

**THERE ARE MANY EVOLUTIONARY  
PATHWAYS TO COOPERATION**

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### Abstract

Current sociobiological discussions attribute the evolution of cooperation to only two main influences: kinship and reciprocity. As a baseline, the paper analyzed the extent of cooperation achieved in three important 2x2 payoff environments (Prisoners' Dilemma, Chicken, and Tender Trap) under the two simplest "rules of the game" or protocols of play (single-round simultaneous-move and single-round sequential move). Kinship promotes cooperation beyond these base levels, to a degree, by modifying payoffs of selfish versus unselfish behaviors. Reciprocity may also promote cooperation, but its expression requires protocols of play that widen available strategy sets (in comparison with the underlying 2x2 payoff matrices). Once payoff modifications and/or more elaborate protocols are allowed, many other pathways to cooperation are opened up as well. Among them are punishment options, complementary strategy mixes, recognition effects, coordination using external clues, and group selection.

## THERE ARE MANY EVOLUTIONARY PATHWAYS TO COOPERATION

A key question for all the social sciences is why cooperation occurs in some contexts but not in others. Cooperation poses an especially pressing challenge for sociobiology, founded as it is upon the central principle of the selfish gene -- that the elements of our genetic heritage have been selected solely for strictly self-interested reproductive survival. The issue is, how can unselfish genes out-compete selfish ones? Or put another way, how can selfish genes translate into unselfish organisms?<sup>1</sup>

A somewhat impoverished view of this profoundly complex problem has become current in the sociobiological literature. To wit, that genetically driven cooperation stems, almost entirely, from only two sources: kinship and reciprocity.<sup>2</sup> As against this restrictive view, my main intention here is to indicate the richness and daunting complexity of the overall project: explaining the evolutionary sources of cooperation among living beings. First, I provide an interpretation of how evolutionary selection leads to subtly different kinds and degrees of cooperation in a variety of different payoff environments and under differing protocols or "rules of the game". In doing so I will compare evolutionary selection with self-interested rational choice as an alternative process that also might conduce to mutually helpful behavior.<sup>3</sup> Next I review how kinship and reciprocity sometimes do contribute to the evolution of cooperation, but sometimes do not. Finally, without attempting an overview of all possible pathways, I shall describe just a few of the many routes to cooperation that need not involve kinship or reciprocity.

### I. COOPERATION AND HELPING IN ALTERNATIVE SOCIAL CONTEXTS

On the level of unilateral action, the kind of behavior that needs to be explained is best described by the psychologically neutral word helping. A pattern of mutual helping among two or

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<sup>1</sup> Classic treatments include Dawkins [1976] and Trivers [1985]. An important recent discussion is Ridley [1996].

<sup>2</sup> E.g., Ridley [1996]. Some authors admit a third force, parental manipulation: parents, aiming at their own evolutionary advantage, may manipulate offspring to act unselfishly toward one another (Alexander [1974], West Eberhard [1975], Trivers [1985], Ch. 7). Parental manipulation is however only a special kind of kinship effect. A few sociobiological researchers (e.g., Tooby and Cosmides [1988]) have at times proposed a number of other influences. In contrast, social scientists in other disciplines generally recognize a wide range of bases for pro-social behaviors. One attempt to connect these up with sociobiological considerations is Hirshleifer [1982].

<sup>3</sup> It might be thought that, since the realms of evolutionary selection and rational choice do not ordinarily overlap, no actual choice can be exercised between them. Still, in certain contexts -- for example, software design -- in the search for efficient programs researchers could and indeed have intentionally used evolutionary selection as an alternative to explicit optimization.

more parties constitutes cooperation. (An unfortunate rhetorical tradition in the sociobiological literature confounds helping, an action, with altruism, which properly speaking refers to motivation. A person can have altruistic motives without engaging in helpful acts, owing perhaps to their high cost or insufficient effectiveness. Conversely, aid might be provided for any number of reasons apart from friendly feeling.)

Helping that is merely incidental to self-interested behavior must be distinguished from assistance to others that is actually costly to the donor. It might seem that costly helping necessarily requires altruistic motivation. But, as will be seen, this is not always the case.

The matrices in Table 1 are numerical instances<sup>4</sup> of social contexts in which greater or lesser degrees of cooperation might be achieved. Two familiar payoff patterns appear, Prisoners' Dilemma (PD) and Chicken (CH), together with one other called Tender Trap (TT).<sup>5</sup> Letting  $a_{ij}$  and  $b_{ij}$  be the Row and Column players' payoff elements in the cell located at the  $i$ -th row and  $j$ -th column, these matrices display a pattern of symmetry such that  $a_{ij} = b_{ji}$ . Thus the Row and Column roles can be transposed.

[Table 1 about here]

The three matrices illustrate characteristic social problems. Prisoners' Dilemma hardly needs explanation: it represents situations where the players could choose helpful behaviors to their mutual advantage, yet, in terms of unilateral decisions, each is motivated to defect. In the Chicken environment the parties might also cooperate by coordinating on different actions, a kind of complementary division of labor, but the payoff from doing so is asymmetrical. In the hope of getting the better of the bargain each side is tempted to behave aggressively, yet to some extent is deterred by the severe penalties suffered when both sides are too assertive. In Tender Trap, cooperation requires adopting the same action. Here interests are pretty much in harmony, yet unilateral decisions in ignorance of one another's choices may not achieve the needed coordination.<sup>6</sup>

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<sup>4</sup> The specific numbers in the Prisoners' Dilemma matrix are those used in the famous tournaments conducted by Robert Axelrod (Axelrod [1984], p. 8). The numbers in the other two matrices have been designed to correspond.

<sup>5</sup> Tender Trap (Hirshleifer [1982], p. 14) somewhat resembles other payoff patterns known as the Assurance Game and Stag Hunt.

<sup>6</sup> Many more payoff environments exist than the very few considered here. Even counting only the matrices with four distinct levels of payoff to each player -- i.e., excluding ties -- there are 78 essentially distinct 2x2 patterns (Rapoport and Guyer [1966]). Allowing for ties increases the number substantially, and the range of possibilities becomes mind-boggling when more strategy options are allowed (e.g., 3x3 matrices). And of course all this is within the context of two-party games; with three or more players the range of possible situations increases almost unimaginably. ("Parental

Figure 1 illustrates the associated opportunity sets. In each diagram the four labeled nodes correspond to the cells of the associated payoff matrix, that is, to the pure-strategy outcomes. The convex hull bounding the nodes indicates the expanded set of outcomes attainable when mixed strategies are also considered.

[Figure 1 about here]

Full cooperation can be regarded as attaining one or more of the Pareto-efficient outcomes, shown diagrammatically by the northeast boundary of the convex hull. There will always be a unique symmetrical "most cooperative" outcome, for example the (5,5) payoff point in the TT diagram.

As for helping, in Prisoners' Dilemma Row's first strategy  $R_1$  is always "more helpful" to his opponent than  $R_2$  -- since, whatever her strategy might be, Column does better when Row chooses  $R_1$  rather than  $R_2$  -- and similarly Column's  $C_1$  is "more helpful" to the Row player than  $C_2$ . This nice separation holds also for Chicken, but not for Tender Trap. In TT when Column is playing her first strategy  $C_1$ , Row's  $R_1$  is "more helpful" than  $R_2$  -- but when Column is playing  $C_2$  the reverse is true. The matrices of Table 1 have been set up so as to make the move-pair  $[R_1, C_1]$  be the symmetrical "most cooperative" choices in each case.

