Chaos and the evolution of cooperation

MARTIN NOWAK* and KARL Sigmund†

*Department of Zoology, University of Oxford, South Parks Road, OX1 3PS, Oxford, United Kingdom; and †Institut für Mathematik, Universität Wien, Strudlhofgasse 4, A-1090 Vienna, Austria

Communicated by Robert M. May, January 28, 1993

ABSTRACT The “iterated prisoner’s dilemma” is the most widely used model for the evolution of cooperation in biological societies. Here we show that a heterogeneous population consisting of simple strategies, whose behavior is totally specified by the outcome of the previous round, can lead to persistent periodic or highly irregular (chaotic) oscillations in the frequencies of the strategies and the overall level of cooperation. The levels of cooperation jump up and down in an apparently unpredictable fashion. Small recurrent and simultaneous invasion attempts (caused by mutation) can change the evolutionary dynamics from converging to an evolutionarily stable strategy to periodic oscillations and chaos. Evolution can be twisted away from defection, toward cooperation. Adding “generous tit-for-tat” greatly increases the overall level of cooperation and can lead to long periods of steady cooperation. Since May’s paper [May, R. M. (1976) Nature (London) 261, 459–467], “simple mathematical models with very complicated dynamics” have been found in many biological applications, but here we provide an example of a biologically relevant evolutionary game whose dynamics display deterministic chaos. The simulations bear some resemblance to the irregular cycles displayed by the frequencies of host genotypes and specialized parasites in evolutionary “arms races” [Hamilton, W. D., Axelrod, R. & Tenaese, R. (1990) Proc. Natl. Acad. Sci. USA 87, 3566–3573; Seger, J. (1988) Philos. Trans. R. Soc. London B 319, 541–555].

The Prisoner’s Dilemma (PD) is a two-player game: each player can opt for one of the two strategies C (to cooperate) and D (to defect). If both players cooperate, their payoff R is higher than the payoff P for joint defection. But a player defecting unilaterally obtains a payoff T, which is larger than R, while the opponent ends up with a payoff S, which is smaller than P. In addition to this rank ordering, one usually also assumes that 2R < S + T. (For our numerical simulations we shall use the values T = 5, R = 3, P = 1, and S = 0.)

The rational decision in this game is to play D, since this yields the higher payoff no matter whether the opponent uses C or D. As a result, both players defect and earn P instead of the larger reward R for joint cooperation.

If the probability that the players repeat the interaction is sufficiently high, there is no longer a single best strategy for this iterated PD (IPD). But a series of computer tournaments by Axelrod (1) established the success of a remarkably simple strategy, TFT (tit-for-tat), which consists of playing C in the first round and then on repeating whatever the adversary did in the previous round. This led Axelrod and Hamilton (2) to use the IPD for explaining the evolution of cooperation in biological interactions on the basis of reciprocity (see also ref. 3). This approach has proved to be extremely fruitful. It is not the only paradigm, but certainly it is the most current in the field (4–11).

While reciprocal interactions abound in nature, it is usually difficult to find clear-cut empirical evidence for the imple-

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

The Princeton’s Dilemma; IPD, iterated PD; TFT, tit-for-tat; GTFT, generous TFT; AILD, always defect; AIC, always cooperate.

Abbreviations: PD, Prisoner’s Dilemma; IPD, iterated PD; TFT, tit-for-tat; GTFT, generous TFT; AILD, always defect; AIC, always cooperate.
reverts to C again. With initial state C, rule (1, 0, 0, 1) cooperates whenever both players choose the same action in the previous round. It fares poorly against AID, since it reverts each second round to C. For this reason, it has been called “simpleton” by Rapoport and Chammah (25). We think that this appellation is not entirely deserved; following Kraines and Kraines (26), we prefer to call it PAVLOV, since it responds to positive and negative conditioning (switching its behavior whenever one round’s payoff is lower than R) and embodies a learning mechanism of basic interest in social psychology (27–29). There are 16 deterministic rules altogether, which we number from 0 to 15 (the ith quadruple being the binary expression for i). The strategy corresponding to rule i will be denoted by S_i. Thus S_0 is AID, S_6 is PAVLOV, S_9 is TFT, and S_13 is AILC. The S_i strategies are exactly the 16 corner points of the four-dimensional strategy space formed by all (p1, p2, p3, p4) strategies.

We shall now take uncertainty into account by replacing 1 by 1 - $\varepsilon$ and 0 by $\varepsilon$ in the quadruples. The small probability $\varepsilon$ describes the frequency of errors. If $\varepsilon > 0$ the first round no longer matters. The total payoff can be defined as the limit of the mean payoff per round. The game between the two players, S = (p1, p2, p3, p4) and S' = (p1', p2', p3', p4'), is a Markov process given by the transition probability matrix

\[
\begin{pmatrix}
p_1 & p_1(1-p_1) & (1-p_1)p_1' & (1-p_1)(1-p_1') \\
p_2 & p_2(1-p_2) & (1-p_2)p_2' & (1-p_2)(1-p_2') \\
p_3 & p_3(1-p_3) & (1-p_3)p_3' & (1-p_3)(1-p_3') \\
p_4 & p_4(1-p_4) & (1-p_4)p_4' & (1-p_4)(1-p_4')
\end{pmatrix}
\]

The stationary distribution (s1, s2, s3, s4) is the lefthand eigenvector corresponding to the eigenvalue 1. The payoff for strategy S is then given by $R_1s_1 + R_2s_2 + R_3s_3 + P_4s_4$. By this change, the payoff for a TFT player against another drops from 3 to 2.25; against GRIM, it drops from 3 to about 1, etc. On the other hand, a pair of PAVLOV players handle accidental mistakes quite well: they both play D for one round and then revert to C. Against GRIM or TFT, PAVLOV suffers from errors, however. Among the 16 S_i strategies AID and GRIM are the only evolutionarily stable strategies. There are three strategies that receive a payoff very close to full cooperation ($R = 3$) when playing against themselves: these are AILC, (1, 1, 1, 0), and PAVLOV.

