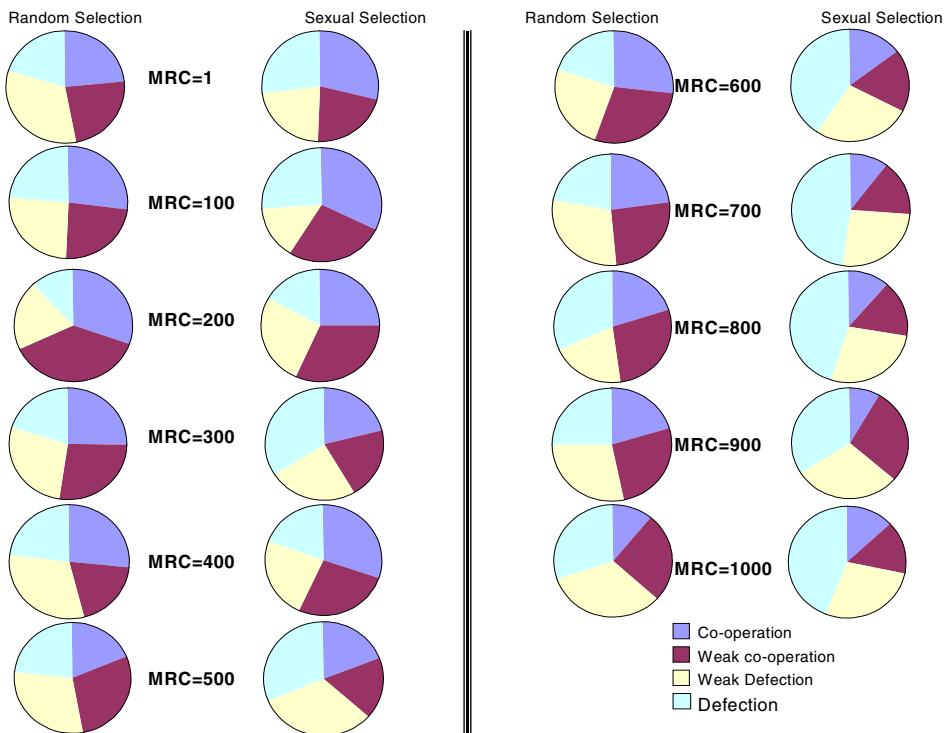
Fig. 3 and Fig. 4 show the mean proportion of males who receive co-operation/weak-co-operation/weak-defection/defection from other males and females under the random selection and sexual selection conditions for various values of MRC. Fig. 5 and Fig. 6 show the mean proportion of females who receive co-operation/weak-co-operation/weak-defection/defection from males and from other females. The results show that in the random selection experiments, males and females co-operate more with members of the opposite sex than they do with members of the same sex. Similarly, when females randomly select mates, they receive more co-operation from males than they offer in turn (especially at low values of MRC) i.e., at low values of MRC males can afford to be suckers. This confirms the results obtained by Key and Aiello (2000).



**Fig. 3.** The mean proportion of males in the 100<sup>th</sup> generation who co-operate/weakly co-operate/defect/weakly-defect with other males in random and sexual selection experiments for various values of MRC.