So, even avoiding the unfortunate term "altruism", the psychologically neutral concepts of helping and cooperation remain somewhat soft around the edges. Still, the meanings are clear enough in many important contexts, and in others they retain at least suggestive validity. I will therefore continue to use these terms, indeed one could hardly do without them, but keeping the possible ambiguities in mind.

## II. OPTIMIZATION VERSUS SELECTION: ONE-ROUND SIMULTANEOUS-MOVE PROTOCOL

The question addressed here is: Can evolutionary selection simulate, replace, or surpass self-interested rational optimization in leading to cooperative outcomes? Despite their limited mental powers, "lower" animals often display impressive patterns of teamwork. And perhaps the cooperation

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manipulation", as described in an earlier footnote, is an example of an interaction involving at least three parties: one parent and two offspring.)

Within the set of two-person 2x2 matrices, the symmetry restriction reduces the number of possibilities. On this basis, and ruling out certain other patterns as well, Heckathorn [1996] boils down the number of patterns to just five -- essentially our three, plus two others that could not be covered here. (In contrast, when it comes to explicit game-theoretic modeling, with a few important exceptions the sociobiological literature deals only with the Prisoners' Dilemma environment.)

observed among humans may stem more from evolutionary selection for "instinctive" behaviors than from calculated rational choices. I will be emphasizing that the relative efficacy of rationality and selection varies depending upon the environmental context (the pattern of payoffs) and also upon the operative "rules of the game" (the protocol).

Starting with the evolutionary mechanism, think of populations of self-interested players randomly encountering one another in alternative payoff environments represented by the PD, CH, and TT matrices in Table 1. And suppose that, in each one-on-one meeting, the protocol of interaction dictates single-round simultaneous-move choices by the Row and Column players. (Other possible protocols will be considered later on.)

The basic principle of evolutionary selection is that more successful strategies multiply, while less successful ones suffer reduced representation within the population. An evolutionary equilibrium (EE) is achieved when, for a given strategy or combination of strategies (the "incumbents"), no other strategies (the "mutants") can successfully invade.<sup>7</sup>

For each matrix of Table 1, let  $\alpha$  be the average payoff over all the individuals following the first strategy and  $\beta$  be the corresponding average payoff for the second strategy. Also, let  $p$  be the fraction of the population following the first strategy. The first strategy will tend to proliferate within the population when  $\alpha - \beta > 0$ , where:<sup>8</sup>

$$(1) \quad \begin{aligned} \alpha &\equiv pa_{11} + (1-p)a_{12} \\ \beta &\equiv pa_{21} + (1-p)a_{22} \end{aligned}$$

For the numerical matrices of Table 1, the associated courses of evolutionary development are pictured in Figure 2. The arrows indicate the direction of movement from any momentarily given level of  $p$ . The evolutionary equilibria pictured in Figure 2 are summarized in the first columns of Table 2.

[Figure 2 and Table 2 about here]

In Prisoners' Dilemma  $\alpha - \beta$  is always negative, hence (as indicated by the arrows) the

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<sup>7</sup> What is here termed evolutionary equilibrium is often referred to by biologists as an Evolutionarily Stable Strategy (Maynard Smith [1982]). The EE terminology is preferable; only in special cases does the equilibrium take the form of a single strategy engaged in by all members of the population.

<sup>8</sup> The symmetry assumption permits us to employ only the  $a_{ij}$  parameters in these equations, omitting Column's  $b_{ij}$  payoff elements.

population inevitably evolves toward an EE at  $p = 0$  -- the familiar PD "trap" -- regardless of the starting point. In each interaction the players end up at the move-pair  $[R_2, C_2]$ , so the mean payoff is 1. Thus, under the assumed protocol, the evolutionary equilibrium for PD excludes both cooperation and helping.

For Chicken the "more cooperative" (first) strategy has higher mean payoff when it is relatively rare (when  $p$  is low) while the reverse occurs when it is numerically more common (when  $p$  is high). Consequently, as the arrows indicate, regardless of the starting point the progression will be toward an interior evolutionary equilibrium at point K where the two strategies are equally profitable:  $\alpha - \beta = 0$ . At this EE a fraction  $p^*$  of the population will be using the first strategy and the remainder the second strategy. Numerically here,  $p^* = 1/3$ . The average payoff to each strategy, and therefore for the population as a whole, is  $5/3$ .

Finally, Tender Trap is the evolutionary reverse of Chicken: now either strategy becomes the more profitable when it is sufficiently popular. The crossover point L occurs numerically at  $p = 3/7$ . So, as the arrows indicate, there are two possible corner EE's. Depending upon whether the starting point is to the right or the left of L in Figure 2, the evolutionary outcome will be the "more cooperative"  $[R_1, C_1]$  strategy combination at point F with payoffs of 5 for each player or the "less cooperative" combination  $[R_2, C_2]$  at point G with payoffs of 3. (Note that the mixed population represented by point L is not an EE.)

To interpret these results in terms of achieved cooperation, it seems reasonable to choose as point of comparison the symmetrical most Pareto-inferior outcome within the opportunity set defined by the convex hull. Measured against this base point, the progress toward cooperation achieved by the evolutionary process under the assumed protocol can be summarized:

For Prisoners' Dilemma -- no progress at all:

At the EE the proportion making the more cooperative (first row or first column) move is  $p = 0$ .

For Chicken -- an intermediate degree of progress:

In evolutionary equilibrium the fraction choosing the more cooperative strategy is  $p^* = 1/3$ . The average payoff to each strategy of  $5/3$  is short of the symmetrical "fully cooperative" payoff of 3 but a considerable improvement over the symmetrical "most Pareto-inferior" payoff of 0.

For Tender Trap -- either full or partial cooperation:

If the initial situation is to the right of the cross-over point in Figure 2, in equilibrium everyone uses the first strategy with payoffs of 5 to each; otherwise, at the EE everyone uses the second strategy with payoffs of 3. In comparison, the "most Pareto-inferior" symmetrical payoffs are 0.5 to each -- midway along the line connecting the (1,0) and (0,1) points in Figure 1.

Thus, depending upon the payoff environment, greater or lesser degrees of cooperation can come about simply by evolutionary selection.

A comparison of these results with what would be achieved under the alternative "rationality mechanism" is provided in Table 2, taking the game theorists' Nash equilibrium (NE) as the standard of rational play.<sup>9</sup>

In Prisoners' Dilemma the unique NE is at the "trap" move-pair [R<sub>2</sub>,C<sub>2</sub>], which of course matches the EE at  $p^* = 0$ . So, in terms of achieved cooperation, the results are equally unsatisfactory under either mechanism.

