Kristian Lindgren,†
Nordita, Blegdamsvej 17, DK-2100 Copenhagen, Denmark †Permanent address: Institute for Physical Resource Theory, Chalmers University of Technology, S-412 96 Göteborg, Sweden.

Evolutionary Phenomena in Simple Dynamics

We present a model of a population of individuals playing a variation of the iterated Prisoner's Dilemma in which noise may cause the players to make mistakes. Each individual acts according to a finite memory strategy encoded in its genome. All play against all, and those who perform well get more offspring in the next generation. Mutations enable the system to explore the strategy space, and selection favors the evolution of cooperative and unexploitable strategies. Several kinds of evolutionary phenomena, like periods of stasis, punctuated equilibria, large extinctions, coevolution of mutualism, and evolutionary stable strategies, are encountered in the simulations of this model.

INTRODUCTION

In the construction of simple models of abstract evolutionary systems, game theory provides a large number of concepts and examples of games that can be used to model the interaction between individuals in a population. Originally, game theory was developed by von Neumann and Morgenstern for the application to economic theory,[1] but it has now spread to other disciplines as well. The work of Maynard-Smith and Price[15,16] has lead to an increasing use of game theory in evolutionary

Artificial Life II, SFI Studies in the Sciences of Complexity, vol. X, edited by
C. G. Langton, C. Taylor, J. D. Farmer, & S. Rasmussen, Addison-Wesley, 1991

ecology. In the social sciences game theoretical methods have been accepted for a long time. A renewed interest in the Prisoner's Dilemma followed the work of Axelrod and Hamilton,[1,4] who performed a detailed analysis of the iterated version of that game, and this has lead to several game theoretic models based on the iterated Prisoner's Dilemma. In large computer networks the presence of interacting agents may lead to computational ecosystems,[13] which can be analyzed from a game-theoretical point of view.

For a population with a fixed number of species, natural selection drives the system towards a fixed point, limit cycle, or strange attractor, assuming an unchanged environment. This process can be modelled by population dynamics, where one usually uses the number of individuals for the different species as variables, so that the dimensionality of the system equals the number of species. Population dynamics models the reproduction, survival, and death of individuals. If the behavior of the individuals (or species) depends on a genetic description inherited by the offspring, the introduction of mutations in the replication process may totally change the dynamic behavior of the system. One way to characterize such a dynamical system is to interpret mutations leading to new species as creations of new variables and extinction of species as the disappearance of present variables. But in both cases these events are due to the (stochastic) dynamic system itself. If there is no limit on the length of the genetic description and the number of phenotypic characters this is coded into, the system may be considered a potentially infinite-dimensional dynamical system. Evolution can then be viewed as a transient phenomenon in a potentially infinite-dimensional dynamical system.[9,20] If the transients continue for ever, we have *open-ended evolution.* Of course, we may still get the same behavior as in the mutation-free population dynamics. Therefore, one of the main problems in the construction of evolutionary models is how to model the interactions between species (and/or environment) so that the transients are infinite or at least long enough for evolutionary phenomena to appear. In this construction one is faced with the dilemma that one wants to achieve both high complexity, which is necessary for evolution to occur, and simplicity, which makes simulation possible for evolutionary time scales. Note that the dynamics used to model the behavior in prebiotic or chemical evolution is usually a form of population dynamics. Such systems have been analyzed by, e.g., Farmer et al.,[9] Schuster,[21] and Eigen et al.[7] in models for evolution of macromolecules.

We have constructed a model of a population of individuals playing the iterated Prisoner's Dilemma. The game is modified so that noise may disturb the actions performed by the players, which makes the problem of the optimal strategy more complicated. This increases the potential for having long transients showing evolutionary behavior. We construct a suitable coding for all deterministic strategies with finite memory, and let such a code serve as the genome for an individual playing the corresponding strategy. By adding mutations to the population dynamics we get a potentially infinite-dimensional dynamical system in which evolution is possible. The "artificial" selection in the model is determined by the result in the game—those individuals who get high scores also have higher fitness.

The idea of using the iterated Prisoner's Dilemma in evolutionary situations is not new, see, e.g., the studies by Axelrod[2] and Miller,[17] and a variety of other kinds of evolutionary models can be found in Langton.[14] The novel approach in this study is the combination of noisy games, simple population dynamics, analytically solvable interactions, and the possibility of increase in genome length, and it appears that this leads to a richness in evolutionary behavior that has not been observed in such models before.

THE PRISONER'S DILEMMA

The Prisoner's Dilemma is a two-person non-zerosum game, which has been used in both experimental and theoretical investigations of cooperative behavior. The game is based on the following situation. Two persons have been caught and are suspected of having committed a crime together. There is not enough evidence to sentence them, unless at least one of them confesses. So, if both stay quiet (cooperate, C) they will be released. If one confesses (defects, D) but the other does not, the one who confesses will be released and rewarded, while the other one will get a severe punishment. Finally, if both confess, they will be imprisoned but for a shorter period. It is assumed that they make their choice of action simultaneously without knowing the others decision.

