

Statistical Mechanics of Evolutionary Dynamics

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Abstract

Evolutionary dynamics is an essential component of a mathematical and computational approach to biology. In recent years the mathematical description of evolution has moved to a description of any kind of process where information is being reproduced in a natural environment. In this manner everything that lives is a product of evolutionary dynamics. Often the behaviour of systems of interacting individuals can be described within game-theoretic models. Evolutionary game theory is such a framework, as a branch of game theory, to study the interaction of non-rational beings like animals or humans under the influence of the changing environment.

Virtually all human societies are based on cooperation of many individuals, which is an important precondition for the development of their complexity. In small groups reciprocal altruism can arise from repeated interactions, whereas in larger human communities cooperation can evolve through indirect reciprocity. In this case, individuals cooperate on the basis of a reputation obtained in previous interactions. Such reputation systems have particular interesting applications in the growing field of anonymous trade via online platforms. While different reputation mechanisms and the effect of unintentional errors have recently attracted a lot of interest, the effect of fake reputations - or fraud - has not been taken sufficiently into account, although such fraud might have a detrimental impact on cooperation based on indirect reciprocity.

In this thesis a simple model is analyzed in which such an effect is taken into account for the first time. After careful consideration of more complicated models this minimal model has been developed. It has several advantages: First, it is simple enough to allow the analytical calculation of the parameter regions that determine the dynamics of the system. And secondary, it allows a direct comparison with behavioral experiments and could be the basis of a further experimental and mathematical analysis of fraud in reputation systems. The results show that cooperation based on indirect reciprocity is robust with respect to fake reputations and can even be enhanced by them. It has been found that fraud does not necessarily have a detrimental effect on social systems. Furthermore, an extension of the usual replicator dynamics is introduced and a mechanism that works in cyclic games as well as in non-cyclic games is developed by introducing a dynamical learning rate. The framework is formulated in finite populations as well as in infinite populations and the relationship between these different approaches is shown. It was shown that a population with such a dynamic learning rate can gain an increased average payoff in transient phases and thereby can also exploit external noise. This mechanism seems to be of particular interest in economic systems.

Kurzfassung

Evolutionäre Dynamik ist eine wesentliche Komponente einer mathematischen und rechnerischen Annäherung an die Biologie. In den letzten Jahren hat sich die mathematische Beschreibung der Evolution stark verändert und liefert nunmehr eine Beschreibung für jeden Prozess, bei dem Information in einer natürlichen Umgebung reproduziert wird. In diesem Sinne ist alles, was lebt, ein Produkt der evolutionären Dynamik. Häufig kann man das Verhalten interagierender Individuen mit spieltheoretischen Methoden beschreiben. Evolutionäre Spieltheorie, als Zweig der Spieltheorie, bietet den Rahmen, um Interaktionen von nicht rationalen Lebewesen, z.B. von Tieren oder Menschen, unter dem Einfluss einer veränderlichen Umgebung zu untersuchen. Nahezu alle menschlichen Gesellschaften basieren auf Kooperation von vielen Individuen, welche eine wichtige Voraussetzung für die Entwicklung ihrer Komplexität ist. In kleineren Gruppen kann sich gegenseitiger Altruismus aufgrund sich wiederholender Interaktionen entwickeln, während in größeren menschlichen Gemeinschaften Kooperation auch durch indirekte Wechselwirkung entstehen kann. In diesem Fall kooperieren die Individuen auf der Basis ihrer Reputation, die sie in vorausgegangenen Interaktionen erworben haben. Solche Reputationssysteme finden eine besonders interessante Anwendung im wachsenden Feld anonymer Online-Plattformen. Während verschiedene Reputationsmechanismen und der Effekt von unbeabsichtigten Fehlern in letzter Zeit großes Interesse erfuhren, wurde der Einfluß gefälschter Reputation - oder Betrug - kaum betrachtet, obwohl solch ein Betrüger möglicherweise einen schädlichen Einfluss auf auf Kooperation basierende indirekte Reziprozität haben könnte. In dieser Arbeit wird ein einfaches Modell analysiert, indem solch ein Effekt zum ersten Mal betrachtet wird. Ausgehend von komplizierteren Modellen wird ein Minimalmodell entwickelt, welches folgende Vorteile hat: Erstens ist es einfach genug für eine analytische Berechnung der Parameterbereiche, die die Dynamik des Systems bestimmen und zweitens erlaubt es direkte Vergleiche mit Verhaltensexperimenten und könnte so die Basis für weitere experimentelle und mathematische Analysen von Betrügern in Reputationssystemen bilden. Die Ergebnisse zeigen, dass Kooperation, basierend auf indirekter Reziprozität, robust ist bezüglich gefälschter Reputation und sogar unter ihrem Einfluss verstärkt werden kann. D.h., Betrüger haben nicht notwendigerweise einen schädlichen Einfluss auf Sozialsysteme. Desweiteren wurde eine Erweiterung der gewöhnlichen Replikatorgleichungen eingeführt und ein Mechanismus sowohl für zyklische als auch für nicht-zyklische Spiele entwickelt, indem eine dynamische Lernrate eingeführt wurde. Dieser Rahmen wurde in endlichen und unendlichen Populationen formuliert und es konnten die Beziehungen zwischen den unterschiedlichen Ansätzen gezeigt werden. Populationen mit einer dynamischen Lernrate erreichen einen erhöhten mittleren Gewinn auf Transienten und können dabei auch externes Rauschen ausnutzen. Diese Ergebnisse könnten auch für das Verständnis wirtschaftlicher Systeme von Interesse sein.

