

SELECTION, MUTATION, AND THE PRESERVATION OF DIVERSITY  
IN EVOLUTIONARY GAMES

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Abstract

Evolutionary models suggesting that in mixed-motive situations only a single strategy, or only a single type of behavior, will ultimately prevail cannot be regarded as satisfactory. Among the forces supporting diversity of strategies and of behaviors are: (i) multiple and/or mixed evolutionary equilibria, (ii) mutation pressure, and (iii) transient dynamic processes. For the Prisoners' Dilemma and the Chicken payoff environments, this paper studies the degree to which "nice" and "mean" behaviors are supported by the alternative reactive strategies TIT FOR TAT and BULLY. Only in exceptional limiting cases does a single strategy or a single form of behavior come to extinguish all others. TIT FOR TAT tends to support the predominance of "nice" behaviors in Prisoners' Dilemma (but not Chicken), while BULLY tends to support a predominance of "mean" behaviors generally.

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In mixed-motive situations combining elements of mutual as well as opposed interests, human behaviors and the underlying strategies are highly varied. Some people show a conciliatory talent, some are belligerent, others give the impression of being aggressive without actually acting violently, while still others may appear pacific yet respond forcefully to attack.

Despite this observed diversity, a rather contrasting claim has gained some acceptance in recent years: that, at least in long-run evolutionary competition, a single optimal strategy does exist -- to wit, the simple reactive strategy known as TIT FOR TAT.<sup>1</sup> TIT FOR TAT was the "winning" contender in the well-known computer tournaments conducted by Robert Axelrod (Axelrod [1984]). And in his evolutionary simulations extending the results of those tournaments, TIT FOR TAT appeared to be driving all other strategies to extinction.<sup>2</sup> Accordingly, Axelrod's well-received book strongly emphasized the optimality and superior survivability of TIT FOR TAT in evolutionary competition.<sup>3</sup> And while Axelrod's own work was limited to the Prisoners' Dilemma payoff environment, somewhat parallel claims have been made for TIT FOR TAT in the Chicken and other payoff environments as well (Lipman [1986]).

The present authors have shown, however, that contentions as to the evolutionary superiority of TIT FOR TAT are valid only under a very narrow "window" of assumptions (Hirshleifer and Martinez Coll [1988], Martinez Coll and Hirshleifer [1991]).<sup>4</sup> As just one example, TIT FOR TAT has very little survival value when the evolutionary competition takes the form of an elimination tournament rather than a round-robin tournament. The purpose of

the present paper is not to offer further criticisms of the sometimes excessive claims made on behalf of TIT FOR TAT, but instead to provide a more systematic analysis of the different strategic elements tending to generate and maintain diversity in evolutionary games.

It is important to distinguish diversity in strategies from diversity in behaviors. Anyone following a "reactive" strategy like TIT FOR TAT must have the capability of engaging in different behaviors: in the Prisoners' Dilemma environment, for example, he must be able to make either a DEFECT move or a COOPERATE move. Conversely, followers of different strategies may find themselves engaging in the same behavior, as when TIT FOR TAT players interact with ALWAYS-COOPERATE players in the Prisoners' Dilemma environment. The evolutionary survival of diversity in both strategies and behaviors will be explored in the analysis that follows.

The two archetype strategies that define Prisoners' Dilemma are the "nice" strategy ALWAYS-COOPERATE (C) and the "mean" strategy ALWAYS-DEFECT (D). (Henceforth we will drop the ALWAYS unless there is danger of confusion.) This paper will place these archetype strategies in competition with each of two reactive strategies: TIT FOR TAT and a less friendly one called BULLY. We then do the same for the payoff environment of Chicken (also known as Hawk-Dove).<sup>5</sup> In Chicken the "nice" archetype strategy will be called COWARD, the "mean" archetype DAREDEVIL (thus retaining the convenient C and D abbreviations).<sup>6</sup>

The analysis concentrates on three elements tending to generate or to maintain diversity in evolutionary processes:

(i) Multiple equilibria: Two distinct types of multiple equilibria will be of importance in what follows. (a) Even if the postulated dynamic

process would lead to a single determinate terminal state -- to what we call an Evolutionary Equilibrium Point (EEP) -- from any given initial population distribution, different starting points might lead to different terminal EEP's. (b) Or, it may be that the dynamic trajectories are not attracted to any single EEP but are attracted to what we call an Evolutionary Equilibrium Region (EER), within which the population distribution may drift without ever settling down to a unique outcome.

(ii) Mutation pressure: Mutations play an essential role in genetic evolution, and are evidently also important in the evolution of social behavior. The term "mutation pressure" suggests that mutation is directional, and may operate more powerfully in some directions than others. The directional effect of mutation pressure is generally to preserve variety, whereas selectional pressures tend to destroy variety.<sup>7</sup>

(iii) Transient vs. equilibrium states: In this paper we will be devoting attention not only to final equilibrium but also to the dynamic trajectories of change. Even if variety is destined ultimately to be extinguished, it persists longer if the rate of dynamic change is slow. And before equilibrium is reached, as will be seen, certain patterns of diversity turn out to be more likely than others ("probability clouds").<sup>8</sup>

## 1. GAMES AND STRATEGIES

Prisoners' Dilemma and Chicken are best thought of as different payoff environments within which a number of simple or complex strategies may be chosen. The two environments have very similar structures. Matrices 1 and 2 show the respective payoffs, ranked ordinally from 1 (lowest) to 4 (highest). (Variations in the actual cardinal payoffs, so long as they

leave these rankings unaffected, will generally not alter the qualitative nature of the solutions.) In the basic 2x2 games involving the archetype strategies only, each player chooses between a nice strategy C (COOPERATE in Prisoners' Dilemma, COWARD in Chicken) and a mean strategy D (DEFECT in Prisoners' Dilemma, DAREDEVIL in Chicken). The crucial difference between the two environments is that in Prisoners' Dilemma the worst outcome (payoff of 1) is suffered by someone playing nice against mean (COOPERATE against DEFECT), while in Chicken the worst outcome is incurred when the contenders both play mean (both choose DAREDEVIL). So in Chicken the two players have a stronger mutual interest in avoiding the D-D behavior combination.

[Table 1 about here]

Turning now to more complex strategies, as already indicated only the reactive strategies TIT FOR TAT and BULLY will be considered in this paper. However, our interpretation of the nature of the reaction differs from the usual one in the literature. Evolutionary analysis necessarily deals with multiple generations, that is, with the changes that selectional and mutational forces bring about between one generation and the next. But whether or not to assume multiple rounds of play in any given one-on-one interaction is a question of fitting the model to the real-world situation.

IRR versus DRR: Consider first TIT FOR TAT. On the usual interpretation, such a player initially makes a nice C move and then, observing what the opponent does, in each following round mirrors the latter's previous choice -- replying C to C and D to D. And a BULLY player would open initially with a mean D move and then respond in each following round with the reverse of the opponent's previous choice.<sup>9</sup> This usual assumption, that reaction can be effectuated only in the next round of play,

we call "deferred recognition and response" (DRR). However, an alternative assumption is employed here, under which the reactive players have the capacity of "immediate recognition and response" (IRR). Thus, the TIT FOR TAT and BULLY players are assumed here to be able to detect immediately whether the opponent is opening with a mean or a nice move, in time for making the appropriate reply in the very same round.

Neither DRR or IRR is right or wrong of itself; which is the correct assumption to make depends upon the situation investigated. Someone playing DEFECT in Prisoners' Dilemma or DAREDEVIL in Chicken would of course always prefer to do so covertly, thus getting away with a mean move for at least one round before the reactive player can respond. And if the actual real-world situation permits such disguise, DRR would be the appropriate assumption to make. But sometimes disguise is impossible and a mean move must be made overtly. Consider the battleship construction race between Britain and Germany in the years preceding World War I. Battleships being too big to hide, mean behavior on either side (building more battleships) had to be quite overt. Thus IRR would have been the appropriate assumption for that competitive interaction. (If on the other hand covert mean play is actually feasible, in real-world situations a reactive player might have to observe behavior in several successive rounds before being able to recognize the opponent's type. Thus, the usual DRR assumption, that exactly one round is both necessary and sufficient, is a very special one that could either be too optimistic or too pessimistic.)<sup>10</sup>

The IRR interpretation permits a much simpler analysis, dealing only with single-round rather than multiple-round play. Under IRR there is no need to be concerned about the "shadow of the future," since a reactive

player is always in a position to make the correct response here and now. Evidently, the IRR assumption favors TIT FOR TAT, since under DRR a TIT FOR TAT player's opening move would leave him open to exploitation in the first round. And of course IRR operates correspondingly to the disadvantage of the archetype D (DEFECT or DAREDEVIL) players. So whenever TIT FOR TAT loses out against overt mean play under our IRR interpretation, it would do even worse against covert mean play under the more usual DRR assumption.

Employing the IRR interpretation, Matrices 3 and 4 show the effect of adding TIT FOR TAT to the available menus of strategies corresponding to the underlying Prisoners' Dilemma and Chicken games, respectively. The only new element needed is the payoff combination when two TIT FOR TAT players encounter one another. Following the definition of TIT FOR TAT, each player will make an opening nice (C) move, to which the other will immediately respond in kind. Thus, as shown, the payoff-pair is (3,3) in each case.

Matrices 5 and 6 show the corresponding payoffs when BULLY is the reactive strategy considered. Here the only new element to be determined is the BULLY-BULLY payoff combination. Following the definition of BULLY, it is reasonable to suppose that whichever player is in a position to go first will open with a mean D move, to which the opponent will instantly respond with the reverse nice C move. Since each player can expect to have the opening move just half the time, the BULLY-BULLY payoffs are calculated as the average of the outcomes of playing C against D and D against C. Specifically, in Matrix 5 for Prisoners' Dilemma the BULLY-BULLY payoffs are calculated as  $(4+1)/2 = 2.5$  for each player. In Matrix 6 for Chicken the corresponding calculation yields  $(4+2)/2 = 3$  for each.



## 2. THE MODEL

### 2.1 Dynamics

The essence of evolutionary dynamics is that more profitable strategies gain increased prevalence over time while less profitable ones suffer diminished representation in the population.