This problem is formalized by assigning numerical values for each pair of choices. An example of such a payoff matrix for the players is shown in Table 1.

If the game is viewed as a single event, each player finds defection to be the optimal behavior, regardless of the opponents action. However, if there is a high probability that the two players will meet again in the same type of game, the question of the most optimal choice of action is more delicate. This kind of "iterated

TABLE 1 The payoff matrix we use in the Prisoner's Dilemma is the same as the one used by Axelrod.[1] The pair (s_1, s_2) denotes the scores to players 1 and 2, respectively

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	(3, 3)	(0, 5)
	Defect	(5, 0)	(1, 1)

Prisoner's Dilemma" has been extensively studied by Axelrod.[1] From the results of a computer tournament, he found that a simple strategy called Tit-for-Tat (TFT) showed the best performance in the iterated game. Tit-for-Tat starts with cooperation and then repeats the opponents last action. Thus, two TFT players meeting each other in a series of games, share the highest possible total payoff and each gets an average score of 3.

In our model we shall let noise interfere with the actions of the players. With probability p the performed action is opposite to the intended one. (We shall assume that the average length T of the game is much longer than the average time between noise-modified actions, $T \gg 1/(2p)$.) For two players using the TFT strategy the result is that they will alternate between three modes of behavior. First they will play the ordinary TFT actions (C, C), but when an error occurs they will shift to alternating (C, D) and (D, C). The third possibility of behavior is sequences of (D, D). The average probability for the three modes are 1/4, 1/2, and 1/4, respectively, giving an average payoff of 9/4. None of the strategies in Axelrod's tournament was able to deal with noise *and* resist exploitation, and TFT turned out to be the best one in that set of strategies.[1] A simple strategy that is more stable to noise is Tit-for-Two-Tats, which defects only if the opponent defects twice in a row, but this strategy is vulnerable to exploiting strategies, and in an evolutionary context it should perform worse. Another way to decrease the sensitivity to noise is to allow for the strategies to choose among different actions according to a certain probability (mixed strategies). This approach has been analyzed by Molander,[18] who found that a strategy which mixes TFT with ALLC (always cooperate) can reach an average score very close to 3. In our model we shall assume that the strategies are deterministic (pure strategies), and in the simulations we shall see that there are deterministic, noise-robust, unexploitable strategies that reach an average score of almost 3.

FINITE MEMORY AND INFINITE GAMES

GENETIC CODING OF STRATEGIES

In the model we allow for deterministic finite memory strategies. This means that a finite history determines the next intended action, although the performed action can be changed by the noise. An m-length history consists of a series of previous actions starting with the opponent's last action a_0, the individual's own last action a_1, the opponent's next to last action a_2, etc. By introducing a binary coding for the actions, 0 for defection and 1 for cooperation, we can label an m-length history by a binary number

$$h_m = (a_{m-1}, \ldots, a_1, a_0)_2 .$$

Since a deterministic strategy of memory m associates an action to each m-length history, it can be specified by a binary sequence

$$S = [A_0, A_1, \ldots, A_{n-1}] .$$

This sequence then serves as the genetic code for the strategy that chooses action A_k when history k turns up. The length n of the genome equals 2^m.

In the population dynamics we shall allow for three kinds of mutations: point mutations, gene duplications, and split mutations. The point mutation changes a symbol in the genome, e.g., [01] → [00], the gene duplication attaches a copy of the genome to itself, e.g., [01] → [0101], and the split mutation randomly removes the first or second half of the genome, e.g., [1001] → [01]. Note that gene duplication does not change the phenotype. The memory capacity is increased by one but the additional information is not used in the choice of action. For point mutations we have used the rate 2×10^{-5} per symbol and genome, and the other mutations occur with probability 10^{-5} per genome. Regarding a position in the genome as a locus and a symbol as an allele rather than a base pair, the point mutation rate we use has the order of magnitude that has been estimated for mutation rates at loci in living systems.[11]

For strategies of memory one, the histories are labeled 0 and 1, corresponding to the opponent defecting and cooperating, respectively. The four memory 1 strategies are [00], [01], [10], and [11]. The strategy [00] always defects (ALLD), [01] cooperates only if history 1 turns up (i.e., the opponent cooperated), and we recognize it as Tit-for-Tat, [10] does the opposite and we denote it Anti-Tit-for-Tat (ATFT), and [11] always cooperates (ALLC). We use equal fractions of these strategies as the initial state in the simulations.

SOLVING THE GAME

If the length of the game is infinite, the stationary distribution over finite histories can be solved analytically. This solution is unique if noise disturbing the actions is present. Although the game is infinite, the strategies can only take into account a finite history when choosing an action, which means that the infinite game is a Markov process. The average payoff for two players meeting in this game can be derived from the probabilities p_{00}, p_{01}, p_{10}, and p_{11} for all possible pairs of action (11), (10), (01), and (00). These can be found if we solve the equation

$$H = MH , \tag{1}$$

where $H^T = (h_0, h_1, \ldots, h_{n-1})$ is the vector of probabilities for different histories $0, 1 \ldots, n-1$, and M is a transfer matrix. The elements of M are determined by the strategies involved in the game including the possibility of making mistakes. The minimal size n of the matrix is given by the memory sizes of the involved strategies and is 2^m if the largest memory is m (or 2^{m+1} if m is odd and both players have the same memory size). Then one gets p_{ij} by summing the appropriate components in H, and the average payoff is

$$s = 3p_{11} + 5p_{01} + p_{00} , \tag{2}$$

according to the payoff matrix in Table 1.