For Chicken there are three NE's. The two solutions in pure strategies -- [R<sub>1</sub>,C<sub>2</sub>] and [R<sub>2</sub>,C<sub>1</sub>] -- are Pareto-efficient but asymmetrical. Of main interest to us is the symmetrical but Pareto-inefficient mixed-strategy NE. For the numerical payoffs of the CH matrix, this mixed strategy has each player choosing the more cooperative move with probability  $\pi = 1/3$  -- numerically the same as the proportion of the population who cooperate ( $p^* = 1/3$ ) in the corresponding EE solution. (In fact, for Chicken it is true generally that  $p^* = \pi$ .)<sup>10</sup> And so once again the two mechanisms arrive at essentially equivalent levels of cooperation, in this case intermediate between full cooperation and none.

For Tender Trap the two symmetrical NE's in pure strategies evidently match up with the corresponding EE's in Table 2. But whereas the "evolutionary mixture" corresponding to point L in Figure 2 was not an EE, the corresponding symmetrical mixed strategy is an NE with  $\pi = 3/7$ , the level of efficiency being lower than at either of the two pure-strategy solutions. It appears that here again the evolutionary process seems to do at least as well as the kind of rationality associated with the

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<sup>9</sup> At a Nash equilibrium, each player's choice is a "best response" to the opponent's strategy. I pass over some subtle intellectual issues about the nature of rationality and how it relates to the Nash equilibrium concept. One approach to the NE, in fact, justifies it not so much as the "eductive" outcome of rational play but rather as the "evolutive" consequence of a trial-and-error process (Binmore [1992]).

<sup>10</sup> In Chicken, at the cross-over proportion  $p^*$  the two strategies have equal payoffs. And it is a feature of all mixed-strategy Nash equilibria that each element of a player's mixture yields the same payoff -- else he would shift out of the mixture to whichever element thereof had highest payoff.



Nash equilibrium concept in game theory.

So, under the single-round simultaneous-move protocol, the two mechanisms -- rational optimization and evolutionary selection -- do about equally well in the PD and CH payoff contexts, while selection has perhaps an edge in the TT environment.

### III. KINSHIP EFFECTS

As has just been seen, a substantial amount of cooperation may -- the Prisoners' Dilemma apart -- emerge simply as a consequence of incidental helping. The next question is the degree to which kinship and/or reciprocity can induce even higher levels of mutual aid. Kinship effects will be examined in this section, and reciprocity in the next.

One of the key propositions of sociobiology is Hamilton's Rule (Hamilton [1964]): Evolutionary selection, other things equal, leads a Donor organism D to unilaterally aid a Recipient organism R if:

$$(2) \quad c_D/b_R = r_{DR}$$

That is, if the cost-benefit ratio is less than the relatedness  $r_{DR}$  of the parties. Cost  $c_D$  and benefit  $b_R$  are measured as increments to fitness (i.e., reproductive survival) of Donor and Recipient respectively. The biological logic is that the "gene for helping" is (so to speak) indifferent between the survival of its own host or the survival of an identical copy in the body of a related organism -- where relatedness measures the chance of an identical copy being present. (Such a gene, for example, instructs an animal to sacrifice its life, other things equal, to save two siblings, four half-sibs, eight cousins, etc.)

Since we are concerned here with the possible evolutionary emergence of additional helping, for any given payoff environment it is natural to take the evolutionary equilibrium EE of the previous section as base point. That leaves some residual ambiguity in the Chicken and Tender Trap environments, where the EE's may be mixed or non-unique. So let us start with Prisoners' Dilemma, where (at least for the simultaneous-move protocol) the EE is not only unique but represents a zero level of helping.

In the PD matrix of Table 1, a unilateral helping act on the part of Row could be interpreted as

a shift from the lower-right  $[R_2, C_2]$  cell with payoffs (1,1) to the upper-right  $[R_1, C_2]$  cell with payoffs (0,5): Row has incurred a cost of 1 while the benefit conferred on Column is 4. Then under Hamilton's Rule, Row would provide the helping act if and only if the relatedness of the parties exceeds  $1/4$ . Suppose we are dealing with a pair of siblings, for whom  $r = 1/2$  either way.<sup>11</sup> Then the same influence would be operative for Column as for Row. So the two would escape the PD "trap" and achieve the improved payoffs (3,3).

An economist might worry, however, whether a hypothetical "gene for helping" H would actually win out in evolutionary competition against the "gene for not-helping" NH. Might not the latter be able to free-ride on the former? Starting at the  $[R_2, C_2]$  base point, the NH strategy is the "incumbent" and the H strategy is the "mutant". Supposing the mutation took place in a parent, one's sibling has only a 50% chance of also carrying it. If the sibling in fact carries the NH gene, he can profitably free-ride and accept the lion's share of the (0,5) payoff after Row's helping act. So siblings bearing the NH gene would do very well indeed.

The difficulty is overcome once we appreciate that helping one's kin means that helping acts will be preferentially directed to fellow-carriers of the helping gene within the population as a whole. The H gene will indeed tend to lose sway within the family, but (if the condition is met) will nevertheless gain in prevalence within the population. To see this, let  $W_H$  and  $W_{NH}$  represent the "fitnesses" of the two genes, and define two new parameters:  $N$  is the population size, and  $m$  is the "discrimination factor" (that is, the proportion of helping acts received by fellow-helpers). Then, for the condition  $W_H > W_{NH}$  to be met, it must be that:<sup>12</sup>

$$(3) \quad -c + \frac{bmNp}{Np} > \frac{b(1-m)Np}{N(1-p)}$$

On the left-hand side,  $-c$  is the cost to the helper (assuming one helping act per unit of time). In the second term on the left, the numerator  $bmNp$  represents the aggregate benefit of helping acts per time-period that are directed at fellow-helpers, while the denominator  $Np$  is the number of helpers in

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<sup>11</sup> Relatedness  $r$  is ordinarily the same in either direction, though some organisms with unusual mating systems may be asymmetrical in this regard.

<sup>12</sup> This discussion is adapted from a development in Hirshleifer [1978], based upon Charnov [1977].

the population. The ratio of the two then shows the average per-helper benefit of helping acts, in fitness units per time-period. The right-hand side similarly shows the average per-non-helper benefit of having helpers in the population. Inequality (3) reduces to:

$$(4) \quad \frac{c}{b} < \frac{m-p}{1-p}$$

As a corollary, for costly helping to evolve, at least the condition  $m > p$  must be met: fellow-helpers must receive helping acts in bigger proportion than their representation in the population. Kin selection is a way of achieving this.

For siblings, and assuming that H is a new mutation in the parent, initially  $p$  is effectively zero in the population. If so, the probability that one's sibling also bears the H gene is one-half. As  $p$  goes to unity,  $m$  must also approach unity, in accordance with the algebraic relation:

$$(5) \quad m = \frac{1+p}{2}$$

Making this substitution in (4) leads directly to:

$$(6) \quad \frac{c}{b} < \frac{1}{2}$$

which is Hamilton's Rule (2) for siblings.

Generalizing, for any level of relatedness  $r$ , if the  $c/b$  ratio is sufficiently favorable the NH gene will eventually be swamped by organisms carrying the H gene.