Denote as  $a_{ij}$  the payoff obtained from playing strategy I in an encounter with strategy J. The mean return  $Y_i$  to a player of strategy I will be weighted by the proportions  $p_j$  of the population actually playing all the different possible strategies:<sup>11</sup>

$$(1) \quad Y_i = \sum_j p_j a_{ij}$$

It will also be useful to define the global mean return  $Y$  received by a population distributed over the different strategies:

$$(2) \quad Y = \sum_i p_i Y_i$$

Let  $F_i$  signify the relative "fitness" of strategy I, that is to say, the difference between its return and the global mean return:

$$(3) \quad F_i = Y_i - Y$$

Evidently, the mean fitness averaged over the population as a whole will be zero.

When the force of selection is considered alone, in each generation the change in the fractional representation of strategy I is given by:

$$(4) \quad \Delta^{SEL} p_i = k p_i F_i = k p_i (Y_i - Y)$$

Here  $k$  is a parameter that reflects the sensitivity of the dynamic process; the higher is  $k$ , the more rapid the change in the population proportions.

Thus, in each generation the change in  $p_i$  due to the force of selection alone will be proportional to the sensitivity parameter  $k$ , to the

current level of  $p_i$ , and to the relative fitness of strategy I (the difference between its mean return and the global mean return in the population).<sup>12</sup> It is easy to verify that (4) implies the logically necessary property that, over the population as a whole, the sum of the increments must be zero. In general, (4) will be a cubic equation in the  $p_i$ .

However, the evolution of the population proportions can also be affected by the force of mutation. Let  $m_{ij}$  denote the rate at which an individual playing strategy I changes to strategy J in any time-period. Let N be the number of distinct strategies available. If  $N = 3$ , for example, then the change in the representation of strategy 1 due to mutation,  $\Delta^{\text{MUT}} p_1$ , will be the algebraic sum of those who shift away from 1 and toward 2 or 3 and those who move toward 1 and away from 2 or 3. Thus:

$$(5) \quad \Delta^{\text{MUT}} p_1 = -(m_{12} + m_{13})p_1 + m_{21}p_2 + m_{31}p_3$$

There are of course corresponding equations for the changes in  $p_2$  and  $p_3$ .<sup>13</sup>

Using the simplification that all the  $m_{ij}$  are equal to a common mutation rate  $m$ , equation (5) reduces to:

$$(5a) \quad \Delta^{\text{MUT}} p_1 = m(1 - 3p_1)$$

Generalizing, an equation valid for any strategy I, when there are N distinct strategies, is:

$$(5b) \quad \Delta^{\text{MUT}} p_i = m(1 - Np_i)$$

Mutation acts as a centripetal force, pulling the population distribution toward interior solutions. If all the  $m_{ij} = m$ , then  $\Delta^{\text{MUT}} p_i$  will be positive whenever  $p_i$  is less than  $1/N$  and negative when  $p_i < 1/N$ .

Summing the effects of selection and mutation, the proportionate representation of strategy I in the following generation, symbolized as  $p_i'$ , will be given by:

$$(6) \quad p_i' = p_i + \Delta^{\text{SEL}} p_i + \Delta^{\text{MUT}} p_i = p_i + kp_i F_i + m(1 - Np_i)$$

## 2.2 Equilibrium concepts

Several different concepts of evolutionary equilibrium have to be distinguished. Unfortunately, some of these involve considerable mathematical difficulties. Rather than attempt a rigorous development and comparison, we limit this discussion to an intuitive interpretation of the fundamental ideas.

Any possible state of the population -- that is, any vector  $p = (p_1, p_2, \dots, p_N)$ , where  $\sum_j p_j = 1$  -- must be one of three types:

Vertex: only one strategy is represented, that is,  $p_i = 1$  for some I, the proportions  $p_j$  for all other strategies being zero.

Edge: more than one strategy, but not all, have positive representation (so that  $p_j = 0$  for at least one strategy J)

Interior: all strategies have positive representation.

A necessary though by no means sufficient condition for a state of the population to be an evolutionary equilibrium is that the proportions  $p_i$  are stationary under the dynamic process considered. A vector meeting this condition is called a Critical Point (CP):

$$(7) \quad p_i' = p_i, \text{ for all } I \quad \text{Definition of CP}$$

Or, combining (6) and (7):

$$(8) \quad kp_i F_i + m(1 - Np_i) = 0, \text{ for all } I \quad \text{Condition for CP}$$

It follows trivially that:

•If only the force of selection is operative, so that  $m = 0$ , the condition for a CP reduces to:

$$(8a) \quad p_i F_i = 0, \quad \text{for all } i \quad \text{CP under selection alone}$$

Thus, when only the force of selection is operative, all vertex states of the population are CP's, while edge or interior states might or might not satisfy the condition for a CP.

•If only the force of mutation is operative, so that  $k = 0$ , the condition becomes:

$$(8b) \quad p_i = 1/N, \quad \text{for all } i \quad \text{CP under mutation alone}$$

Thus, under mutation alone there is only a single interior CP. This would remain true even in the more general case where the  $m_{ij}$  are no longer assumed all equal.

It follows that when the forces of selection and mutation are both operative there may or may not be more than one CP, but all the CP's will lie in the interior. The exact locations will depend upon the ratio  $k/m$ , that is to say, the relative weights of the selectional and mutational forces.

As already indicated, not all CP's are actually evolutionary equilibria. Evolutionary equilibria are points, or sets of points, which are the stable termini of the dynamic evolutionary process considered. An evolutionary equilibrium must be an attractor. All trajectories in its (sufficiently small) neighborhood must lead into it, which of course implies there will be no trajectories leading out.

In more formal language, for a Critical Point (CP) to be an Evolutionary Equilibrium Point (EEP) it must have a convergency zone -- a set of points from which all the dynamic trajectories lead into it -- that

covers all the points in some (sufficiently small) neighborhood. Thus, an EEP is immune to (sufficiently small) shocks: if the population proportions were momentarily displaced, the dynamic process would work to restore the population back to the equilibrium state.<sup>14</sup>

There is also a second type of evolutionary equilibrium, which we call an Evolutionary Equilibrium Region (EER). Such a region is a set of CP's no one of which is an EEP, but the region as a whole attracts all sufficiently nearby trajectories.

Two other classes of equilibria, while less essential for our present purposes, have been discussed extensively in the literature:

Nash Equilibrium (NE): A Nash Equilibrium in pure strategies exists when, at some cell in the payoff matrix, neither player can gain by deviating. An NE is strict if the deviating player actually loses thereby, or weak if the deviator merely does no worse.

Considering only the symmetrical NE's (corresponding to the cells along the main diagonal of the payoff matrix), the NE condition can be expressed as:

$$(9) \quad F_s(S) \geq F_j(S) \quad \text{Condition for symmetrical NE}$$

This means that when all the population is following strategy S, that strategy must have no less fitness than any other strategy J.<sup>15</sup>

Only a partial listing of the relationships between this NE condition and our other equilibrium concepts will be relevant for us here: (i) A strict NE along the main diagonal of the payoff matrix, i.e., where the strict inequality in (9) holds, corresponds to a vertex EEP, in which only the single strategy associated with that row and column of the matrix is represented. (ii) A weak NE along the main diagonal may or may not be an

EEP, or the end-point of an EER. (iii) If there is no NE along the main diagonal, any NE must correspond to an edge or an interior state in which the various pure strategies are being played by corresponding fractions of the population. Any such edge or interior vector might or might not be an EEP.

Evolutionarily Stable Strategy (ESS): The Evolutionarily Stable Strategy concept (Maynard Smith [1976]) is a strengthening of the NE condition. Considering once again only symmetrical states, the condition for an ESS is:

$$(10) \quad F_s(S) > F_j(S) \quad \text{or} \quad \text{Condition for symmetrical ESS}$$

$$F_s(S) = F_j(S) \quad \text{and} \quad F_s(J) > F_j(J)$$

That is, strategy S must have strictly superior fitness when the population is all-S, or, if an equality with some other strategy J holds there, then S must be strictly superior when the population is all-J. It can be shown that the conditions (10) are sufficient but not necessary to identify an EEP at a vertex.

### 2.3 Graphical Representation

In the 3-strategy case it is convenient to represent the possible states of the population as points associated with an equilateral triangle. In Figure 1, the vertex C represents a population distribution in which  $p_C = 1$ , that is, all the individuals are following the archetype nice strategy C (COOPERATE in Prisoners' Dilemma, COWARD in Chicken). Vertex D similarly corresponds to  $p_D = 1$ , where everyone plays the mean strategy D (DEFECT in Prisoners' Dilemma, DAREDEVIL in Chicken). Vertex T corresponds to  $p_T = 1$ .

representing a population all of whom are playing the reactive TIT FOR TAT strategy. (When BULLY is substituted for TIT FOR TAT as the reactive strategy considered, the third vertex will be labelled B.) For the state represented by any point in the triangle, the proportion  $p_C$  is shown by the distance from that point to the opposite side DT, and similarly for the other proportions  $p_D$  and  $p_T$ . At the specific point X in Figure 1, the associated distribution is  $(p_C, p_D, p_T) = (.7, .2, .1)$ .<sup>16</sup>

[Figure 1 about here]

Starting from any given point, the dynamic represented by equation (6) generates a series of points or trajectory, whose course and direction depend solely upon the associated payoff matrix and the values of the parameters  $k$  and  $m$  -- representing the sensitivities to the forces of selection and mutation, respectively. Figure 1 pictures a trajectory starting at point X and ending at point Z. In each simulation to be described, 200 evolutionary trajectories are pictured (beginning from initial positions spaced randomly throughout the triangle). Every trajectory is represented by 50 points, corresponding to 50 iterations of equation (6). Arrows are used to suggest the general direction of the trajectories within regions.

For given  $k$  and  $m$ , the separations between successive points along a trajectory depend exclusively upon the profitability differences among the strategies considered. For the trajectory in Figure 1 the points are widely separated to begin with, but as the final point Z is approached the distances from one point to the next normally diminish, since the profitability differences are becoming smaller. Of course, as  $k$  and  $m$  become larger, other things equal the dynamic rates of change and therefore

the separations between points increase.