1 Introduction

1.1 Motivation

Responding to a growing interest over the past years the theory of “Complexity” is an emerging interdisciplinary field of study that spans fields as diverse as physics, mathematics, biology, economics, organizational science and computational intelligence. Basically, a system is complex if we cannot understand it through simple cause-and-effect relationships or other standard methods of system analysis. Furthermore, in a complex system we cannot reduce the interplay of individual elements to the study of those individual elements considered in isolation. This means that often several different models of the complete system, each at a different level of abstraction, are necessary. Nevertheless, modern science often does not reflect all of reality, but only the part of reality that is ordered, linear, ergodic, isolatable, predictable, observable, and controllable. The trend toward disciplinary specialization¹ stands in opposite to the major need for knowledge integration and transdisciplinarity to understand complex systems. Recently, life sciences, in particular biology, are on the brink of an unmatched theoretic expansion. For example, mutation and selection have been described by exact mathematical equations using methods from statistical physics. The theory of evolution became more and more a mathematical theory². Other typical examples of “complex systems” are the immune system, nervous system, social and economic networks, prebiotic evolution or insect colonies.

This thesis deals with evolutionary dynamics and evolutionary games which are also considered as typical examples for complex adaptive systems (Bak, 1996; Jensen, 1998; Schuster, 2002; Nowak, 2006; Schuster, 2007).

1.1.1 Statistical Physics and Biological Systems

During the last twenty years, theoretical physicists got more and more into contact with biology (computational neuroscience). Artificial neural networks which cover fields as cognitive sciences, natural and artificial intelligence, brain, mind and behaviour, perception and

¹For example our knowledge in medical science is doubled all six years and this is the typical time scale a medical student needs to finish its education in a german university

²Charles Darwin regretted in his autobiography not to have a deeper knowledge of mathematical methods.

action, learning and memory, robotics, man-machine communication, etc. are well established in statistical physics (Amit, 1989; Hertz, Krogh and Palmer, 1991; Churchland, 1992; Arbib, 1998). In the beginning of the 1980s the famous physicist John Hopfield (Hopfield, 1982) introduced a recurrent artificial neural network which works as an associative memory, and thus is capable to store patterns. If in these networks a perturbed version of a stored pattern is presented, the network becomes attracted to the correct stored pattern if it falls into its basin of attraction. Hopfield showed that there exists an energy function which ensures that, if units are randomly chosen to update their activations, the network will converge to states, which are local minima in the energy function. Thus, if a state is a local minimum in the energy function, it is a stable state for the network. Furthermore, Hopfield showed that this energy function belongs to a general class of models in physics, called Ising models. It can be shown with methods of theoretical physics that this so called “Hopfield model” has a storage capacity of L patterns depending on the network size N . If $L/N < 0.138$ the recall of patterns is possible.