In the Chicken and Tender Trap environments, since a positive level of incidental cooperation is achieved at the EE, the scope for improvement is not so great. Nevertheless, with appropriate changes, the argument above holds. For example, consider the environment represented by the Tender Trap matrix of Table 1, Under the simultaneous-move protocol one possible EE was the inferior  $[R_2, C_2]$  move-pair with payoffs (3,3). Bilateral helping means shifting to the Pareto-superior solution with payoffs (5,5), but could such a shift evolve thanks to kinship effects? Unilaterally, the cost of

helping is  $c = 3$  while the benefit to the other party is only  $b = 2$ . Since relatedness is necessarily less than unity, here kinship would not do the trick. (However, a somewhat more favorable TT matrix -- for example, if the payoffs at the upper left were (10,10) instead of (5,5) -- could reverse this conclusion.)

The upshot is that, in a variety of environments, the kinship factor can induce a higher level of cooperation than what could be achieved through merely self-interested helping. But of course, only when the  $c/b$  ratio is sufficiently low relative to the degree of relatedness  $r$ .

Next, although this consideration applies even beyond the context of helping due to kinship, it will be helpful here to bring in one other important factor: competition. The cost and benefit parameters  $c$  and  $b$  (and the payoff patterns from which they were derived) have so far been taken as given constants. But any fitness gain due to mutual helping would presumably lead to population growth, leading to increased pressure upon resources. The consequent intensification of rivalry could then be expected to affect the cost-benefit calculations adversely.

This influence of competition can be explored using a generalized helping/hurting rule (following West Eberhard [1975]):

$$(7) \quad \sum_{\text{losers}(i)} r_{iD} c_i < \sum_{\text{gainers}(j)} r_{jD} b_j$$

That is, a donor D will be motivated to take any action on the margin for which the relatedness-weighted sum of benefits exceeds the corresponding sum of costs, where  $i$  is an index running over all the losers whereas  $j$  is an index running over all the gainers. (The donor will count himself, with a relatedness of unity, on whichever side of the inequality is appropriate.)

Turning now to the constraints upon the costs and benefits dictated by pressure on resources, as an extreme absolute competition could be defined by the condition (Hirshleifer [1978]):

$$(8) \quad \sum_i c_i = \sum_j b_j$$

That is, the individuals are playing a constant-sum game.

In two-party absolute competition the ratio  $c_i/b_j$  is necessarily unity, so in such an environment we would not expect to observe costly helping even toward close kin. In fact, extreme

sibling hostility has been known to evolve -- for example, in bird species for whom within-nest competition is severe -- and possible human analogs come to mind.

Rewriting the generalized helping/hurting rule (7), where  $\bar{r}$  is the average relatedness of members of the population to the donor:

$$(9) \quad \sum_i c_i (r_{iD} - \bar{r}) < \sum_j b_j (r_{jD} - \bar{r})$$

So, under absolute competition, it is not simple relatedness but relatedness greater or less than the average in the population that serves as the factor weighting costs and benefits. Paraphrasing Hamilton [1970]: "Anyone is your enemy who is less closely related to you than the average in the population".

In sum, kinship effects do certainly tend to promote cooperation with close kin. But as competition intensifies, such helping diminishes; it may actually become selectively advantageous to injure not only strangers but more remote kin as well, even at some cost.

#### IV. RECIPROCITY AND OTHER SEQUENTIAL STRATEGIES

The discussion so far has analyzed three important payoff patterns, each representing a possible environment in which one-on-one interactions might take place, but under only a single protocol: single-round simultaneous-move play. Under that protocol there was no way for reciprocative behavior to express itself. In this section I will consider two (among an indefinitely large number of) alternative "rules of the game" that allow reciprocity to play a role.<sup>13</sup> The first to be considered is the simplest possible sequential arrangement: a single round, but now the players move in turn. Then the later-mover can adapt his choice in response to the opponent's earlier move in the same round. The other protocol to be examined involves simultaneous moves in any given round, but allows for an indefinitely large number of rounds. In that case a player's subsequent-round choices could be conditioned upon what the opponent has done in prior rounds.<sup>14</sup>

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<sup>13</sup> Comparative studies of different protocols are quite rare in the game-theoretic literature. One important exception is Brams [1993].

<sup>14</sup> Reciprocity brings to mind the institutions of contract and market exchange. These forms of interaction involve a variety of possible negotiation protocols too complex to be examined here. In addition, owing to the need for enforcement, contract and market exchange typically constitute games with three or more players and so are beyond the scope of the present paper. (Some further comments on negotiation and exchange will be offered below.)

Single-round sequential protocol:

The change from single-round simultaneous play to single-round sequential play opens up a surprising range of strategy choices. The earlier-mover still has only two options: the "more helpful"  $R_1$  or the "less helpful"  $R_2$ . (It will be assumed that the Row player has the earlier move.) The later-mover has four reactive options:

- i. Respond to  $R_1$  with  $C_1$  and to  $R_2$  with  $C_1$   
(always follow with the more helpful  $C_1$ )
- ii. Respond to  $R_1$  with  $C_1$  and to  $R_2$  with  $C_2$   
(echo the opponent's earlier move)
- iii. Respond to  $R_1$  with  $C_2$  and to  $R_2$  with  $C_1$   
(reverse the opponent's earlier move)
- iv. Respond to  $R_1$  with  $C_2$  and to  $R_2$  with  $C_2$   
(always follow with the less helpful  $C_2$ )

Since any individual might either be the earlier-mover or later-mover, there are in all eight possible sequential strategies.

In this context, reciprocity is represented by the strategy 1,ii: pick the "more helpful"  $R_1$  on the earlier move, and the echoing option ii on the later move.<sup>15</sup> Interacting with one another, reciprocative players would always end up at the move-pair  $[R_1, C_1]$  achieving payoffs (3,3) in PD and CH and payoff (5,5) in TT. I will be asking here, for the different payoff environments, whether reciprocative behavior is consistent with equilibrium under the rationality or the evolutionary mechanisms.

The "rational" game theory solution concept for this sequential protocol is subgame-perfect equilibrium (SGPE). The essential idea is that the player with the earlier move will choose his most profitable option, on the assumption that the reactive later-mover will similarly be choosing whatever is most profitable for herself when her turn comes up.

Table 3 indicates that, for Prisoners' Dilemma, the SGPE is 2,iv -- in short, never cooperate. Thus the adopted move-pair remains  $[R_2, C_2]$  with payoff 1 to each player. (Reciprocity behavior is an available strategy, but it is not consistent with self-interested rational play.) Despite the changed protocol, under the rationality mechanism the PD "trap" still grips as tightly as ever.

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<sup>15</sup> This form of reciprocity corresponds to the "Tit for Tat" strategy that has received a great deal of attention in the sociobiological literature (see below).

[Table 3 about here]

For Chicken the SGPE solution is 2,iii: as earlier-mover choose the less helpful option, and as later-mover always reverse the opponent's prior choice. In any single run of the game the result is asymmetrical, the earlier-mover having the advantage. But recall that each player is equally likely to be the earlier-mover or later-mover. Then, taking the average of the asymmetrical (5,1) and (1,5) payoffs, the mean return is 3 -- exactly the same as at the reciprocative outcome. This equivalence is however an accidental result of the specific payoff numbers used in the CH matrix of Table 1. If the payoffs in the upper-left cell were changed from (3,3) to say (2,2), the game would still be Chicken but the parties would now both do better under self-interested rationality than by following the reciprocity strategy! The opposite would hold if, say, the upper-left payoffs were changed to (4,4).