POPULATION DYNAMICS

We shall consider a system consisting of a population of N individuals interacting according to the iterated Prisoner's Dilemma with noise. Each individual acts according to a certain strategy encoded in its genome. We think of a population sharing the same niche, fighting or cooperating with each other, to get a part of the available resources for survival and reproduction. In *each* generation all individuals play the infinitely iterated Prisoner's Dilemma against all, and the score s_i for individual i is compared to the average score of the population, and those above average will get more offspring in the next generation. In the reproduction, mutations may occur leading to the appearance of new strategies.

We model this situation as follows. First, we identify the different genotypes present in the population, and let them meet in the game described above. Let g_{ij} be the score for the strategy of genotype i playing against the strategy of j, and let x_i be the fraction of the population occupied by genotype i. Then, the score s_i for an individual with genotype i is

$$s_i = \sum_j g_{ij} x_j \,, \tag{3}$$

and the average score is

$$s = \sum_i s_i x_i \,. \tag{4}$$

The fitness w_i of an individual is defined as the difference between its own score and the average score,

$$w_i = s_i - s \,. \tag{5}$$

From one generation t to the next $t+1$, we assume that due to the result of the interactions, the fraction $x_i$of the population for genotype i changes according to

$$x_i(t+1) - x_i(t) = d w_i \; x_i(t) \,, \tag{6}$$

where d is a growth constant. This equation can also be written in the following form

$$x_i(t+1) - x_i(t) = d s_i \; x_i(t) \left(1 - \sum_j \frac{s_j x_j(t)}{s_i} \right) , \tag{7}$$

which is a logistic equation for a population of competing species.[11] The carrying capacity is normalized to 1, and the competition coefficients for species i are $s_j/s_i (j = 1, 2, \ldots)$. Note that this growth equation conserves the total population size. If x_j falls below $1/N$ for a certain genotype j, we set $x_j = 0$ and that species has died out. When this happens, the fractions x_i have to be renormalized for the population size to be constant. When mutations are present there is an additional stochastic term m_i in the growth equation. If the mutation rates are small ($p_p + p_d + p_s \ll 1/N$), the additional term is well approximated by

$$m_i = \frac{1}{N} \sum_j (Q_{ij} - Q_{ji}) \,, \tag{8}$$

where Q_{ij} is a stochastic variable taking the value 1 if a gene j mutates to the gene i, and 0 otherwise. The probability for Q_{ij} to be 1 is

$$P(Q_{ij} = 1) = N x_j q_{ij} \,, \tag{9}$$

where q_{ij} is the probability that genotype j mutates to i, obtained from the mutation rates and the genotypes i and j. (This mutation may be composed of one gene duplication and several point mutations, although this is less frequent.) Due to the term m_i, new genotypes may appear in the time evolution, and we get a model with a potentially infinite state space.

SIMULATION RESULTS AND DISCUSSION

The system described above consists of a population of N individuals interacting according to the iterated Prisoner's Dilemma with a probability p for mistake (noise). Individuals who get high scores get more offspring in the next generation than those who get low scores. In this reproduction we allow for mutations to occur and new strategies to enter the game.

We model the dynamics of this system by Eqs. (6)–(9), and the parameters that enter are the growth rate d, the mutation rates p_p, p_d, and p_s, the population size N, and the error probability p. In the simulation example the parameter values are $N = 1000, p = 0.01, p_p = 2 \times 10^{-5}, p_d = p_s = 10^{-5}$, and $d = 0.1$, and we have also restricted the length of the genetic code to be at most 32, i.e., at most strategies of memory 5. For the first generation we have chosen equal fractions of the four strategies with memory one, i.e., $x_{00} = x_{01} = x_{10} = x_{11} = 1/4$.

Almost all simulations have in common that during the evolution the system passes a number of long-lived metastable states (periods of stasis) that appear in a certain order. These periods are usually interrupted by fast transitions to unstable dynamic behavior or to new periods of stasis. Below we shall discuss the evolutionary phenomena observed in a typical simulation of the model. In the four most common periods of stasis we find examples of coexistence between species, exploitation, spontaneously emerging mutualism (symbiosis), and unexploitable cooperation.

THE EVOLUTION OF STRATEGIES OF MEMORY 1.

In Figure 1 the development of the population for the first 600 generations is shown. During the first 150 generations, the dynamics drives the system of the 4 strategies towards a population mainly consisting of TFT strategies. The All-D strategy [00] exploits the kind All-C strategy [11] and the ATFT strategy [10], and consequently [00] increases its fraction of the population. When the strategies [11] and [10] are extinct, the average score for All-D is close to 1 and the more cooperative Tit-for-Tat strategy takes over the population.