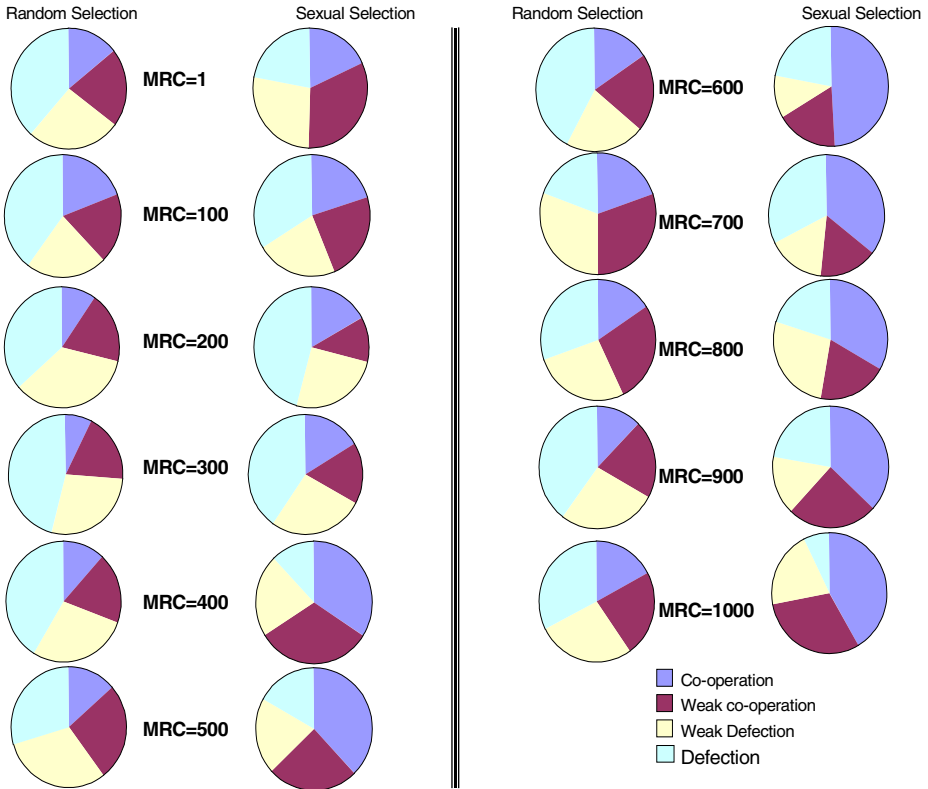
Comparing the sexual selection experiment results with random selection results shows that sexual selection of co-operative males by females results in an increase of co-operation between members of the same sex for most values of MRC. However, co-operation between members of opposite sex increases under some conditions while it decreases under different conditions. At very small values of MRC ( $MRC < 200$ ) proportion of females receiving co-operation from males increases as predicted by the null hypothesis but then it declines as MRC increases further. We performed t-tests to see if the increase in male co-operation with females was statistically significant. The graph shown in Fig. 7 plots the t-test values of the difference in the proportion of males co-operating with females between the sexual selection and the random selection populations. The t-test values initially increase and then drop but the increases are not statistically significant at any point. These results contradict our null hypothesis that the sexual selection by females of the most co-operative mate leads to a significant increase in the proportion of females receiving co-operation from males.

The main reason why the proportion of males co-operating with females does not increase (especially at large values of MRC where it actually decreases) is that the male population in the sexual selection environment faces two conflicting selection pressures. Besides the selection pressure exerted by female selection favoring cooperative males, value of male reproductive cost (MRC) also exerts a selection pressure by allowing only those males to mate and pass their genes if they have collected enough points during their game playing phase. The reproductive cost pressure selects for those males who have more competitive strategies and are better point collectors. The two selection pressures would pull in the same direction if co-operation with females also improved a male player's point collection. This would happen if all females adopted reciprocal co-operation strategies (such as tit-for-tat) in which female co-operation with males depended on male co-operation with them.



**Fig. 4.** The mean proportion of males in the 100<sup>th</sup> generation who co-operate/weakly co-operate/defect/weakly-defect with females in random and sexual selection experiments for various values of MRC.