Relatively dense concentrations of points or "probability clouds" appear in certain regions of the diagrams. Those are regions attracting and retaining, at least for a while, a large number of the trajectories passing nearby. Such clouds tend to appear in the neighborhood of any Evolutionary Equilibrium Point (EEP) or Evolutionary Equilibrium Region (EER). But even a Critical Point that is not an EEP or part of an EER may have a probability cloud nearby, owing to the stationarity property of equation (7) that defines a CP.

### 3. PRISONERS' DILEMMA SIMULATIONS

In this section we picture and analyze the evolutionary survival of diversity in the Prisoners' Dilemma (PD) payoff environment. The available strategies include the archetype strategies COOPERATE (C) and DEFECT (D) plus one or the other of the reactive strategies TIT FOR TAT and BULLY. The section following provides a corresponding analysis for the Chicken environment.

#### 3.1 TIT FOR TAT as reactive strategy in PD -- under selection alone

Figure 2 suggests the nature of the evolutionary process in the Prisoners' Dilemma environment, when TIT FOR TAT (T) is the reactive strategy considered and only the force of selection is operative. Thus, the mutation coefficient is  $m = 0$ . The value  $k = .4$  was employed for the selection coefficient. The payoffs are as shown in Matrix 3.

[Figure 2 about here]

The curve LD in Figure 2 connects those points where  $F_d = 0$ , that is.



where the relative fitness of the mean strategy D is zero. Its equation, using the payoffs of Matrix 3, is:

$$(11) \quad p_c = (2p_d - p_d^2 - 1)/(p_d - 2)$$

where  $0 \leq p_c, p_d \leq 1$  and of course  $p_c = 1 - p_s - p_d$ . In the region above LD, the relative fitness of D is positive;  $p_d$  is increasing, and all the trajectories progress toward vertex D. Below the curve,  $F_d$  is negative and all the trajectories move away from D.

The diagram suggests that there is no interior Critical Point. From equations (6) and (7), such a CP would require that all the fitnesses  $F_i$  equal zero. But it is easily seen from the payoff matrix that the curves corresponding to  $F_c = 0$  and  $F_t = 0$  would lie along the side TC of the triangle. In other words, when there are no D players in the population, COOPERATE (C) and TIT FOR TAT (T) have equal fitness. And of course, these relative fitnesses must be zero since they equal the population average. It follows that point L where  $F_d$  also equals zero, which is located at  $(p_c, p_d, p_t) = (.5, 0, .5)$ , is an edge Critical Point. But a moment's further reflection reveals that each and every point along the TC edge is also a CP -- since, even where  $F_d$  differs from zero along this edge, condition (8a) is still met because  $p_d = 0$ . So the CP's in Figure 2 are the three vertices and the entire side TC.

Let us now consider the evolutionary equilibria. Along the side TC, looking first at the upper range LC, the diagram shows that all the trajectories are moving away in the direction of vertex D. Thus this upper range does not contain any evolutionary equilibria, as is evident also from the consideration that the DEFECT strategy has positive fitness in this range -- lying as it does above the curve LD -- while COOPERATE and TIT FOR

TAT have zero fitness. But the lower range TL along the side TC does represent a set of terminal points of the evolutionary process. However, as the diagram suggests, every point in the range TL has a convergency zone consisting only of one single curve (trajectory) leading to that point as terminus. Consequently, no single point within the range TL is an Evolutionary Equilibrium Point (EEP), but the range as a whole is an Evolutionary Equilibrium Region (EER). And, as would be expected, there is a somewhat diffuse "probability cloud" in the neighborhood of the EER represented by the range TL.

Near the CP at vertex D, representing an all-DEFECT population, there is also a faint probability cloud, particularly below the curve LD. Nevertheless, vertex D is not an Evolutionary Equilibrium Point. As has been seen, while above LD all the trajectories are moving toward D, below that curve they are all heading away. More formally, an EEP must have a convergency zone that consists of all the points in its (sufficiently small) neighborhood. Starting from D, a finite displacement of radius  $\epsilon$ , no matter how small, would have some chance of falling below the curve LD -- thus initiating a trajectory leading away from rather than back toward vertex D. What generates the denser concentration below curve LD is that, whereas the trajectories above that curve approach vertex D from a wide spread of directions, those departing the close neighborhood of D are all funneled into a narrow "channel of high probability" below.

Digression on "evolutionary equilibrium" versus "collective stability":

In view of the wide attention his work has received, at this point we digress to make a brief comparison of Axelrod's analysis (Axelrod [1984, Appendix B]) with ours. So far as results are concerned, Axelrod contends

that DEFECT (the D vertex) and TIT FOR TAT (the T vertex) are both evolutionary equilibria -- more specifically, in his terminology, they are "collectively stable" -- whereas in our analysis neither of the two is an EEP (although the T vertex is the end-point of an EER).

First, with regard to the T vertex. Here the explanation for the discrepancy lies in Axelrod's inappropriate formal definition of what he calls "collective stability." (While a definition cannot be said to be incorrect, it is inappropriate if it fails to describe the intended referent.) From his non-technical discussion and interpretations, it is evident that the evolutionary equilibrium concept Axelrod had in mind was the same as ours: a strategy or distribution of strategies that is an attractor and thus secure from invasions, i.e., is stable as against sufficiently small shocks. However, his formal treatment defined a strategy S as "collectively stable" whenever no other strategy S' has strictly higher payoff in an all-S population. This corresponds to equation (9) above, which is the condition for a symmetrical Nash Equilibrium (NE). But, we have seen, (9) is not strong enough to define an evolutionary equilibrium. It is true that a strict NE along the main diagonal is always a vertex EEP. But a weak NE, while still "collectively stable" on Axelrod's definition, need not be an EEP. So Axelrod's "collective stability" is not sufficient for an EEP.<sup>17</sup> And specifically, the T-T strategy-pair in Matrix 3, corresponding to the T vertex in the diagram, is only a weak NE since a COOPERATE player does equally well in an all-TIT FOR TAT population. Such a weak NE could still be an EEP if had a convergency zone including all the points in its sufficiently small neighborhood, but it can be seen in Figure 2 that the convergency zone for vertex T consists only of one single

trajectory.

Next, with regard to the D vertex. Here, under the usual DRR (deferred recognition and response) assumption used by Axelrod, in an otherwise all-DEFECT population a single TIT FOR TAT player would actually do worse than any of the D players, losing out in the very first round of a multiple-round interaction and doing no better in any of the later rounds. Thus, under the DRR assumption Axelrod is quite correct in claiming that all-D is an EEP: there is a neighborhood of D in which all arbitrary shocks would initiate trajectories leading back toward D. But as seen above, under our IRR (immediate recognition and response) assumption the D vertex is not an EEP, since its convergency zone fails to cover all the points in its neighborhood.

### 3.2 TIT FOR TAT as reactive strategy in PD -- selection and mutation

The evolutionary outcome in Prisoners' Dilemma + TIT FOR TAT, under selectional forces alone, is therefore a range of population mixtures of the COOPERATE and TFT strategies. Since this is an edge solution, or a set of edge solutions, rather than a vertex solution proper, in equilibrium there is diversity in strategies. But there is no diversity in behavior, since the two surviving strategies are both "nice": only cooperative moves will actually be observed in equilibrium. To model the survival of both nice and mean behaviors, in a previous paper we expanded the underlying payoff environment to allow a strategy called PUNISHER.<sup>18</sup> This paper employs a different method of achieving an interior equilibrium, namely, introducing mutational pressure.

Figure 3 shows the effect of allowing mutation as well as selection,

the mutation coefficient being  $m = .01$  while the selection coefficient remains  $k = .4$  as before. As follows from equation (6), if  $p_s = 0$  in any generation for any strategy S, then in the next generation  $p_s' = m$ . Thus the edges of the triangle "reject" any nearby trajectory. The darker probability clouds of the previous Figure 2, in the neighborhood of the previous Critical Point at vertex D and of the Evolutionary Equilibrium Region TL along the vertical axis, here have both been displaced somewhat into the interior and converted into a single channel of high probability. The vertex at D is no longer even a Critical Point, and there no longer is an Evolutionary Equilibrium Region. And in fact, in Figure 3 there is only a single Evolutionary Equilibrium Point, in the interior, located approximately at  $(p_c, p_d, p_t) = (.268, .056, .676)$ .<sup>19</sup>

[Figure 3 about here]

The exact position of the EEP will depend upon the numerical values in the payoff matrix, and also upon the ratio  $m/k$  which reflects the relative strength of the mutational and selective forces. As the mutation rate  $m$  increases relative to the selection rate  $k$ , the EEP will shift inward toward the center of the triangle. This is pictured in Figure 4 where  $m$  has been increased to .03 (with  $k = .4$  remaining unchanged). Here the trajectories are forming a definite "whirlpool" in the neighborhood of the EEP located approximately at  $(p_c, p_d, p_t) = (.254, .164, .580)$ .

[Figure 4 about here]

### 3.3 BULLY as reactive strategy in PD

Building on the previous discussion, a more compact treatment will suffice when BULLY replaces TIT FOR TAT as the reactive strategy played

against the two archetype strategies of Prisoners' Dilemma.

After replacing the T vertex by the B (all-BULLY) vertex, Figure 5 is like Figure 2 in representing selectional forces alone ( $m = 0$  while  $k = .2$ ). The probability cloud in Figure 5 is dense only in the neighborhood of the all-DEFECT vertex. Indeed, it is easy to verify that all-DEFECT is now the sole Critical Point CP and sole Evolutionary Equilibrium Point EEP. That BULLY does so poorly is not surprising when we notice that its payoffs in Matrix 5 are dominated by DEFECT.<sup>20</sup> Figure 6 shows the effect of introducing a mutational element ( $m = .02$ ) into the simulation, with the anticipated consequence of shifting the probability cloud and the EEP somewhat into the interior. The single EEP here is at the vector  $(p_c, p_d, p_d) = (.077, .832, .092)$ .