We now consider a large population of players using the strategies S_0 to S_15. By $x_i$, we denote the frequency of S_i in a given generation. In each generation all the strategies play the infinitely iterated PD among one another (subject to a small error frequency, $\varepsilon$). It is easy to compute the average payoff $f_i$ for an S_i player (which depends on the composition
of the population. The evolutionary dynamics map the frequencies \( x_i \) after one generation into \( x'_i \) according to the following rule: first selection provides each \( S_i \) strategist with a number of offspring proportional to its expected payoff \( f_i \) (the higher the payoff, the more offspring). To this is added a tiny number of invaders, \( u \), which may be caused by mutation. This yields a deterministic recurrence equation for the frequencies of the strategies:

\[
x'_i = \left( \frac{x_i f_i}{\sum x_j f_j} + u \right)/(1 + nu), \quad i = 1, \ldots, n.
\]

Here \( n \) denotes the total number of strategies in the population.

This modification of the usual game dynamics allows for recurrent and simultaneous invasion attempts. The resulting dynamics can exhibit complicated periodic and even chaotic orbits (see Figs. 1 and 2). The most interesting dynamics occur around \( u = 0.0004 \). Here the strategies \( S_4, S_6, S_7, \) and \( S_{12} \) are driven almost to extinction, but the other strategies and the total payoff for the population display violent oscillations (with large amplitudes for strategies \( S_5, S_6, S_9, S_{10}, \) and \( S_{11} \)). The minima of their frequencies are very close to 0, except for the TFT-like strategy \( S_{10} \), which is best protected against extinction and is in this sense the “safer bet.” But whenever the proportion of TFT players is large, they are superseded by the more generous strategy \( S_{11} \) [whose transition rule (1, 0, 1, 1) forgives a defection by the other player if it was matched by a defection of its own] and PAVLOV (\( S_0 \)). The \( S_{11} \) and PAVLOV population, in turn, is invaded by the parasitic \( S_1 \) (which cooperates only if its defection has met with instant chastisement). This paves the way for the strategies close to AllD (\( S_0 \)) and to GRIM (\( S_4 \)), which in turn leads to the resurgence of TFT. This is the main cycle in the selective mechanics, but the other strategies introduce the twists leading to chaos. Figs. 1 and 2 show the dynamics for the error frequency \( \epsilon = 0.01 \), but other values of \( \epsilon \) give essentially the same results; for example, \( \epsilon = 0.001, \epsilon = 0.0001 \), and even the limiting case, \( \epsilon \to 0 \). Thus the observed complicated dynamics is not a consequence of using highly erroneous strategies, it can also be observed for arbitrary small values of \( \epsilon \). (But note that for \( \epsilon = 0 \) the first moves become important in some interactions. These additional complications will be analyzed in a more technical paper.)

For large error frequencies—e.g., \( \epsilon = 0.1 \)—the interesting dynamics disappear and the population is dominated by defection strategies.

Chaos and irregular oscillations seem to be robust features of the IPD. Not all the 16 \( S_i \) strategies are necessary to display chaotic behavior. Smaller systems can be chaotic as well. (The smallest chaotic system that we found consists of the 10 \( S_i \) strategies AllD, \( S_1, S_5, S_7, \) GRIM, PAVLOV, TFT, \( S_{11}, S_{10}, \) and \( S_{14} \).) Chaos can also be found if one includes a number of other stochastic strategies, given by some arbitrary probabilities \( p_1, p_2, p_3, p_4 \). Complicated dynamics can also be observed within the subset of simpler strategies which are specified by the opponent’s last move (33).

This erratic evolution can be strongly biased toward cooperation if one includes GTFT. We have studied the evolutionary dynamics of a population which consists of the 16 \( S_i \) strategies and GTFT. For larger mutation rates, GTFT makes the oscillations more regular (allowing only period 2) and increases slightly the overall level of cooperation. For small mutation rates, we even find a stable equilibrium dominated by GTFT. For \( u = 0.00001 \), for example, the equilibrium frequency of GTFT is 0.98 and the overall level of cooper-

---

**Fig. 2.** The evolutionary dynamics of the 16 \( S_i \) strategies lead to chaos. Four two-dimensional projections of the chaotic attractor are shown: TFT versus AllD, TFT versus (1, 0, 1, 1), PAVLOV versus AllD, and PAVLOV versus (1, 0, 1, 1). Invasion rate \( u = 0.0004 \); error frequency \( \epsilon = 0.01 \).
ation is 2.96 (rather than 1.15 in the system without GTFT). This success of GTFT is surprising, because AllD and GRIM are still the only evolutionarily stable strategies, and GTFT can be invaded by AllC, (1, 0, 1, 1), (0, 1, 1, 1), and the alternating strategy (0, 0, 1, 1). It seems that very small repeated invasion attempts can twist this system from defection to cooperation. For $\mu = 0$, we observe convergence to either AllD or GRIM.

Chaos and unpredictability may play important roles in the evolution of cooperation. Simple strategies in the IPD can lead to very complicated evolutionary dynamics.

We thank Bill Hamilton, Bob May, and Jon Seger for discussion and comments.