However, Tit-for-Tat only reaches an average score of 9/4 since noise interferes with the interaction. Then, through a point mutation [01] → [11], the All-C strategy enters the scene again. The mutant gets an average score of almost 3, and thus the fraction of [11] rapidly increases. Next, it is favorable for a mutant [11] → [10] to survive, since ATFT exploits ALLC and plays fairly well against TFT. Actually, ATFT gets the same score $s = 9/4$ as TFT when playing against ATFT or TFT. When the population of ATFT has grown large enough, mutations from [01] and [10] to [00] will survive, and the fraction of ALLD increases again. The system oscillates, driven by the relatively fast population dynamics in combination with the point mutations.

In Figure 2 the time scale is compressed by a factor of 50, and the evolution of the first 30000 generations is shown. The picture we get is a history with stable periods interrupted by fast transitions or unstable dynamics. The average score for the same simulation is drawn in Figure 3, which shows that there is no general tendency towards higher scores, although the simulation seems to end in a stable high score state. In the same figure the number of species per generation is depicted, showing that the dimensionality of the system can increase and decrease in the evolution.

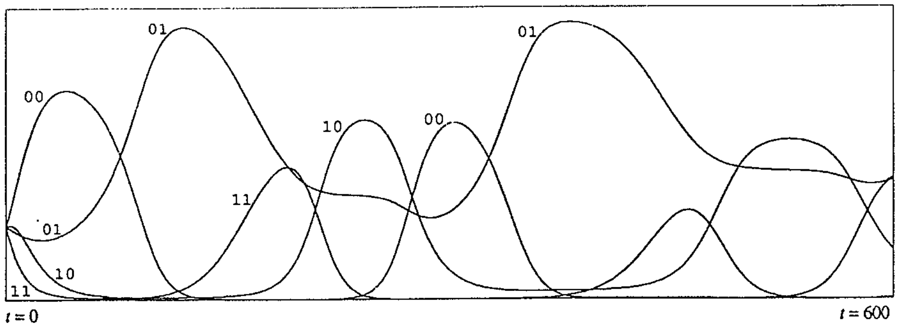

FIGURE 1 The evolution of a population of strategies starting with equal fractions of the memory one strategies [00], [01], [10], and [11] is shown for the first 600 generations. The fractions of different strategies are shown as functions of time (generation).

After some thousands generations the oscillations observed in Figure 1 are damped out, and the system stabilizes with a mixture of TFT [01] and ATFT [10]. If only the four simplest strategies are taken into account, this situation is easily analyzed. Assume that the population is divided into two fractions, one consisting

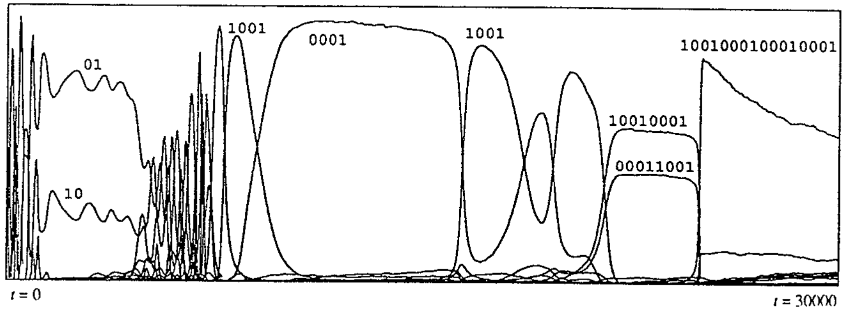

FIGURE 2 The simulation of Figure 1 is continued for 30000 generations, showing that four periods of stasis appear in the evolution. The oscillations observed in Figure 1 are damped and the system reaches a period of stasis with coexistence between [01] (TFT) and [10] (ATFT). This stasis is punctuated by a number of memory 2 strategies, and after a period of unstable behavior the system slowly stabilizes when the strategy [1001] increases in the population. This strategy cooperates if both players performed the same action last time. For two individuals using this strategy, an accidental defection by one of the players leads to both players defecting the next time, but in the round after that they return to cooperative behavior. Thus, the strategy [1001] is cooperative and stable against mistakes, but it can be exploited by uncooperative strategies. Actually, one of its mutants [0001] exploits the kindness of [1001], which results in a slow increase of [0001] in the population. This leads to a long-lived stasis dominated by the uncooperative behavior of [0001]. A slowly growing group of memory 3 strategies is then formed by mutations, and the presence of these species causes the fractions of the strategies [0001] and [1001] to oscillate. Two of the memory 3 strategies, M_1=[10010001] and M_2=[00011001], manage to take over the population, leading to a new period of stasis. Neither M_1 nor M_2 can handle mistakes when playing against individuals of their own kind, but if M_1 meets M_2 they are able to return to cooperative behavior after an accidental defection. This polymorphism is an example of mutualism which spontaneously emerges in this model. The stasis is destabilized by a group of mutants, and we get a fast transition to a population of memory 4 strategies which are both cooperative and unexploitable.