[Figures 5 and 6 about here]

Summarizing for the Prisoners' Dilemma payoff environment: (1) With TIT FOR TAT as reactive strategy, under selection alone there is no single Evolutionary Equilibrium Point (EEP) but rather an Evolutionary Equilibrium Region EER representing a range of mixtures of TIT FOR TAT and COOPERATE. Under our assumption of immediate recognition and response (IRR), an all-DEFECT population is a Critical Point but not an EEP or part of any EER. Since TIT FOR TAT and COOPERATE are both "nice" there is strategy diversity but no behavioral diversity. When mutation pressure is introduced, a single EEP does emerge, displaced somewhat into the interior from the EER under selection alone. So mutation pressure generates a degree of behavioral diversity as well as strategy diversity. (2) With BULLY as reactive strategy, under selection alone there is only an all-DEFECT EEP; neither strategy diversity nor behavior diversity exist in equilibrium. Introducing

mutations displaces this equilibrium somewhat into the interior, generating as before some diversity of both types. (3) Apart from the diversity that persists in equilibrium, the transient non-equilibrium diversity displays some systematic patterns: probability clouds near the various EEP's or EER's and, with the introduction of mutation pressure, channels of high probability that tend to attract all nearby trajectories in the course of their dynamic progress.

#### 4. CHICKEN SIMULATIONS

Figure 7 is the analog for the Chicken environment of Figure 2 for Prisoners' Dilemma, portraying selectional forces alone with TIT FOR TAT serving as the reactive strategy (Matrix 4), but the diagrams have some notable differences. Like Figure 2, Figure 7 contains a curve LD that divides two convergence zones. (However, LD in Figure 7 is a separatrix, whereas in Figure 2 the curve LD represented the set of points where  $F_d = 0$ .) Like Figure 2 again, the trajectories in Figure 7 suggest the existence of an Evolutionary Equilibrium Region (EER) running along the side TC from vertex T to point L -- located at  $(p_c, p_d, p_t) = (.667, 0, .333)$  and surrounded by a loose probability cloud. However, what looks very different from Figure 2 is the second, denser probability cloud in the region near point N, at the population proportions  $(p_c, p_d, p_t) = (.5, .5, 0)$  representing a mixture of COWARD and DAREDEVIL. The directions shown for the trajectories correctly suggest that the range TL is indeed an EER while point N is indeed an EEP. Which of these multiple equilibria is actually attained will depend upon the initial state of the population.<sup>21</sup>

[Figure 7 about here]

When mutations are introduced, we see in Figure 8 that (as in the comparable Figures 3 and 4 for Prisoners' Dilemma) only a single interior CP survives, and it may be verified that this is also an EEP. The numerical solution is  $(p_c, p_d, p_t) = (.532, .357, .111)$ . What is rather remarkable is the difference between the fates of the two selection-alone equilibria after mutation pressure is introduced. The EEP at point N in Figure 7 (representing a mixture of COWARD and DAREDEVIL) is displaced in Figure 8 only slightly into the interior. In contrast, the former EER in Figure 7 (representing "nice"-behavior mixtures of COWARD and TIT FOR TAT along the TC edge) disappears entirely in Figure 8, having been converted into an interior channel of high probability that leads inexorably to the EEP near point N. We might say that the selection-alone EEP at N is "resilient," while the EER along the TC edge is not, with regard to the introduction of mutation pressure; the former bends a bit, the latter falls apart entirely.

[Figure 8 about here]

Turning to BULLY as the reactive strategy in the Chicken environment (Matrix 6), the picture in Figure 9 under selection alone (using  $k = .4$ ) leads to a unique edge EEP at point H located at  $(p_c, p_d, p_b) = (0, .5, .5)$ . This equilibrium is a mixture of BULLY and DAREDEVIL, both involving "mean" behaviors! In this case, introducing mutations ( $m = .02$ ) leads only to the expected minor change as shown in Figure 10, in which the single EEP is displaced somewhat into the interior of the triangle, the solution being  $(p_c, p_d, p_b) = (.077, .461, .461)$ .

[Figure 9 about here]

Summarizing for the Chicken environment: (1) With TIT FOR TAT as reactive strategy, under selection alone there is an Evolutionary



Equilibrium Region EER representing a range of mixtures of TIT FOR TAT and COWARD (paralleling the Prisoners' Dilemma EER involving TIT FOR TAT and COOPERATE) and an alternative Evolutionary Equilibrium Point EEP representing a unique specific mixture of COWARD and DAREDEVIL players. So there are two types of mixed equilibria, one involving uniformly nice behavior and the other both nice and mean behaviors. However, introducing mutational pressure eliminates the first of these equilibria, leading to a unique EEP quite close to the second equilibrium in which TIT FOR TAT is unrepresented. (2) With BULLY as reactive strategy, under selection alone there is a single EEP mixture of BULLY and DEFECT (both involving mean behaviors); introducing mutations leads only to a small shift of this equilibrium into the interior. (3) As before, the dynamic process generates probability clouds near the evolutionary equilibria and channels of high probability that attract the dynamic trajectories before ultimate equilibrium is attained.

Comparing the evolutionary outcomes, in the Chicken environment TIT FOR TAT does not do nearly so well as in Prisoners' Dilemma, while BULLY does better. Correspondingly, in Chicken TIT FOR TAT is noticeably less effective in eliciting or supporting survival of nice behavior generally.

## 5. SUMMARY AND DISCUSSION

(1) In the actual world a wide diversity of strategies and behaviors persist. Our central aim has been to explore several factors that can support this diversity, even in narrowly specified environments like Prisoners' Dilemma or Chicken and with restricted menus of strategies. Special attention was paid to three sources of diversity: (i) multiple

equilibria and/or equilibria involving mixtures of strategies and behaviors; (ii) random mutations, and (iii) the fact that equilibrium may be approached only slowly, so that high probability may attach to some states or sets of states that are not absolutely stable.

(2) In both Prisoners' Dilemma and Chicken there is a nice strategy C (COOPERATE in Prisoners' Dilemma, COWARD in Chicken) and a mean strategy D (DEFECT in Prisoners' Dilemma, DAREDEVIL in Chicken). As against these two archetype strategies in each environment, we considered two reactive strategies: TIT FOR TAT, and a less friendly one termed BULLY. In contrast with most recent analyses, we allowed reactive players the capacity of "immediate recognition and response" (IRR). This worked to the advantage particularly of TIT FOR TAT, since under IRR a TIT FOR TAT player cannot be exploited by a D player even in the very first round.

(3) For a state of the population to be an Evolutionary Equilibrium Point (EEP), under the dynamic process considered it must be a stationary state or Critical Point (CP) that, in addition, has a convergency zone covering all the points in its (sufficiently small) neighborhood. Intuitively, all nearby trajectories must lead into it. There has been some confusion in the literature as to the necessary and sufficient conditions for evolutionary equilibrium. In particular, Axelrod's "collective stability" is not sufficient for an EEP. We also defined an Evolutionary Equilibrium Region (EER), for which the convergency condition is satisfied by the region as a whole though not for any single point within it.

(4) Without recapitulating the detailed results, TIT FOR TAT in the Prisoners' Dilemma environment, while not as successful as has sometimes been claimed, does support a tendency toward the predominance of nice

behaviors. BULLY, in contrast, survives only thanks to mutation pressure and otherwise has little influence upon the outcome. In the Chicken environment, the picture is somewhat reversed: TIT FOR TAT has little survival value, at least in the presence of mutation pressure, while BULLY survives and supports a tendency of mean behaviors to predominate.

(5) When transient as well as equilibrium states are considered, the possible diversity is of course greater. Transient diversity is not merely random, and a number of systematic patterns can be observed. Most evident are the "probability clouds" in the neighborhood of the various equilibria. Perhaps more interesting, the dynamic process tends to generate "channels of high probability" attracting the trajectories along which the population distributions progress on the way to equilibrium. Transient as against equilibrium states take on enhanced importance if we think of a higher-level process that extinguishes and regenerates populations as a whole at random moments of time. If so, then our probabilistic diagrams can be regarded as snapshots showing how the "population of populations" will be distributed over transient and equilibrium states.

(6) Apart from the sources of diversity considered here, in the world at large wider menus of strategies are available in both Prisoners' Dilemma and Chicken environments. Even more important, strategies are chosen and behaviors take place not only under these payoff conditions but simultaneously under many other payoff conditions as well. Thus there is no reason to expect any single strategy like TIT FOR TAT to emerge as universally superior. Rather, our models and simulations predict (as is in fact observed) a great variety of strategies and behaviors coexisting, each doing relatively well in some environmental contexts but not in others.

## ENDNOTES

<sup>1</sup>Marimon (1988) translates TIT FOR TAT as OJO POR OJO.

<sup>2</sup>"Simulated future rounds of the tournament suggested that TIT-FOR-TAT would continue to thrive, and that eventually it might be used by virtually everyone." [Axelrod (1984), p. 55]

<sup>3</sup>Axelrod also correctly indicated a number of the necessary qualifications. For one thing, if TIT FOR TAT is to be an equilibrium evolutionary outcome the "shadow of the future" must be sufficiently great - the discounting of future payoffs cannot be too severe. Also, in his analyses the all-DEFECT strategy always remained an alternative possible evolutionary outcome (Axelrod [1984], Appendix B).

<sup>4</sup>Other authors, including Molander (1985), Boyd and Lorberbaum (1987), and Mueller (1987), have obtained somewhat analogous results.

<sup>5</sup>The evolutionary equilibrium application to Chicken, under the alternative name Hawk-Dove (Maynard Smith [1976]), actually preceded Axelrod's work on Prisoners' Dilemma. An early contrast of evolutionary outcomes under Chicken and Prisoners' Dilemma was provided in Hirshleifer (1982). Lipman (1986) is a more recent comparison.

<sup>6</sup>While this paper examines only 3-way competitions, elsewhere we have explored 4-way competitions in which both reactive strategies, TIT FOR TAT and BULLY, are simultaneously in play against the two archetype

strategies (Martinez Coll and Hirshleifer [1991]).