Finally, for Tender Trap, the SGPE is 1,ii. Here, under the assumed sequential protocol, reciprocity behavior coincides with rational self-interest, and leads to the unique "most cooperative" outcome with payoff 5.

Now let us turn to the evolutionary process. Having to deal with eight different strategies is more than a little troublesome. In addition to a number of more complicated possibilities, the evolutionary equilibrium EE could involve only one strategy surviving, or two, or any number up to the full eight.<sup>16</sup> To keep the problem within bounds, I ask only whether the reciprocity strategy 1,ii can ever be a single-strategy evolutionary equilibrium.

In the Prisoners' Dilemma environment, 1,ii cannot be a single-strategy EE. In a population with 1,ii as sole "incumbent", every possible "mutant" strategy involving C<sub>2</sub> or R<sub>2</sub> -- that is, any strategy for which the less cooperative option is chosen on the earlier move or on the later move or both -- will strictly defeat 1,ii in one-on-one play and thus successfully invade. True, the reciprocative players will be making [R<sub>1</sub>,C<sub>1</sub>] moves with one another and achieving handsome (3,3) payoffs. But against these incumbents a mutant choosing the less cooperative R<sub>2</sub> on the earlier move will be earning the higher of the payoff-pair (5,0), and similarly an entrant choosing the less cooperative C<sub>2</sub> on the later move will receive the higher of (0,5).

The analysis of Chicken is very similar. If 1,ii is the incumbent, once again the reciprocative players receive (3,3) when they interact with one another. But a less cooperative mutant would now earn the higher of (5,1) on the earlier move and/or the higher of (1,5) on the later move.

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<sup>16</sup> Up to eight distinct single-strategy EE's might coexist, as many as  $8 \times 7 / 2 = 28$  EE's involving mixtures of two strategies, etc.

For Tender Trap the situation is somewhat trickier. As incumbent, the reciprocative strategy  $1,ii$  cannot be strictly defeated by any other. However, the Always-Cooperate (AC) strategy  $1,i$  ties  $1,ii$  in any one-on-one interaction between them -- since both lead to the move-pair  $[R_1, C_1]$  with payoffs (5,5). So we can expect a kind of meta-stable "drifting equilibrium" for some range of combinations of  $1,i$  and  $1,ii$ .

Summarizing, in both the Prisoners' Dilemma and Chicken environments under the single-round sequential protocol, reciprocative behavior does not in general succeed in maintaining itself either as the rational subgame-perfect equilibrium or as an evolutionary equilibrium. However, in Tender Trap the reciprocative strategy is indeed the sole SGPE, and it is an element in a "drifting" EE in combination with the Always-Cooperate strategy  $1,i$ .

#### Multiple-round simultaneous-move protocol:

A variety of other "rules of the game" provide ways for reciprocity behavior to be expressed. Let us suppose here that the players choose simultaneously in any given round, but the interaction is repeated over an indefinite number of rounds. Then a less cooperative move in a prior round could conceivably be penalized by the opponent's refusal to play cooperatively in one or more subsequent rounds.

Under the famous Tit-for-Tat (TFT) strategy popularized in the well-known work of Axelrod [1984], initially the player would choose the more helpful option (first row or column in the matrices of Table 1), thereafter echoing the opponent's behavior in the previous round. Unhelpful behavior would be punished, but in a proportionate eye-for-an-eye way that leaves open the possibility of later reversion to more cooperative play. In two tournaments conducted by Axelrod using the Prisoners' Dilemma payoffs of Table 1, TFT scored higher than any other of the strategies considered. It has come to be widely believed that TFT is, in a very sweeping sense, the "best" strategy to follow and constitutes the key to the emergence of cooperation.<sup>17</sup>

A systematic investigation of these issues is out of the question here. Instead, I shall limit myself to a few points bearing specifically upon TFT as one possible reciprocative strategy.

1. Not all social interactions correspond to evolutionary competition. So even if TIT FOR TAT were a universal evolutionary equilibrium, that would not warrant using the TFT strategy in non-evolutionary

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<sup>17</sup> For a critique of these claims see Martinez Coll and Hirschleifer [1991]. Some qualifying statements also appear in Axelrod [1984], pp. 176-177.



contexts such as labor-management relations or international policy.<sup>18</sup>

2. But of course TFT is far from being a universally valid EE. Even if it were the "best" strategy or constituted the only EE in the iterated simultaneous-move Prisoners' Dilemma, those results need not apply to other environments and protocols.

3. In fact, for evolutionary processes quite generally, it is unreasonable to expect a "corner solution" in which only a single strategy survives. In almost all real-world contexts a coexisting mix of strategies -- more cooperative ones together with less cooperative ones -- is observed.<sup>19</sup> (This point will be discussed further under the heading of "complementary strategy mixes" in the next section.)

4. There are a huge number of EE's in the multiple-round simultaneous-move Prisoners' Dilemma, but an all-TFT population is not one of them! In parallel with the corresponding result for the single-round sequential-move PD, here again Tit for Tat as incumbent can never do better than tie with (and thus be subject to invasion by) the Always-Cooperate strategy.

The upshot, then, is that reciprocity, like kinship, can indeed promote cooperation in a number of important specific contexts. But it is no panacea.

## V. OTHER PATHWAYS

So far the analysis has examined two influences -- kinship and reciprocity -- that, in certain circumstances, lead to cooperation. These are the forces emphasized in sociobiological summaries and textbook discussions. Yet appearing here and there in the vast literatures of sociobiology, economics, and other social sciences are indications of a great many other possible pathways to cooperation.

Kinship promotes cooperation by modifying the payoffs of helpful actions. (Discounted by the degree of relatedness, benefits to others are counted as equivalent to benefits to self.) And reciprocative behavior requires consideration of a number of alternative protocols of play, with a consequent need to deal with extended strategy sets in comparison with the elemental Row and Column strategies of Table 1. However, once adjustments of payoffs, protocols, and/or strategy sets are permitted, many other possible routes to cooperation are opened up. A very few of these additional routes are briefly covered in this section.

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<sup>18</sup> Contra occasional suggestions in Axelrod [1984], for example p. 190.

<sup>19</sup> See, e.g., Dugatkin [1990]. For the PD environment and the multiple-round simultaneous-move protocol, Boyd and Lorberbaum [1987] have shown that no single strategy can ever be an EE.

### Punishment opportunities:

Reciprocative strategies penalize an opponent's failure to cooperate by what might be termed "reactive non-cooperation". But this is a mild penalty. In some circumstances it may be possible to impose stronger penalties, as exemplified by what has been termed the Punisher strategy (Hirshleifer and Martinez Coll [1988]). Punisher players gain at the expense of non-cooperators, just as the latter "make a living" by exploiting cooperators. In the realm of Nature, for example, super-predator species prey upon lower-level predators. In human terms, bounty-hunters make a profit by capturing criminals.

When Punisher strategies are available in the PD environment, the typical evolutionary outcome is a mixed population in which the more cooperative, less cooperative, and Punisher strategies are all represented -- rather like the continuing survival of ranchers, rustlers, and bounty-hunters in the Old West. Thus, introducing Punisher is a way of modeling the fact that what we observe in the real world is almost never the total victory of any single strategy but rather a co-existing set of differentiated strategies.