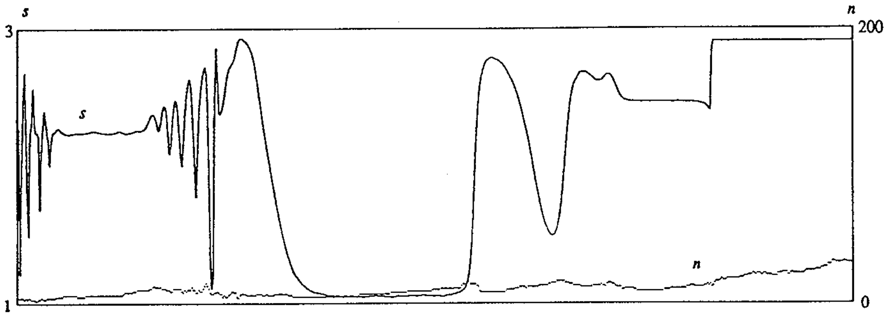

FIGURE 3 The average score s (continuous line) and the number of genotypes n (broken line) are shown for the simulation of Figure 2. When the exploiting memory 2 strategy dominates the scene, the average score drops close to 1. The last stasis, populated by the evolutionary stable memory 4 strategies, reaches a score of 2.91, close to the score of 3 achieved by the best strategies in a noise-free environment. Before the transitions and in the periods of unstable behavior, it appears that there are more mutants that survive and the number of genotypes increases, suggesting that most of the evolution takes place in these intervals.

of TFT and one of ATFT, and denote the fraction of the first by x. Then, for a large population, if $x < 7/16$ a mutant [00] will start to replicate, and if $x > 3/4$ any mutation to [11] will survive and replicate. But, if $7/16 < x < 3/4$ there is a meta-stable state consisting of a mixture of TFT and ATFT. This state is long-lived because none of the one-step mutations [00], [11], [0101], and [1010] are able to disturb the system. Actually, a detailed analysis shows that the only strategy with memory 2 that can invade this population alone and survive is the strategy [1100] which alternates between C and D, regardless of the opponent's action. However, this is not the usual way the stasis collapses, since one gene duplication and two point mutations are needed to get [1100] from [01] or [10]. Usually, a number of strategies, all having small fractions of the population, have a combined effect and cause the destabilization.

THE EVOLUTION OF STRATEGIES OF MEMORY 2.

The first stasis is usually followed by a period of unstable behavior, as is examplified in Figure 2. When the system stabilizes the strategy A=[1001] manages to dominate the population for some time. This strategy chooses C when the last pair of actions (the own and the opponent's) was CC or DD, which means that two individuals, both playing this strategy, get scores close to 3 when playing against each other. A typical history including a misaction **D** looks as follows (CC, C**D**, DD, CC, CC, ...), showing that the strategy is not sensitive to the noise. On the other hand the strategy can be exploited by one of its mutants, B=[0001]. When the strategy A plays against B, there are two modes of behavior, examplified by the following types of histories: (CC, CC, CC, ...) and (DD, CD, DD, CD, ...) where the second action in each pair is due to B. The second mode appears with frequency 0.80 and its average payoff is 3 for B and only 1/2 for A. Although the strategies A and B have totally different behavior (cooperative and uncooperative, respectively), the scores they receive are very close. This leads to a slow increase of B, while A decreases in the population, see Figure 2. Even a small group of mutants can then influence their scores so that the dominant strategy scores less than the rival species, which explains the oscillatory pattern that follows.

THE EVOLUTION OF STRATEGIES OF MEMORY 3.

During the time period dominated by the memory 2 strategies, a group of mutants containing memory 3 strategies is slowly growing. In Figure 2 we see two new strategies $M_1 = [10010001]$ and $M_2 = [00011001]$ spread in the population. A new stasis is reached between M_1 and M_2, and we shall analyze their behavior in more detail. The histories below exemplify how these strategies act when a single noise-induced **D**-action occurs.

M_1:M_1	M_2:M_2	M_1:M_2	M_2:M_1
C C	C C	C C	C C
C **D**	C **D**	C **D**	C **D**
D D	D D	D D	D D
C D	D C	C C	D D
D D	D D	C C	D C
C D	C D	C C	D D
D D	D D	C C	C C
C D	D C	C C	C C
.	.	.	.
.	.	.	.
.	.	.	.

Individuals playing against the same strategy type are not able to handle the noise, but when the strategies M_1 and M_2 play against each other they manage to return to a cooperative mode after a series of intermediate actions. The strategies respond to a disturbance D with a certain pattern of actions which fits to the opponents actions. This leads to a payoff close to 3 when they meet, but the payoff when M_1 meets M_1 is $S_{1:1} = 2.17$, and this is even worse for M_2, $s_{2:2} = 1.95$, because M_2 also has a mode consisting of a series of defect actions. Obviously, this strategy mix is an example of mutualism. The success of one of them is dependent on the success of the other one, and in Figure 2 we see that they spread simultaneously in the population.