<sup>7</sup>Mutation has no close connection with another type of chance variation known as "trembling hand" -- in which a player, while intending to follow some particular strategy, with some small probability accidentally behaves in a way consistent with a different strategy. In mutation the random variation has the player permanently changing his type; in trembling hand, the player's type remains the same but the actual executed move is subject to variation. The latter comes closer to, though still is not quite the same as, the "probability of error" (POE) considered in Hirshleifer and Martinez Coll (1988). The latter concept, applicable only to reactive strategies, referred to recognition errors rather than to execution "trembles."

<sup>8</sup>A number of other sources of variety could be generated by breaking out of the bind of the very simple underlying Prisoners' Dilemma or Chicken game. Members of a single population might be interacting via several distinct games simultaneously, or a single game could be played by interacting populations (buyers encountering sellers, say). Or, it might be possible to append additional archetype choices to either Prisoners' Dilemma or Chicken, for example the PUNISHER strategy mentioned below.

<sup>9</sup>There are actually four rather than only two simple reactive strategies, since a double dichotomy is involved: (i) the initial move can be hard or soft, and (ii) the reactive reply can either mirror or reverse the opponent's move. TIT FOR TAT combines a soft opening with a mirroring reply while BULLY combines a hard opening with a reversing reply. The other two possible combinations do not lack interest, but for reasons of space are not considered here; under a somewhat different approach, they were analyzed

in Martinez Coll (1986).

<sup>10</sup> Interestingly, the biologist John Maynard Smith, who may be regarded as the founder of evolutionary game theory, employed the DRR assumption in one of his earliest articles (Maynard Smith and Price [1973]) but in later papers has more usually used the equivalent of our IRR assumption. In particular, the RETALIATOR strategy in Maynard Smith (1976) is the equivalent of TIT FOR TAT with our IRR assumption; each round lasts long enough for effective recognition and response to influence the payoff in that same round.

<sup>11</sup> We are assuming that only pure strategies are ever employed.

<sup>12</sup> This is one of a number of possible variants of what has been called "replicator dynamics" in the biological literature. The form of equation (4) has the desirable property that  $\Delta^{SEL} p_i$ , the step size, approaches zero as  $p_i$  approaches extinction (goes to zero) or as  $p_i$  approaches fixation (goes to unity). Nevertheless, in any such discrete dynamic formulation the possibility remains of a too-big step that would take  $p_i$  outside the allowable range between zero and one. In our simulations, we took care to keep the sensitivity parameter  $k$  sufficiently small to avoid such an eventuality. Alternatively, it would have been possible to employ a continuous rather than a discrete dynamic equation, replacing  $\Delta p_i$  with the time-derivative  $dp_i/dt$ .

<sup>13</sup> While the individual mutations are probabilistic, equation (5) is expressed in deterministic form. This is equivalent to assuming a population of infinite size.

<sup>14</sup>Mutations are not momentary displacements in this sense; mutations represent a systematic dynamic force in the evolutionary process.

<sup>15</sup>An NE off the main diagonal of the payoff matrix corresponds to a non-vertex Critical Point involving a distribution of the population over the associated row and column strategies. Adjusting equation (9) for such a case, the S within the parentheses describing the state of the population would have to be interpreted as a population distribution. We will not consider such NE's in this paper.

<sup>16</sup>This representation makes use of the geometrical proposition that, for any equilateral triangle, the sum of the distances from any point to the three sides equals the altitude. By setting the altitude equal to 1, the three distances become the population proportions.

<sup>17</sup>And, comparing it with equations (10), we see that it is not sufficient for an ESS either.

<sup>18</sup>Rather like bounty-hunters in the Old West, PUNISHER players make a living from profitable encounters with DEFECT players (criminals). Thus, in an all-COOPERATE population, DEFECT is most profitable; in an all-DEFECT population, PUNISHER is most profitable; in an all-PUNISHER population, COOPERATE is most profitable. (Note the analogy with the children's game of Rock-Paper-Scissors.) It follows that when the PUNISHER strategy becomes available in the Prisoners' Dilemma environment, only interior solutions can maintain themselves even under selection alone.

<sup>19</sup>As an important qualification, the possibility of an EEP depends also upon the values of  $k$  and  $m$ . If  $k$  were sufficiently large relative to  $m$ , all the trajectories might be spiralling outward rather than inward, and no EEP would exist. In this paper we will always be assuming, as pictured in the simulation diagrams, that whenever an evolutionary equilibrium is otherwise possible the dynamic parameters will be such as to permit its existence.

<sup>20</sup>A dominated strategy may sometimes survive as some positive proportion of the population at a Critical Point or at points within an Evolutionary Equilibrium Region, although not at an Evolutionary Equilibrium Point. For example, COOPERATE (which is dominated by TIT FOR TAT in Matrix 3) comprises a fraction of the population in the Evolutionary Equilibrium Region of Figure 2. The explanation is that, once in that region, COOPERATE has the same payoff as TIT FOR TAT. However, in Figure 5 DEFECT dominates BULLY increasingly as the all-DEFECT vertex is approached.

<sup>21</sup>These results are somewhat at variance with Lipman (1986). The main explanations parallel those discussed in our comment on Axelrod: Lipman follows Axelrod in (i) mistaking the so-called "collective stability" concept (i.e., the Nash Equilibrium condition) for an evolutionary equilibrium, and (ii) employing the "deferred response" DRR instead of the "instant response" IRR assumption for the reactive strategies. (The first of these is an analytical error, the second only a modelling difference.)



# SELECTION, MUTATION, AND THE PRESERVATION OF DIVERSITY

## IN EVOLUTIONARY GAMES

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TABLE 1: Prisoners' Dilemma and Chicken -- Basic and Expanded Matrices

<u>Prisoners' Dilemma</u>				<u>Chicken</u>			
Matrix 1				Matrix 2			
	C	D		C	D		
C	3,3	1,4		C	3,3	2,4	
D	4,1	2,2		D	4,2	1,1	
Matrix 3				Matrix 4			
	C	D	T		C	D	T
C	3,3	1,4	3,3	C	3,3	2,4	3,3
D	4,1	2,2	2,2	D	4,2	1,1	1,1
T	3,3	2,2	3,3	T	3,3	1,1	3,3
Matrix 5				Matrix 6			
	C	D	B		C	D	B
C	3,3	1,4	1,4	C	3,3	2,4	2,4
D	4,1	2,2	4,1	D	4,2	1,1	4,2
B	4,1	1,4	2.5, 2.5	B	4,2	2,4	3,3