### Complementary strategy mixes:

Extending this idea for the Prisoners' Dilemma payoff environment and multiple-round simultaneous-move protocol, Lomborg [1996] generated simulations taking account of all the strategies that can "remember" and thus react to the opponent's three prior moves. (There are 32,768 such strategies!) Over the evolutionary generations meta-stable (but never fully stable) equilibria<sup>20</sup> emerge. These typically involve a considerable number of mutually supportive strategies, commonly falling into two types labeled "nucleus" and "shield". The nucleus strategies are highly cooperative ones, reacting very little or not at all to opponents' unhelpful moves but scoring well in encounters with other members of the incumbent strategy set. The shield strategies, in contrast, provide protection by reacting adversely to uncooperative deviants.

Despite chaotic periods that show up when an existing meta-equilibrium collapses, the system as a whole spends most of its time at or near the meta-equilibria. Furthermore, these equilibria yield very high average payoffs (high levels of cooperation). In fact, the mean evolutionary payoffs were

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<sup>20</sup> Meta-stable equilibria are strategy combinations that persist more or less unchanged over a considerable number of generations, but eventually succumb to the invasion of "mutants" who find a basis for entry.

generally higher than what an all-TFT population would achieve!<sup>21</sup>

Recognition and prompt response:

While ordinarily it is assumed that a TFT player can react to the opponent's prior move in the very next round of play, that is only one of many possibilities. If response delay were greater, the TFT strategy would not do so well. Conversely, however, Tit-for-Tat would do even better than in the standard formulation if a TFT player could recognize and respond to the opponent's choice earlier, perhaps even in the very same round. This last could occur if, for example, the situation dictated that the opponent's action, hostile or friendly, had to be overt rather than covert. In the arms race preceding World War I, it was impossible for open societies like Britain or Germany to hide the numbers of battleships under construction. So a hostile move by either nation (deciding to build more battleships) could not gain much lead time over the opponent's response. Alternatively, by paying a "cost of scrutiny" (Frank [1988], pp. 59-63) it might be possible to identify a covertly hostile action in good time -- an instance of trading off payoff numbers to gain promptness of response.

Allowing perfect recognition and timely response makes Tit-for-Tat an available strategy even when the protocol is single-round simultaneous-move.<sup>22</sup> Martinez Coll and Hirshleifer [1991] analyzed the Prisoners' Dilemma and Chicken environments under this protocol, with three strategies in contention: TFT, Always-Cooperate (AC), and Never-Cooperate (NC). In such a simple context it was possible to find all the evolutionary equilibria. For PD a "drifting" EE was found involving TFT and AC, provided the proportion of the latter was not too large. In the Chicken environment there was a similar drifting equilibrium, but also a separate non-drifting EE in which the population ended up with a specific division between AC and NC. (Note the similarity of the latter equilibrium to the EE for Chicken in Figure 2.)

Once again, these extended strategy sets allowed the continuing survival of more and less cooperative players in a variety of contexts.

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<sup>21</sup> This was possible because the simulations allowed for "noise", that is, for the possibility that a TFT player misperceives and therefore responds incorrectly to the opponent's prior move. Absent noise, in a hypothetical all-TFT world everyone would score 3 per move, and it is not possible to do better. But the all-TFT payoffs decline considerably with even modest levels of noise.

<sup>22</sup> Recall that we have heretofore allowed TFT to play a role only in the single-round sequential-play or the multiple-round simultaneous-play protocols.

Control:

In some circumstances a person might be in a position to "commit" to a particular strategy, or alternatively to foreclose his ever employing certain other strategies. (As in "burning your bridges behind you".) Commitment or foreclosure can affect the rational equilibrium. If you burn your bridges behind you the enemy knows you can no longer retreat, which might affect his calculation whether or not to attack. However, neither commitment nor foreclosure on the part of an individual can affect the evolutionary equilibrium, since your self-denied strategies still remain available to other players present in the population.

Conceivably, however, a player might have the ability to dictate or control the opponent's possible actions. Such control might conceivably be effected by physical means like imprisonment, or psychological means like hypnotism or indoctrination.<sup>23</sup> The controlling party would ordinarily incur some cost, yet the trade-off might prove advantageous.

As one example, for Prisoners' Dilemma using the single-round simultaneous-play protocol "with recognition" (as described just above), Heckathorn [1996] found that the reciprocative Tit for Tat strategy was driven to extinction by a control strategy termed "hypocritical cooperation". Under that strategy the player does not cooperate voluntarily, but is willing to incur a cost to force the opponent into a cooperative move. In a world where such control is not too costly, a great deal of cooperation might emerge, even if unwilling.

Coordination by external clues:

The three payoff contexts of Table 1 displayed different types of obstacles hampering mutually advantageous coordination of strategies. Sometimes, however, external clues may provide the basis for harmonizing the players' moves.

Starting from the underlying Chicken environment under the single-round simultaneous-move protocol, Maynard Smith [1978] described a strategy termed Bourgeois. The idea is that, in competing for use of a resource, one animal typically arrives earlier and the other later. Using this external clue, the Bourgeois strategy is: As earlier-comer, play aggressively, as later-comer, play submissively. In terms of the CH matrix of Table 1, the moves would be [R<sub>2</sub>,C<sub>1</sub>] with payoffs (4,2), the earlier-comer having the advantage. But on average each animal can expect to be in either situation half the time, so

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<sup>23</sup> Parental manipulation, discussed in an earlier footnote, is an example of such control.

the mean payoff would be 3 -- higher than 5/3 payoff shown in Table 2 for the symmetrical EE when only the simpler more cooperative and less cooperative strategies are available.

Group selection:

While currently highly controversial among biologists, group selection as a possible force favoring cooperation has a long intellectual history. Darwin suggested that the habit of cooperation, even where disadvantageous to the individual, might be evolutionarily viable owing to its impact upon the differential survival of groups (Darwin [1871] n.d.: 498).

But, at least if we think in terms of environments like the Prisoners' Dilemma matrix of Table 1, group selection for cooperative behavior runs against the fact that individual selection favors selfish actions. And in fact the current standard view among sociobiologists is that individual selection for selfishness must dominate (Williams [1966]). The key argument has been that individuals within a population have shorter 'turnover times' (are differentially selected faster) than populations as a whole. So the internal within-group trend toward selfishness will proceed more rapidly than any collective between-group gain from the displacement of less unselfish populations.

But recall that kin selection, whose power no sociobiologist questions, operates essentially by concentrating helping acts upon fellow-carriers of the helping gene. Much the same would hold even for unrelated individuals living in groups characterized by preferential interaction with one another -- possibly due simply to propinquity. Group selection is also favored by frequent exterminations of entire clans and tribes, a condition that very likely characterized primal mankind (Alexander [1979], Ch. 4). In recent years biological opinion has been swinging back toward assigning a substantial evolutionary role to group selection (Wilson and Sober [1994]).

The discussion in this section could do no more than suggest the huge number of pathways to cooperation opened up once we allow for wider ranges of payoff patterns and protocols, and consequently enlarged strategy sets. Sociobiologists have not overlooked these other pathways, indeed, most of the examples in this section derive from the sociobiological literature. What I have tried to critique is the tendency in textbooks and other summary discussions to recognize only kinship and reciprocity as systematic factors tending to produce cooperative evolutionary outcomes.