THE EVOLUTION OF STRATEGIES OF MEMORY 4.

During the stasis of the two symbiotic strategies a group of mutants is formed and their fraction of the population is slowly increasing. The stasis ends with a fast transition to a new meta-stable state, consisting of two leading strategies and a growing group of mutants. All of these strategies have memory 4, i.e., they take into account the actions performed by both players the previous 2 time steps. There are several genotypes that can take the role of the leading one in this transition, because there is a class of genotypes coding into phenotypes or strategies that have practically the same behavior. All of them are cooperative, and if one player accidently defects both players defect twice before returning to the cooperative mode again. This assures that the strategy cannot be exploited by evil strategies at the same time as the mistakes only marginally decrease the average payoff. In the schematic genome E = [1xx10xxx0xxxx001] the most frequently used positions are shown and each x corresponds to a history occurring with a probability of order p^2 or less. There are 512 strategies fitting this mask, which explains the formation of a large genetic variety in this population, although some of these may have imperfections that can be exploited by other strategies. A typical game involving an accidental defect action **D** is shown below.

E : E
C C
C **D**
D D
D D
C C
C C
.
.
.

In Figure 2 [1001000100010001] has taken the lead, but there are others present in the growing group of quasi-species. The fact that the fraction of the leading genotype decreases can be explained by the small difference between the leading strategy and many of the strategies among the mutants. It should also be noted that since the length of the genome doubles each time the memory capacity is increased by 1, the probability for point mutations also doubles.

An important stability criterion for a strategy in a population dynamics model is given by the concept of an *evolutionary stable strategy.*[15] Assume that all individuals in a large population play a certain strategy S. The strategy S is evolutionary stable if any sufficiently small invading group of strategies dies out. It has been shown that, in the iterated Prisoner's Dilemma without noise, the Tit-for-Tat strategy is not evolutionary stable, because there are other strategies playing on equal terms with TFT at the same time as they perform better against other strategies. It has been shown by Boyd and Loberbaum[6] that there is no pure strategy that is evolutionary stable in the iterated Prisoner's Dilemma. A generalization of their result shows that this also holds for any finite population mixture of pure strategies.[10]

For the iterated Prisoner's Dilemma used in our model the presence of noise implies that every strategy can be regarded as a mixture of two opposite pure strategies, which allows for evolutionary stable strategies to exist.[5] Actually, the leading strategy in Figure 2 is evolutionary stable. A strategy that is simpler to analyze is $E_0 = [1001000000000001]$, which defects whenever the behavior deviates from the pattern in the game example above. This implies that no strategy can exploit it, and no strategy can invade a population of these by trying to be more cooperative, because any such attempt would be favorable to E_0 and it would reduce the payoff for the intruder. (Note that E_0 actually exploits the kind strategy [11].) However, even if the one-step mutants play slightly worse than the master species the mutation rate may be large enough for a net increase of these mutants, which leads to a growing group of quasi-species. In the simulations of our model we find that a large group of quasi-species is formed.

PATHWAYS FOR OPEN-ENDED EVOLUTION?

The scenario described above, passing periods of stasis dominated by strategies of increasing memory and then getting stuck in the evolutionary stable stasis, occurs with a probability of about 0.9. There are, however, evolutionary pathways that avoid the evolutionary stable memory 4 strategies. In Figure 4 an example of such a simulation is shown, and instead of getting to the stasis of the symbiotic species (see Figure 4(a)), the system takes a new way in state space and in Figure 4(b) we find the population dominated by memory 4 strategies not present in the ordinary simulations. The bottom diagram of Figure 4(b) shows that the number of genotypes (most of these are also of different phenotype) may increase to more than 200. In the figure it is seen that the system undergoes a collapse in which most of the genotypes disappears in a few hundred generations. Similar extinctions occur also in Figure 4(c), but they do not involve that many genotypes. In all these events the average score drops fast, suggesting that the extinctions are due to a mutant that exploits the present strategies but is unable to establish a cooperative behavior with its own species.