1.1.1.1 Statistical Physics and Evolutionary Dynamics

Beyond artificial neural networks we will demonstrate in this paragraph corresponding basic principles between evolutionary dynamics and statistical physics (Hauert and Szabo, 2005; Sella and Hirsch, 2005). Evolutionary dynamics is at the interface of dynamical systems and evolutionary game theory. If we characterize the requirements of an evolutionary model we can say that an evolutionary model combines two processes called *selection* and *mutation*. The *selection process* favors certain individual varieties between a given population. The *mutation process* creates these varieties. Usually, in evolutionary game theory these processes are iterated in time, thus, we could say that evolution is a process composed of selection and mutation iterated in time (Jacob, 1997). This requires, of course, that we have a sufficiently clear picture of the relevant selection and mutation processes. If we model these processes from a physical point of view and apply methods from physical to biological systems then we have two quite different possibilities. In a *bottom-up* point of view the biological systems (think of populations or ecosystems) are described, despite of their complexity, with physical laws on a low level representation. On the one side we might lose important details of the system, but on the other side we can describe the main behaviour of the systems by using simple physical laws. In a second step trails are made to get from this low level description to more complex descriptions of the whole biological system. A different approach is to consider similarities between a well understood physical system and a reduced biological system, provided that the biological system is sufficiently complete. The advantage of this approach is that we can use tools used in physical science for the description of biological systems. For example Hertz, et al. (1991) used the Hopfield model (Hopfield, 1982) de-

scribed in the previous paragraph to demonstrate the analogy between neural networks and spin glasses (Hertz, Krogh and Palmer, 1991).

We now will describe the mathematical analogy between evolutionary and thermodynamic systems to understand the interest of physicists in evolutionary dynamics. This illustrates how established tools of statistical physics can be applied to evolutionary dynamics. One analogy between evolutionary and thermodynamic systems is their description with state variables (Table 1.1). In statistical physics state variables are for example certain particles in a gas with given position, velocity or momenta. In evolutionary systems the gene with its four-letter code A, T, C and G, denoting the nucleotides adenine, thymine, cytosine, and guanine and organised in a double-stranded DNA to carry the genomic information, can be used as a corresponding state variable. Another possibility is to use the frequency of a population as a state variable. Another analogy exists concerning the fitness f of a given population

	Evolutionary dynamics	Statistical physics
State variable	$\vec{x} = (A, C, C, \dots, T)$	$\vec{s} = (\vec{q}_k, \vec{p}_k)$
Additive fitness and energy	$W = \ln(f(\vec{x}))$	$E = \hat{H}(\vec{s})$
Population size and temperature	$\nu = N - 1$	$\beta = \frac{1}{k_B T}$
Boltzman factor	$E_i \propto e^{-\nu(-x_i)}$	$E_i \propto e^{-\beta E_i}$
Invariance	$W_i \rightarrow W_i + C$	$E_i \rightarrow E_i + C$

Table 1.1: Analogy between evolutionary dynamics and statistical physics. There exists a mathematical analogy between certain evolutionary and thermodynamic systems, allowing the application of established methods of statistical physics to analyze evolutionary models. All parameters are explained in the text in detail (Sella and Hirsch, 2005).

and the energy E . The fitness f is a central concept in evolutionary theory. It describes the capability of an individual of a certain population to reproduce. An individual with higher fitness becomes more common. This process is called natural selection. It is convenient to define the additive fitness as the logarithm of f with $W = \ln(f(\vec{x}))$ because this allows us to identify an analogy to a physical system at thermal equilibrium. The Boltzmann distribution $E_i \propto e^{-\beta E_i}$ with $\beta = \frac{1}{k_B T}$ gives the probability that a system is found in a microscopic state i with a given energy E_i . Here, k_B is the Boltzmann constant and T is temperature. In analogy the probability that a given population is fixed (in the state variable i) is $E_i \propto e^{-\nu(-x_i)}$. Thus, we can say that ν is equivalent to β and the additive fitness $-x_i$ to the energy E_i . In applications of evolutionary dynamics the “temperature” of an evolutionary system is of course not related to the physical temperature, but is simply a parameter controlling the dynamics.