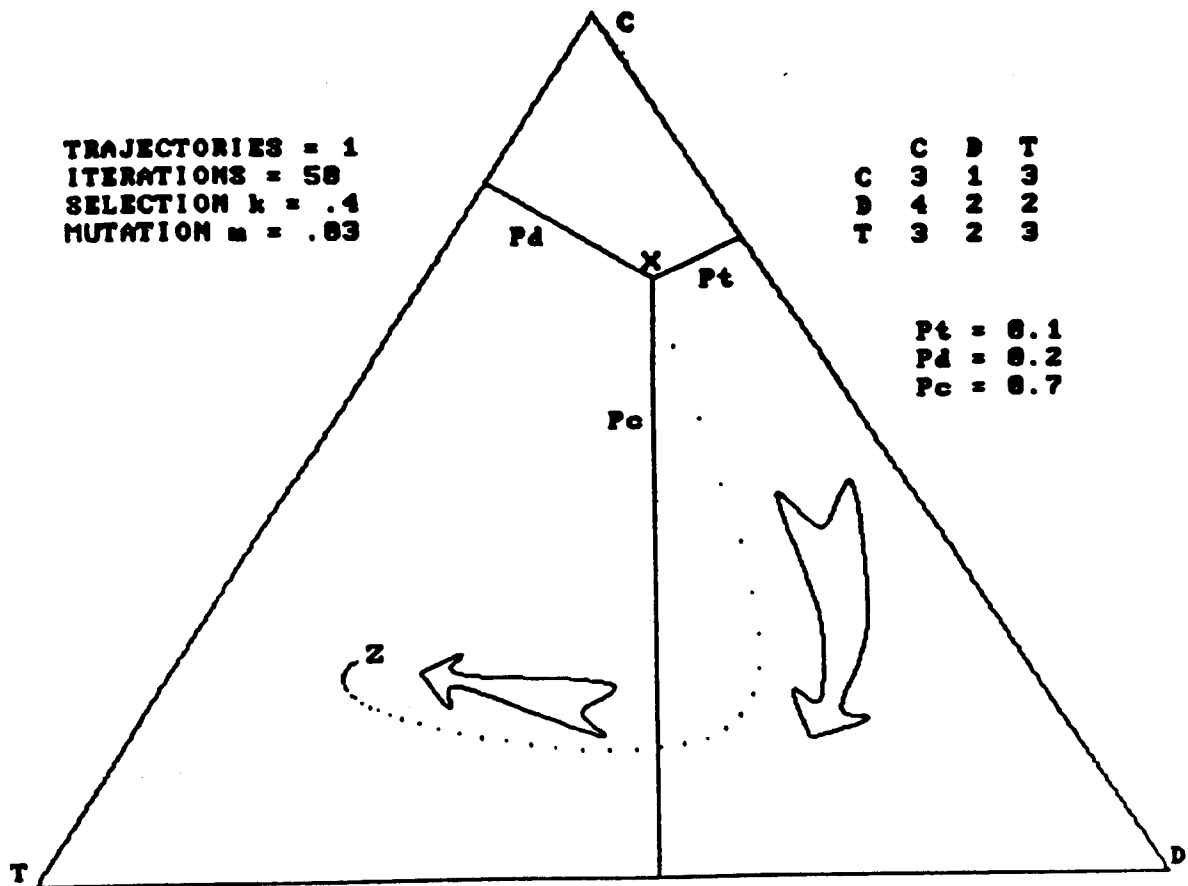


Figure 1: Triangular representation of population states

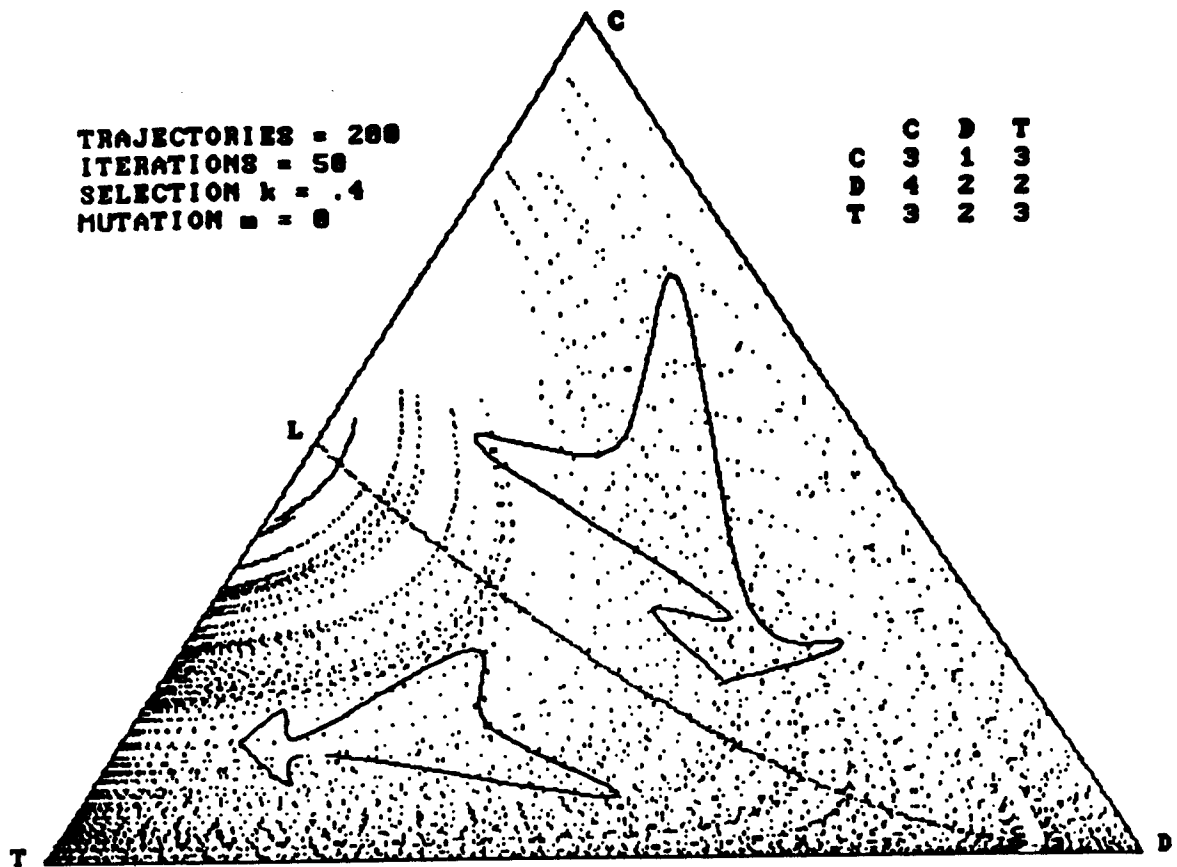
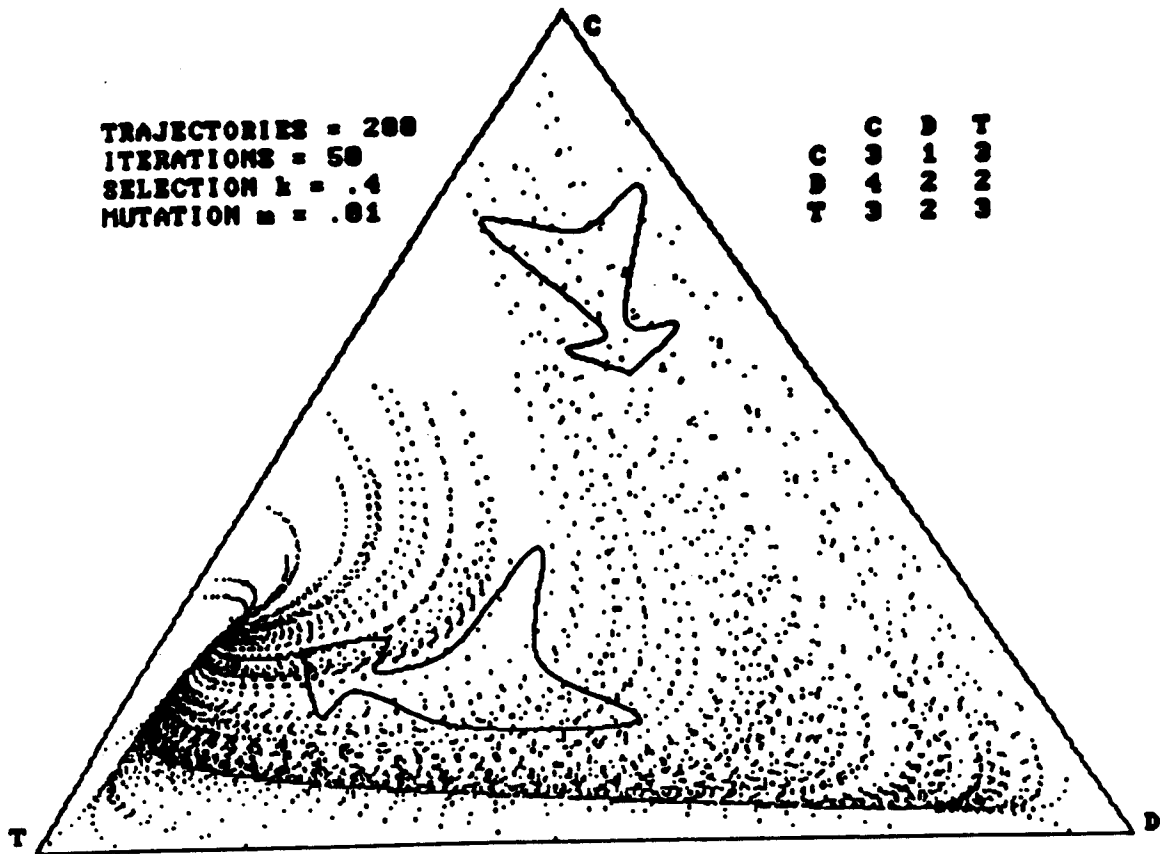


Figure 2: Prisoners' Dilemma plus TIT FOR TAT -- selection alone



**Figure 3:** Prisoners' Dilemma plus TIT FOR TAT -- selection and mutation  
 ( $m = .01$ )

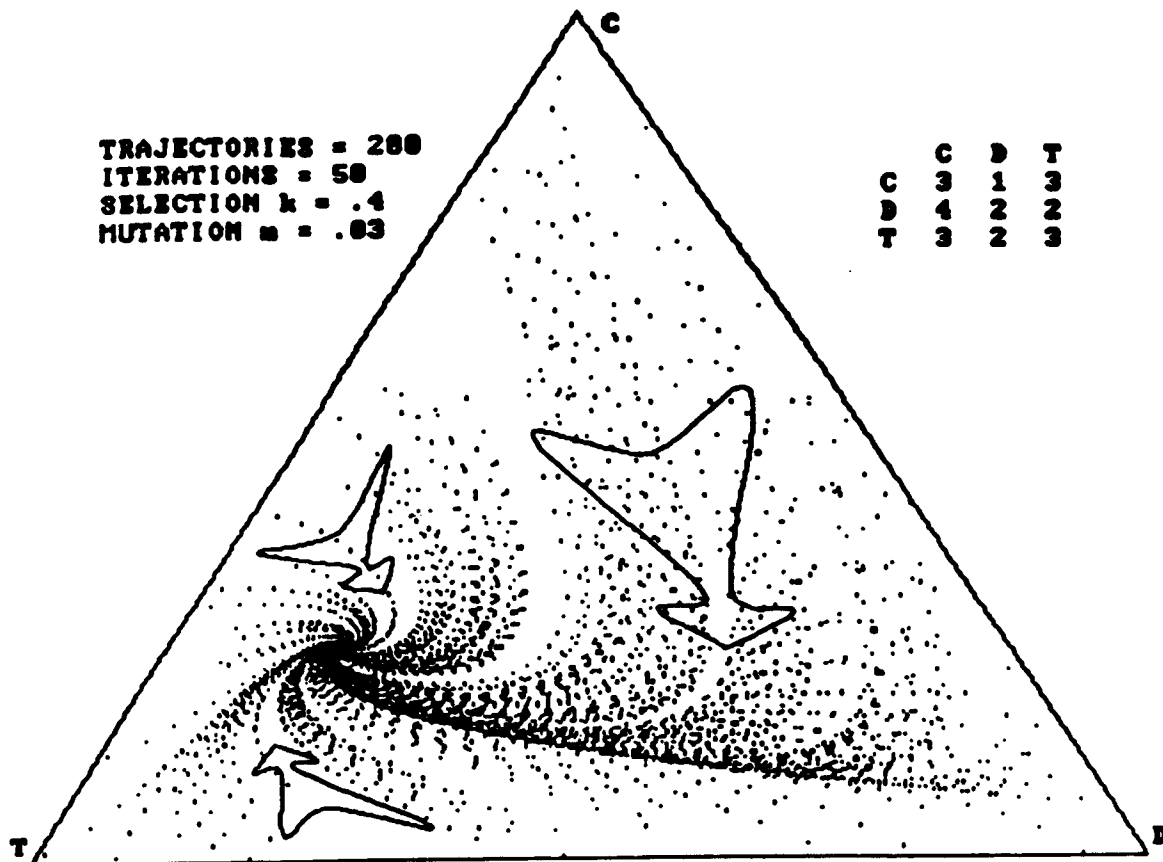


Figure 4: Prisoners' Dilemma plus TIT FOR TAT -- selection and mutation  
 ( $m = .03$ )