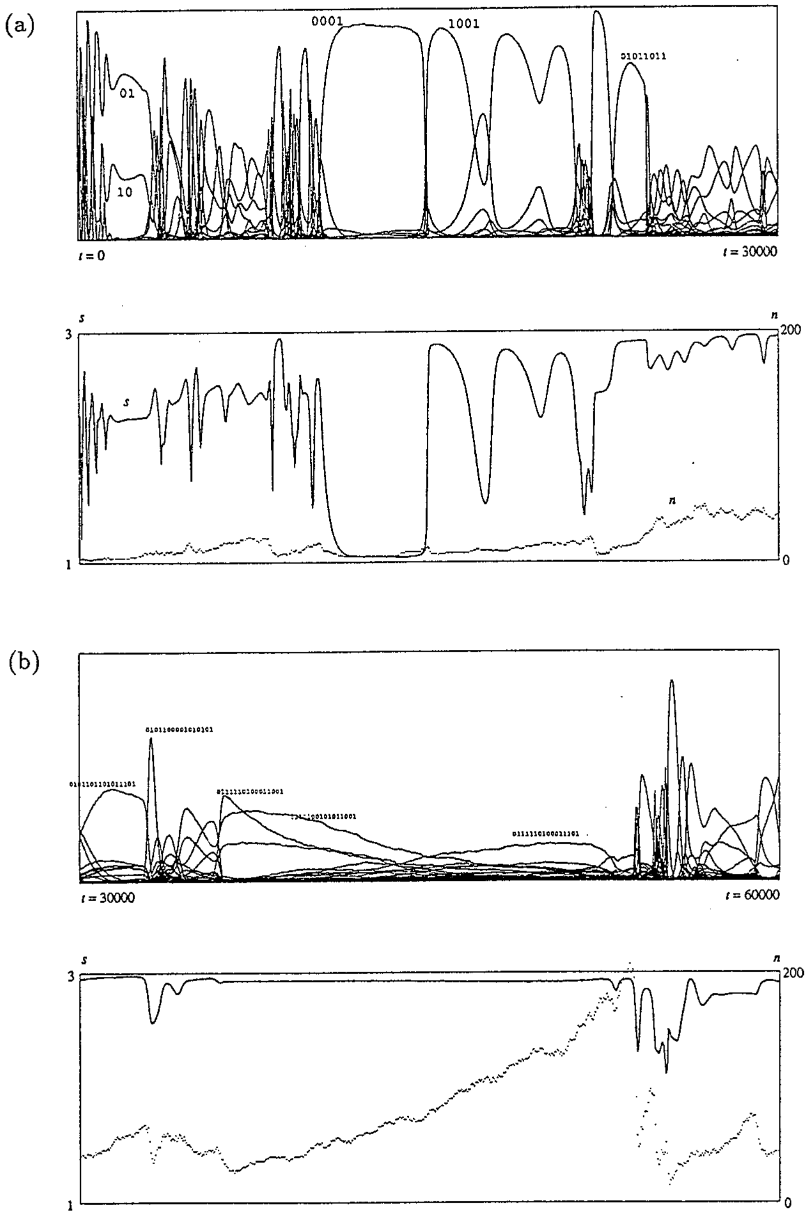

FIGURE 4 See caption next page.

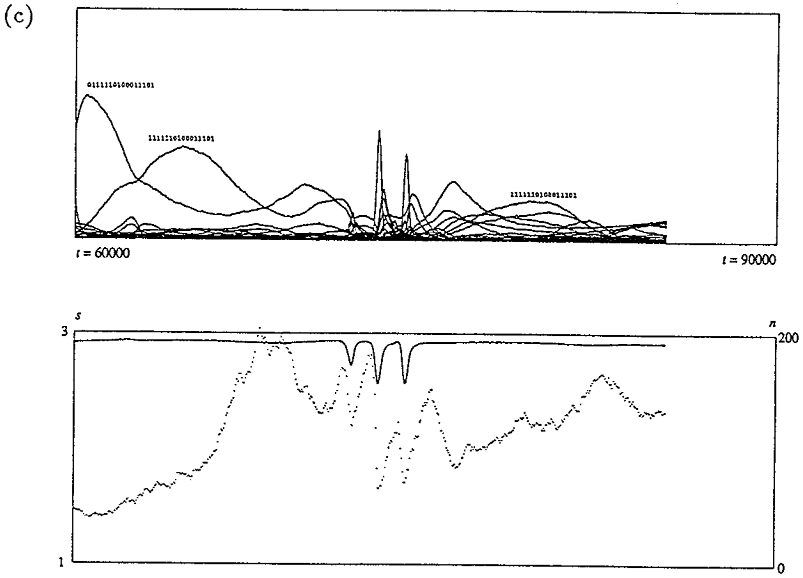

FIGURE 4 In (a) through (c) the evolution of a system avoiding the stable memory 4 stasis is shown for more than 80 000 generations. The bottom graphs show the average score and the number of genotypes (cf. Figure 3). (a) In this simulation the system never reaches the symbiotic stasis but finds another way in state space leading to new strategies dominating the population. (b) Several new memory 4 strategies appear and dominate the population. The system reaches a dimensionality of more than 200, and after that a collapse occurs in which most of the genotypes disappears. At the same time, the average score drops, indicating that this large extinction is caused by a parasite mutant exploiting the present species. (c) Some new large extinctions occur, and a few of them are accompanied by a decrease in the average score.

CONCLUSIONS

The presence of mutations in the population dynamics leads to intrinsical changes of the dimensionality of the system. The dynamic behavior observed is highly complicated with extremely long transients. One important characteristic of the model is that the game-theoretic problem used is complicated enough for complex strategies to evolve, at the same time as we can solve the game analytically, letting us simulate the population dynamics over evolutionary time scales. If one instead uses the iterated Prisoner's Dilemma without noise the potentiality for evolutionary transients is essentially lost. Another important aspect is that we use an effective way to code the strategies in genomes, and that the genome is easily modified by mutations. Having these aspects in mind it should be possible to model other situations as well, for example evolutionary models with more realistic assumptions, including, e.g., spatial dependence and sexual reproduction.