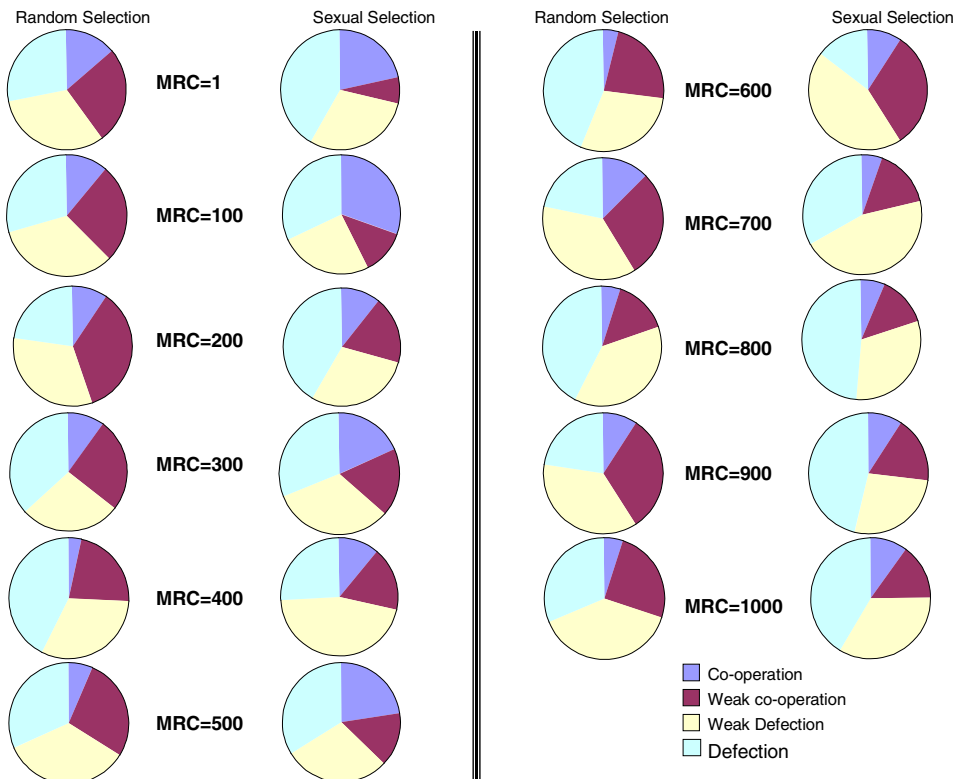
Increase in co-operation by males in response to other simple female strategies such as always co-operate or always defect would decrease a male's point collection and hence the two selection pressures will pull in the opposite directions. When the two



**Fig. 5.** The mean proportion of females in the 100<sup>th</sup> generation who co-operate/weakly co-operate/defect/weakly-defect with males in random and sexual selection experiments for various values of MRC.

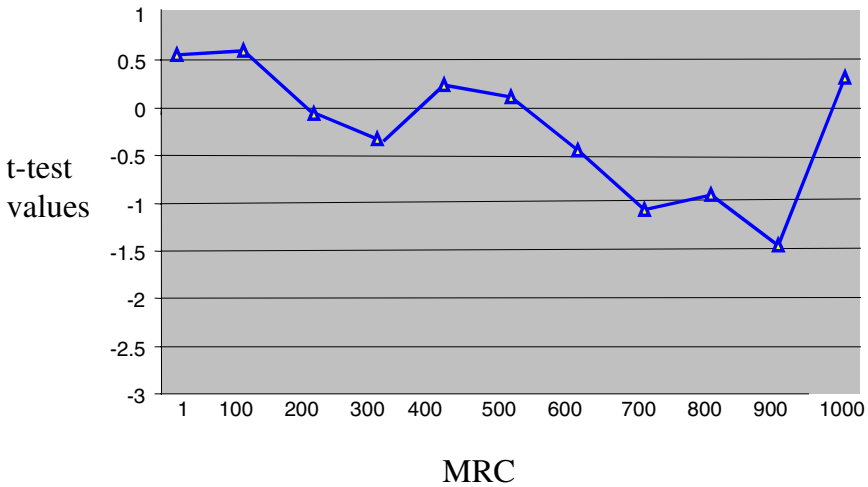
pressures select for different strategies more complicated interactions ensue. However, even when both selection pressures favor more co-operative male strategies, males may never evolve to adopt the strategy of “always co-operate with females”. This is because such strategies are not evolutionarily stable. If males become mostly co-operative towards females, females would learn the strategy of always defect because that allows them to collect more points. Females have a stronger selection pressure on them to be competitive because of a higher reproductive cost in most cases. Faced with the “always defect with males” strategy, reproductive pressure on males will favor “always defect with females” strategy which runs counter to the co-operative strategies favored by sexual selection pressure. When male reproductive cost is low, male co-operation with females will arise because the sexual selection pressure dominates the reproductive selection pressure. This is what happens as the graph in Fig. 7 illustrates. However, as the male reproductive cost increases, co-operative males despite being favored by the females are simply not able to collect enough points to enable them to mate and propagate their genes.





**Fig. 6.** The mean proportion of females in the 100<sup>th</sup> generation who co-operate/weakly co-operate/defect/weakly-defect with other females in random and sexual selection experiments for various values of MRC.