## VI. CONCLUDING THOUGHTS

Cooperation takes many forms and emerges through many channels and pathways. Game-theoretic analyses in the sociobiological literature have concentrated excessively upon just one or a very few payoff environments (notably Prisoners' Dilemma) and similarly only one or a very few of the enormous range of possible protocols of play ("rules of the game"). It is probably owing to this excessive narrowness of viewpoint that usually only kinship and reciprocity are recognized as systematic influences favoring the rise of cooperation.

As a baseline, this paper first assessed the extent of cooperation emerging in three important payoff environments (Prisoners' Dilemma, Chicken, and Tender Trap) illustrating different types of obstacles hampering the evolution of mutual helping, and the two simplest possible protocols (single-round simultaneous-move and single-round sequential move). In these contexts, by and large, comparable levels of cooperation were achieved by the different mechanisms of evolutionary selection and rational self-interested choices. The degree to which kinship and/or reciprocity improved upon these results varied with the specifics of the payoff environment and protocol assumed.

However, allowing for kinship and reciprocity already involves a certain widening of horizons in comparison with the baseline conditions -- that is, they involve modifications of payoffs and/or consideration of more complex protocols (and consequent extensions of the sets of strategies assumed available). Once such alterations are permitted, a vast number of other routes to cooperation are opened up. The final main section of the paper summarized a number of these other pathways: punishment opportunities, complementary strategy mixes, recognition effects, techniques of control, coordination with the help of external clues, and group selection.

A few other points relate to limitations of the present analysis.

First, not all competition is evolutionary competition. The relations among nations and social classes certainly change over time, but are not usually best modeled as involving large populations of entities subject to evolutionary influences such as inheritance, mutation, multiplication, and selection.

Second, the analysis here dealt almost exclusively with symmetrical solutions. But a degree of cooperation is often achieved in asymmetrical ways, for example by systems of dominance and deference that keep internal power struggles within bounds.

As a coda to the main discussion, I will offer a further comment on a secondary theme of the paper: the relative efficacy of evolutionary selection versus rational optimization as mechanisms of competition and cooperation. A possibly surprising result here was that there usually did not seem to

be much to choose between them; if anything, the edge lay with selection. But, I want to argue, the very simple protocols of play taken into account led to an under-estimate of what interacting rational choices could achieve in the way of cooperation. In the single-round sequential-move Prisoners' Dilemma, for example, the Subgame-perfect equilibrium associated with rational play offers no escape from the PD "trap" outcome (Table 3). However, rational players can (and are observed to) do much better under quite reasonable though somewhat more complex protocols, in particular one that might be termed the Standard Negotiation Protocol (SNP).<sup>24</sup>

The SNP, while single-round, allows for an indefinite number of negotiation cycles before moves are finalized and payoffs are made. In each cycle players tentatively choose either the more cooperative move (first row or column of the PD matrix in Table 1) or the less cooperative move (second row or column). After these tentative choices are revealed at the end of a cycle, either or both players may stand pat or switch. Since any player can always switch away from the exploitative outcome in which he/she would have received zero payoff, there is no reason not to try the cooperative move. The only stable equilibrium involves the mutually advantageous (3,3) payoffs. So rational players can, given this quite realistic protocol, escape the PD trap after all.

More generally, rational players can frequently treat the rules of the game as endogenous, and hence should be able to hit upon a protocol leading to mutually advantageous outcomes. Economists will of course recognize this as a version of the famous Coase Theorem.

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<sup>24</sup> This discussion is an adaptation of a development in Brams [1993]).

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Table 1

THREE PAYOFF ENVIRONMENTS (numerical illustrations)

Prisoners' Dilemma (PD)

	C1	C2
R1	3,3	0,5
R2	5,0	1,1

Chicken (CH)

	C1	C2
R1	3,3	1,5
R2	5,1	0,0

Tender Trap (TT)

	C1	C2
R1	5,5	0,1
R2	1,0	3,3

Figure 1  
THREE PAYOFF ENVIRONMENTS

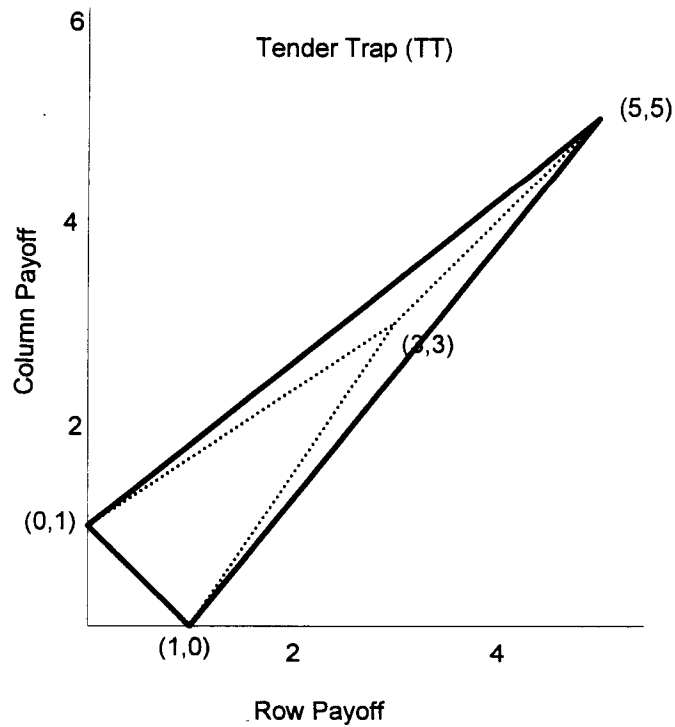
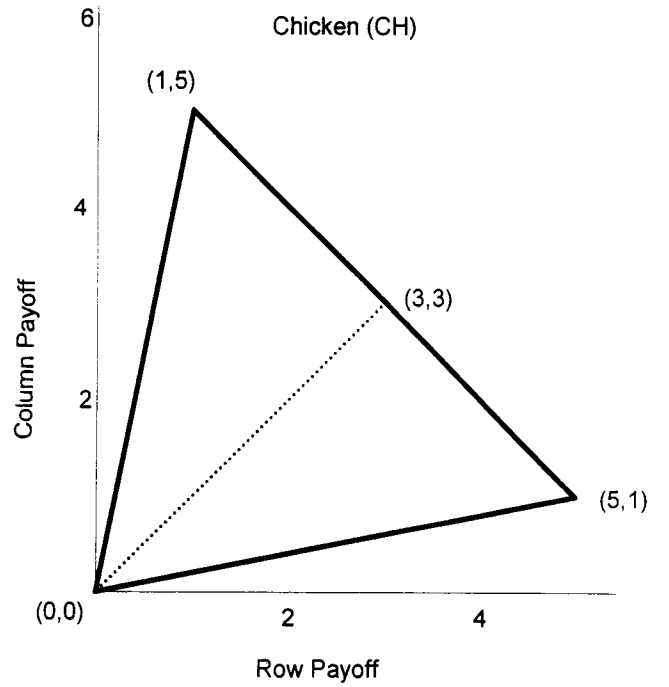
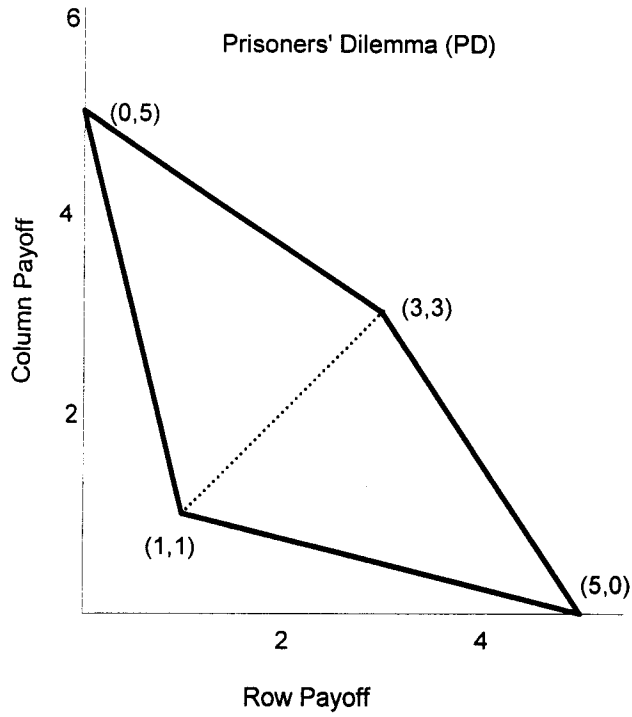