From the game-theoretical point of view we have found that when the iterated Prisoner's Dilemma is modified by noise, there is an unexploitable strategy that is cooperative. The evolutionary simulation, which actually is a kind of genetic algorithm[12] for finding good strategies for the noisy iterated Prisoner's Dilemma, indicates that the minimal memory for this kind of strategy is 4, i.e., the strategy should take into account the action of both players the previous 2 time steps. By answering a single defection by defecting twice the strategy is prevented from exploitation by intruders.

We have found periods of stasis punctuated by rapid transitions to new stasis or to periods of unstable dynamics. These rapid transitions are reminiscent of punctuated equilibria,[8] and it appears that the destabilization usually is due to a slowly growing group of mutants reaching a critical level. The coevolution of mutualism emerges spontaneously, and it serves as an example of a higher level of cooperation than the actions on the single round level provide. The appearance of an evolutionary stable strategy is interesting from the game-theoretic point of view, but in the construction of models possessing open-ended evolution one tries to eliminate such stabilizing phenomena. Therefore, from the evolutionary point of view, one should pay more attention to the less probable evolutionary pathways that avoid this evolutionary stable stasis. In particular, the large extinctions that appear in these simulations should be studied in more detail, since these collapses are triggered by the dynamical system itself and do not need external catastrophes for their explaination. The analysis of these results is in progress and shall be reported elsewhere. The major result of this model is that it establishes the fact that several evolutionary phenomena, like those described above, can emerge from very simple dynamics.

ACKNOWLEDGMENTS

I thank Tomas Kåberger for inspiring me to start the construction of this model, Mats Nordahl and Doyne Farmer for stimulating discussions, Gunnar Eriksson and Karl-Erik Eriksson for collaboration in game theory that also provided inspiration for the present study, and Torbjörn Fagerström for useful biological remarks. Financial support from Erna and Victor Hasselblad Foundation is gratefully acknowledged.

REFERENCES

1. Axelrod, R. *The Evolution of Cooperation.* New York: Basic Books, 1984.
2. Axelrod, R. In *Genetic Algorithm and Simulated Annealing*, edited by D. Davies, 32–42. London: Pitman, 1987.
3. Axelrod, R., and E. Dion. "The Further Evolution of Cooperation." *Science* **242** (1988): 1385–1390.
4. Axelrod, R., and W. D. Hamilton. "The Evolution of Cooperation." *Science* **211** (1981): 1390–1396.
5. Boyd, R "Mistakes Allow Evolutionary Stability in the Repeated Prisoner's Dilemma Game." *J. Theor. Biol.* **136** (1989): 47–56.
6. Boyd, R., and J. P. Lorberbaum. "No Pure Strategy is Evolutionarily Stable in the Iterated Prisoner's Dilemma Game." *Nature (London)* **327** (1987): 58–59.
7. Eigen, M., J. McCaskill, and P. Schuster. "Molecular Quasi-Species." *J. Phys. Chem.* **92** (1988): 6881–6891.
8. Eldredge, N., and S. J. Gould. *Models in paleobiology*, edited by T. J. M. Schopf, 82–115. San Fransisco: Freeman, Cooper and Company, 1972.
9. Farmer, J. D., S. A. Kauffman, and N. H. Packard. "Autocatalytic Replication of Polymers." *Physica* **22D** (1986): 50–67.
10. Farrell, J., and R. Ware. "Evolutionary Stability in the Repeated Prisoner's Dilemma." *Theor. Pop. Bio.* **36** (1989): 161–166.
11. Futuyma, D. J. *Evolutionary Biology* (2nd ed.). Sunderland: Sinauer Associates, 1986.
12. Holland, J. H. *Adaptation in Natural and Artificial Systems.* Ann Arbor: University of Michigan Press, 1975.
13. Kephardt, J. O., T. Hogg, and B. A. Huberman. "Dynamics of Computational Ecosystems." *Phys. Rev.* **A40** (1989): 404–420.
14. Langton, C. (Ed.). *Artificial Life.* Redwood City, CA: Addison-Wesley, 1989.
15. Maynard-Smith, J. *Evolution and the Theory of Games.* Cambridge: Cambridge University Press, 1982.

16. Maynard-Smith, J., and G. R. Price. "The Logic of Animal Conflict" *Nature (London)* **246** (1973): 15–18.
17. Miller, J. "The Coevolution of Automata in the Repeated Prisoner's Dilemma." Santa Fe Institute preprint 89-003, 1989.
18. Molander, P. "The Optimal Level of Generosity in a Selfish Uncertain Environment." *J. of Conflict Resol.* **29** (1985): 611–618.
19. von Neumann, J., and O. Morgenstern. *Theory of Games and Economic Behavior.* Princeton: Princeton University Press, 1944.
20. Rössler, O. E. "A System Theoretic Model of Biogenesis." *Zeitschrift für Naturforschung* **26b** (1971): 741–746.
21. Schuster, P. "Dynamics of Molecular Evolution." *Physica* **22D** (1986): 100–119.