There is another solution to the male point collection problem namely to collect more points from other males to compensate for the loss of points that males incur by becoming more co-operative with females. As Fig. 3 shows, this is indeed what happens; male-male co-operation increases at most points. Female-female co-operation also increases at most points as shown in Fig. 6 because females also need to compensate for the loss of points resulting from a drop in male co-operation. However, regardless of how competitive females are against other females, they cannot obtain all their points from females simply because players cannot select the sex of their opponent during the game playing phase (which is done randomly). The reproductive cost selection pressure assures that females must be good at collecting point from both males as well as females. Even though males become less co-operative in the sexual selection population than they were in the random selection population, they are still more co-operative to females than females are to other females.

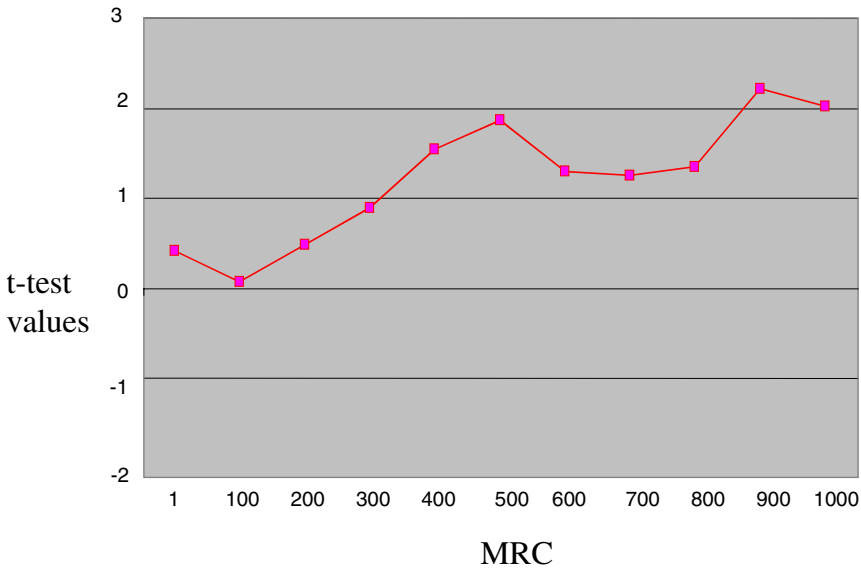


**Fig. 7.** Student t-test values for the difference between the mean proportion of males cooperating with females between the sexual selection and the random selection population plotted against the value of MRC varied from 1 to 1000.

As male strategies become more competitive, they evolve from being mostly co-operative towards females to more complicated strategies such as reciprocal co-operation strategies that co-operate with only those females who co-operate with them. This means that female strategies of mostly defection gather less points. This means that females must co-operate more with males in order to gain points from them. This is what happens as shown in Fig. 5. Initially, at very small values of MRC ( $MRC < 200$ ) as the male co-operation with females increases (as discussed earlier) female co-operation with them declines. However, at larger values of MRC, as male strategies become more competitive, female co-operation with males increases. We performed t-tests to see if the increase in female co-operation with males in the sexual selection population over the random selection population was statistically significant. As Fig. 8 shows, the t-test values are above the 0.05 threshold at most points (especially at points with larger values of MRC). This shows that there is an emergent selection pressure on the female population favoring those females who are more co-operative to males even though no such selection pressure were explicitly programmed (nor expected when we began this study).

## 4 Conclusion

Advocates of sexual selection theory have argued that various male traits such as male co-operative behavior towards females can evolve through female preference for males who co-operate with them. This paper presents the results of simulation experi-



**Fig. 8.** Student t-test values for the difference between the two population means plotted against the increasing value of MRC from 1 to 1000.

ment we performed to test this hypothesis in a simple population of male and female agents only distinguished by their reproductive costs. Our results show that sexual selection of co-operative males by females does not lead to a significantly larger proportion of males co-operating with females. What we found instead was that it is the proportions of females co-operating with males that ends up increasing. It remains to be seen if these results will hold up in other environments such as n-person Prisoner's Dilemma and the game of Chicken (Nowak 1995).

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