Figure 2

PROGRESS TOWARD COOPERATION IN  
THREE EVOLUTIONARY ENVIRONMENTS

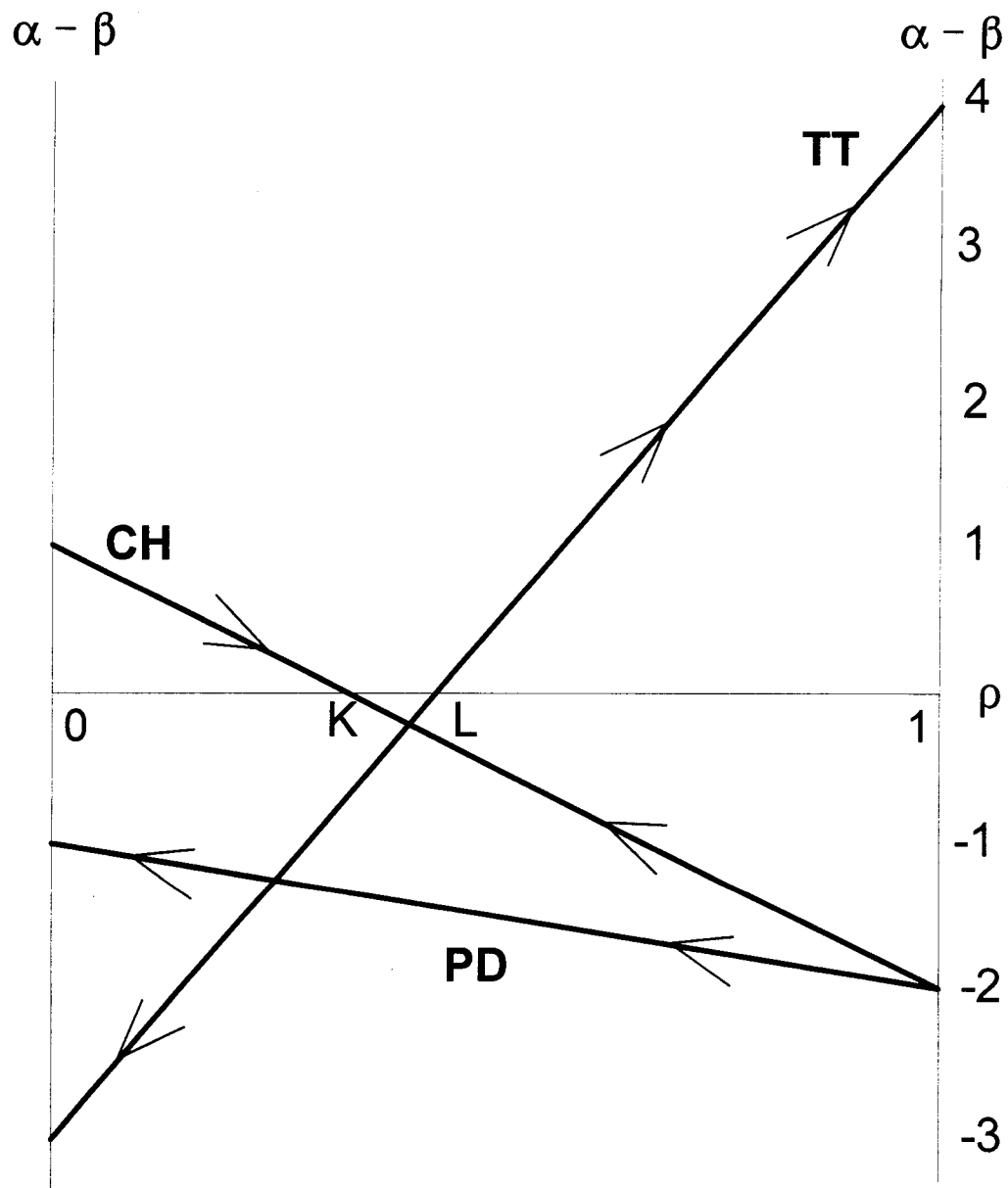


Table 2  
RATIONALITY VERSUS SELECTION IN THREE PAYOFF ENVIRONMENTS  
(simultaneous-move protocol)

	<u>Evolutionary Equilibrium (EE)</u>		<u>Nash Equilibrium (NE)</u>	
	<i>Proportion cooperating (<math>p^*</math>)</i>	<i>Payoffs</i>	<i>Strategy-pair</i>	<i>Payoffs</i>
<b>PD</b>	0	1	[R2,C2]	(1,1)
<b>CH</b>	1/3	5/3	(i): [R2,C1] (ii): [R1,C2] (iii): mixed-strategy ( $\pi = 1/3$ )	(5,1) (1,5) (5/3,5/3)
<b>TT</b>	(i): 1 (ii): 0	5 3	(i): [R1,C1] (ii): [R2,C2] (iii): mixed-strategy ( $\pi = 3/7$ )	(5,5) (3,3) (15/7,15/7)

Table 3  
 RATIONALITY VERSUS SELECTION IN THREE PAYOFF ENVIRONMENTS  
 (sequential-move protocol)

	<u>Evolutionary Equilibrium (EE)</u>		<u>Subgame-perfect Equilibrium (SGPE)</u>	
	<i>Is Reciprocity strategy 1,ii a possible EE?</i>	<i>Payoffs</i>	<i>Strategy (earlier-move, later- move) [see text]</i>	<i>Payoffs</i>
<b>PD</b>	No	--	2,iv	(1,1)
<b>CH</b>	No	--	2,iii	(3,3)*
<b>TT</b>	Yes**	5	1,ii	(5,5)

\*Average of (5,1) and (1,5). (Earlier-mover has advantage, but each player has a 50% chance of being the earlier-mover.)

\*\*As part of “drifting equilibrium” with 1,i.