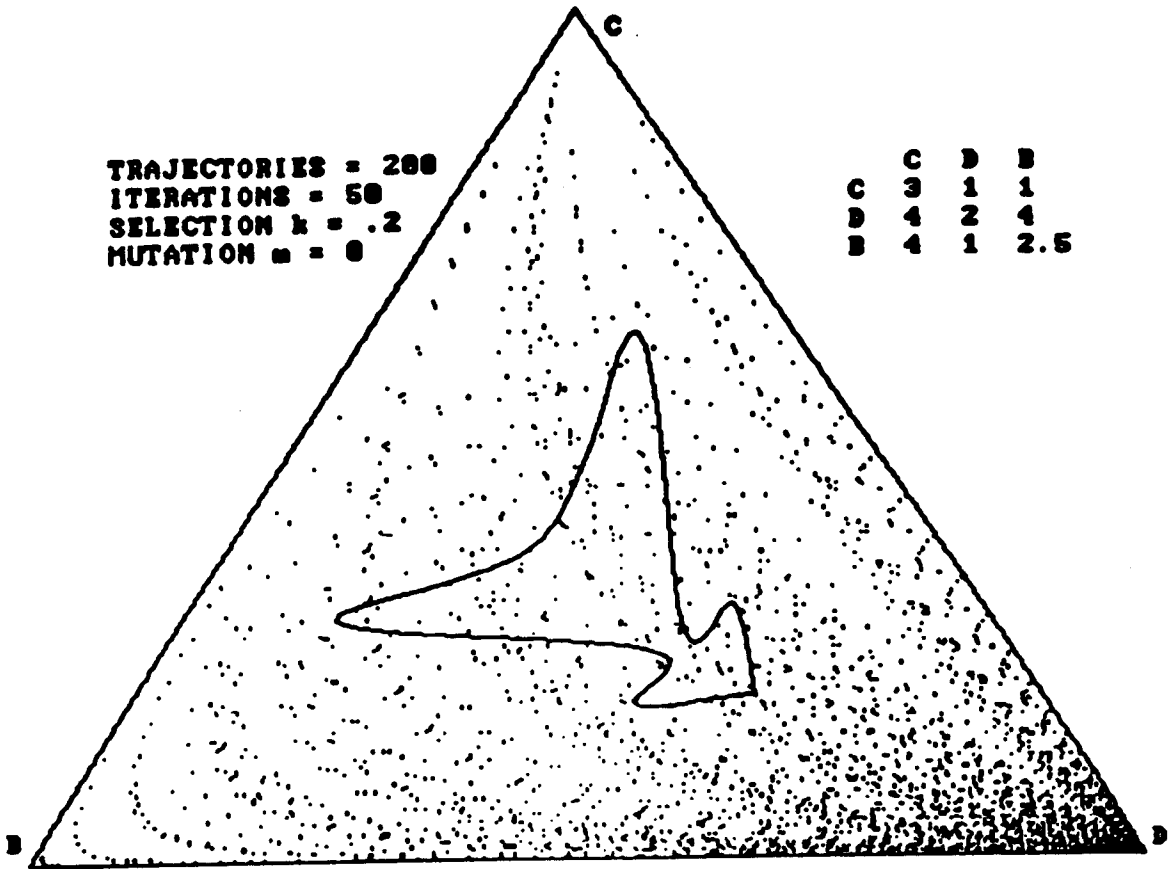


Figure 5: Prisoners' Dilemma plus BULLY -- selection alone



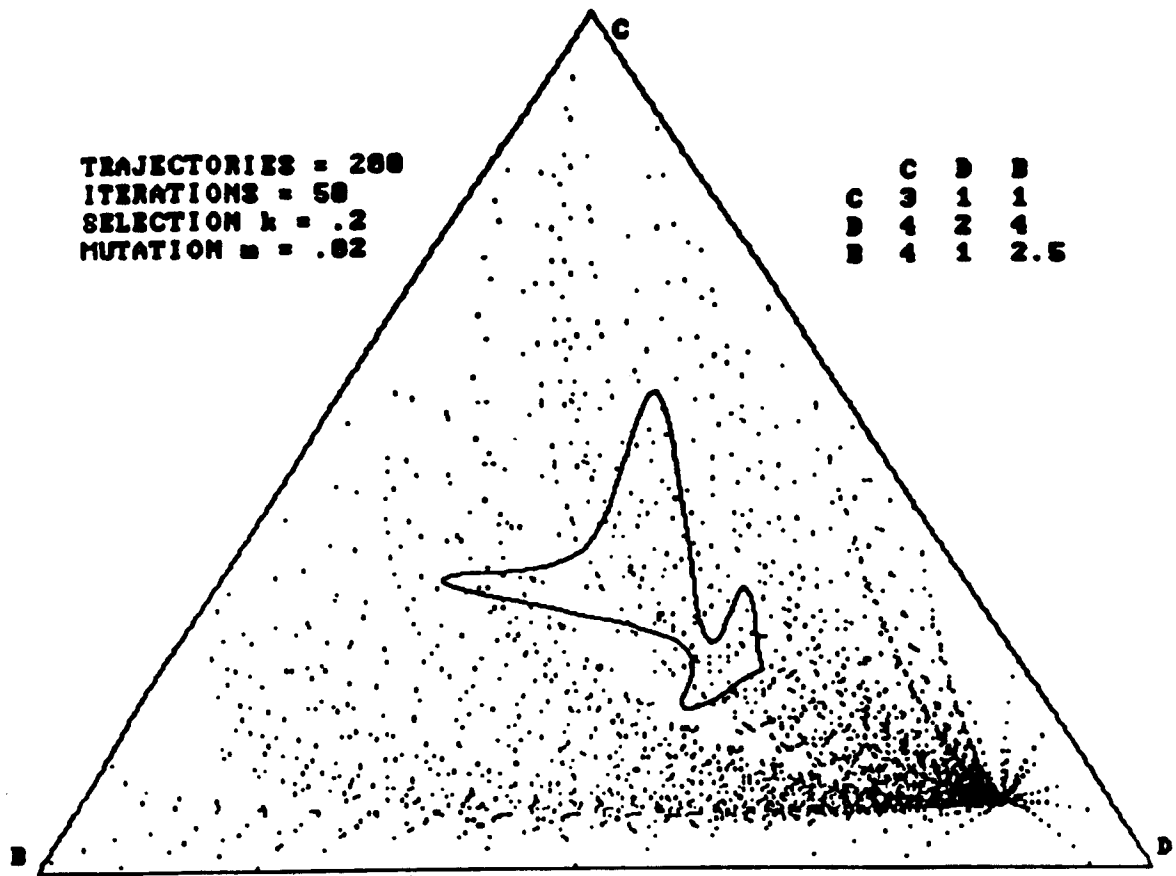


Figure 6: Prisoners' Dilemma plus BULLY -- selection and mutation ( $m = .02$ )

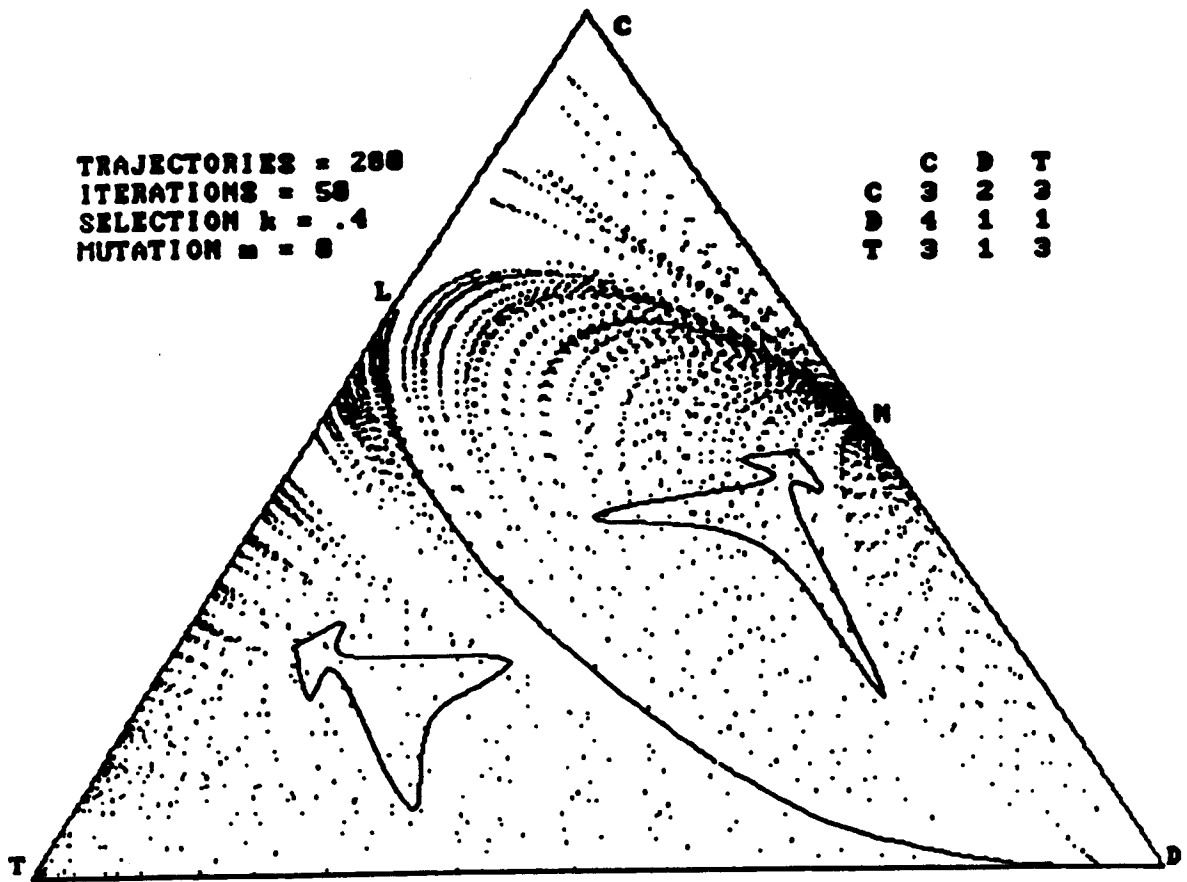


Figure 7: Chicken plus TIT FOR TAT -- selection alone

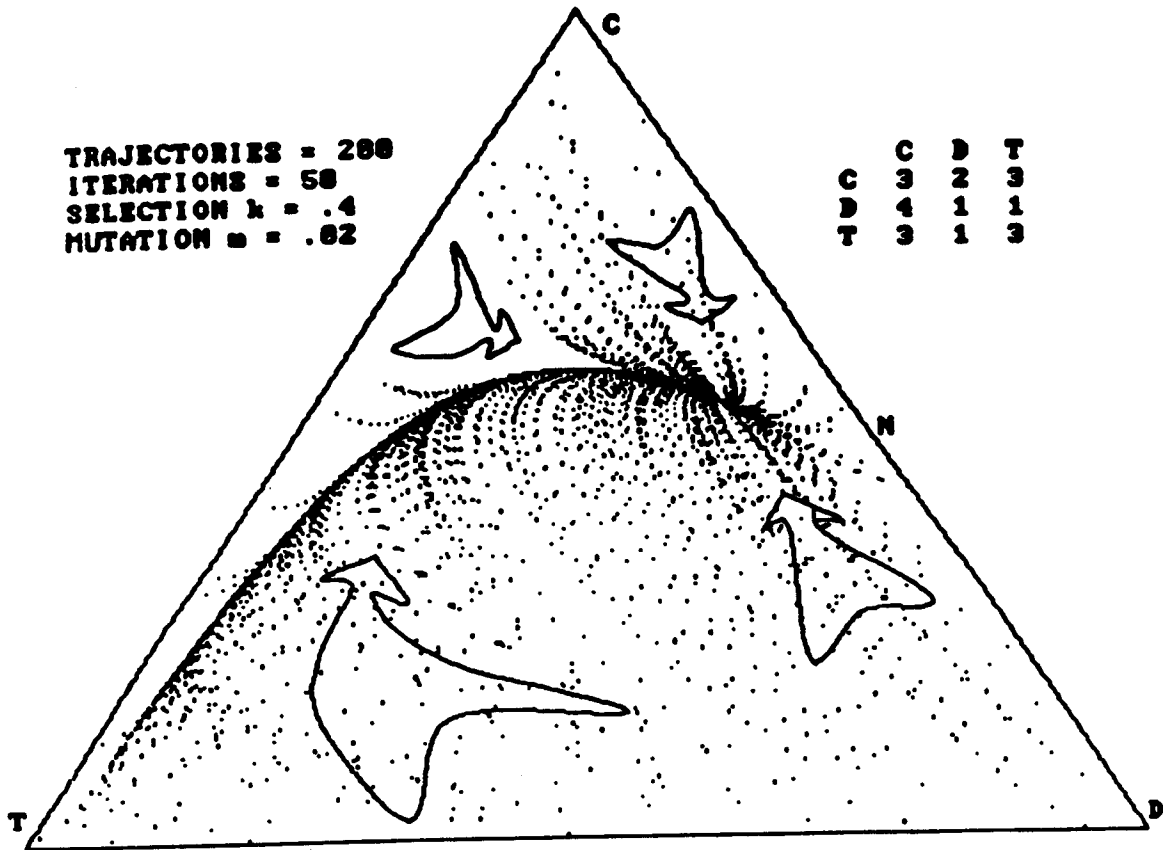


Figure 8: Chicken plus TIT FOR TAT -- selection and mutation ( $m = .02$ )

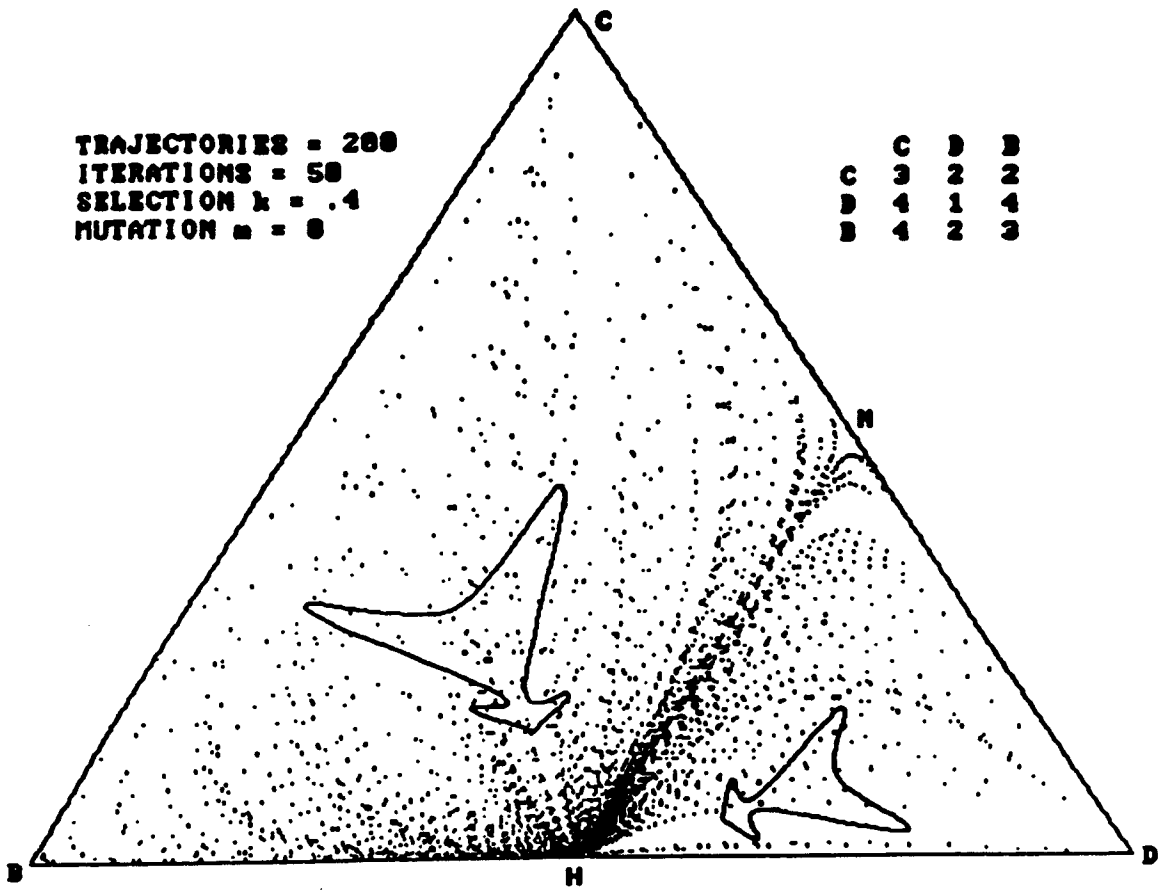


Figure 9: Chicken plus BULLY -- selection alone

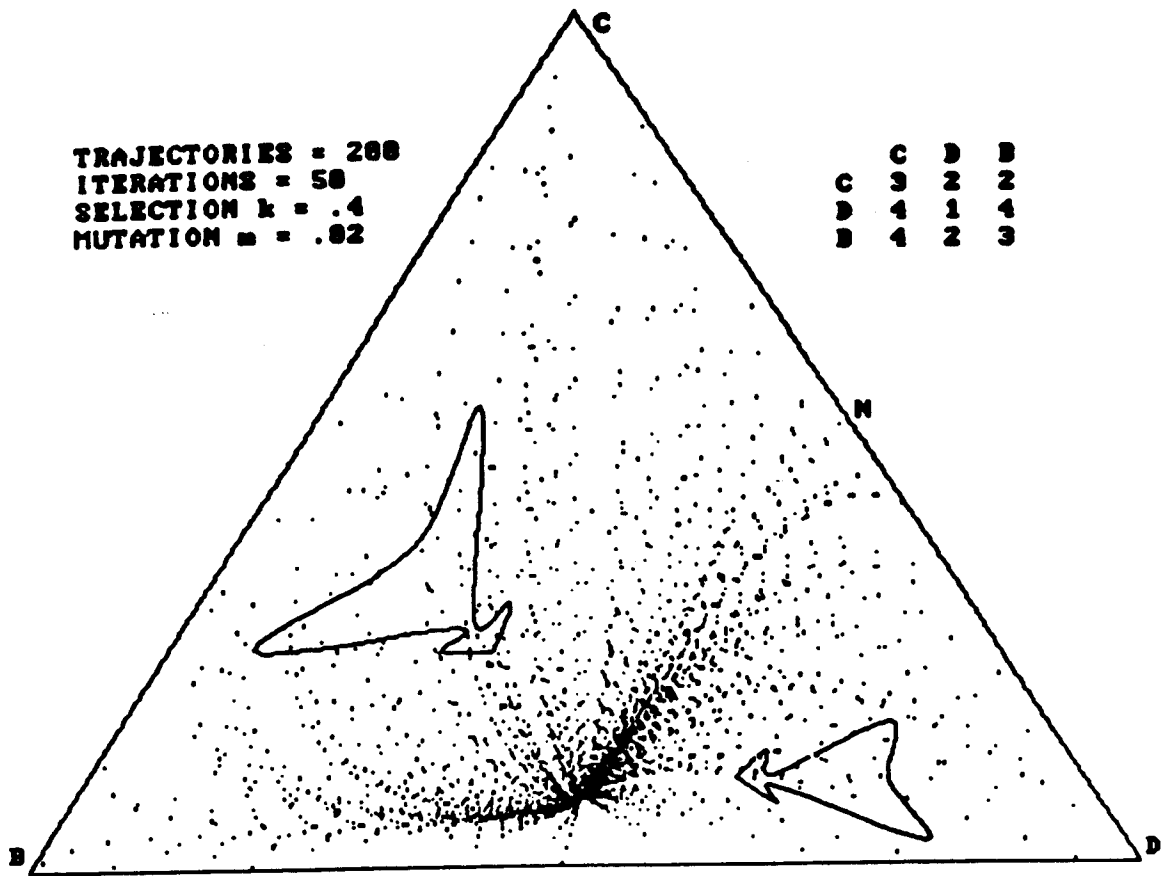


Figure 10: Chicken plus BULLY -- selection and mutation ( $m = .02$ )