The parameter β is inversely proportional to the temperature. If the temperature is zero and a physical system is in thermal equilibrium, it is found allways in the lowest energy state. In this manner a given infinite population, as long as the evolutionary system is at steady state, is always in the state of highest fitness. Otherwise, if the temperature is greater zero, the probability to find the system in a certain microscopic state is depending alone on the state's energy. Similarly, in evolutionary systems, the probability to find a finite population in a certain state depends only on the fitness of the population type. Even though in evolutionary models the interactions between individuals such as animals in ecological and evolutionary models, genes in population genetics, and people in social processes, is closely related to statistical physics, which deals with systems of interacting particles, we have to distinguish between these two systems. Whereas physical systems show a tendency to reach by-and-by states characterized by the minimum of some global quantity, such as the total energy of the system, population dynamics does not exhibit necessarily such general principle. For example, agents in social models tend to maximize their own payoff, and genes or animals maximize their individual fitness. If we now compare the energy E in physical systems with the fitness W , which are both additive quantities, it has to be taken into account that in physical systems the energy is defined in such a way that it is reduced already by the physical process itself. In contrast, in evolutionary systems the fitness increases during the dynamical process. Consequently, the minus sign is introduced to complete the translation. In physical systems the addition of a constant C to the energy of the microscopic states remains the dynamics unchanged. This invariance can occur also in evolutionary systems. Here the system is invariant by adding a constant to the additive fitness. If we use the fitness f instead of the additive fitness W the constant must be multiplying ($f_i \rightarrow C f_i$).

Taken together, the mathematical description of evolution of a population in a constant environment has interesting analogous to that of a thermodynamic system. Thus, the methods used to describe systems in statistical physics seem to be appropriate to describe evolutionary systems.

1.1.2 Outline

Let us now briefly summarize the train of thoughts pursued in this thesis.

In the remaining paragraphs of chapter one, the game theoretical background is given, followed by surveys of evolutionary dynamics and statistical physics providing the methodological framework for subsequent studies on dynamics and evolution of games in finite and infinite populations. Chapter two is the main chapter and contains three published articles. Finally, the questions that were raised in this thesis are discussed and an outlook is given.

- In **paragraph 1.2** a basic overview of the classical game theory is given to facilitate the dynamic evolutionary theory. The famous prisoner's dilemma game and the matching pennies game are discussed in detail, because these games are important subjects of the publications. In particular, the fundamental notion of the Nash equilibrium is introduced.
- In **paragraph 1.3** a basic concept of evolutionary dynamics in finite and infinite populations is introduced. The games described in the previous paragraph are then analysed in the context of evolutionary game theory. To address the problem of the equilibrium selection in games with multiple equilibria, basic properties of the deterministic replicator dynamics and of the stochastic dynamics of finite populations are reviewed. Additionally, the important concepts of evolutionary stability are explained.
- In **paragraph 1.4** a survey of the publications presented in chapter two is given.
- In **chapter 2** the publications are presented.
- In **chapter 3** a conclusion and an outlook are given.

1.2 Game Theory

1.2.1 Classical Game Theory

Game theory is a branch of mathematical analysis developed to study decision making in conflict situations. Important in this decision making process is that the result depends not only on the own decision but also on the behaviour of the opponent. So game theory is a theory of social interactions between agents. Generally, these agents (decision makers) are called players, which can be any kind of object such as individuals, groups, companies, consumers, or any combination of these. In this general manner we can define a game as a formal model of an interactive situation. The fundamental and formal conception of game theory was first presented in John von Neumann and Oskar Morgenstern's book "Theory of Games and Economic Behaviour" (von Neumann and Morgenstern, 1944). Nevertheless, many illustrious predecessors worked on problems belonging to the so-called "game theory". For example contributions of Bernoulli (1738), Cournot (1883), Bertand (1883), Borel (1924) and Hotelling (1929) brought forward new ideas, rather than an independent theory.

The following three constituent parts are essential to setup a game:

1. the *player* (decision maker)
2. the *rules* of the game
3. the *outcome* (the payments made between the players: win, lose or draw)

The outcome of the game comprises that any possible combination players made, according to the rules of the game, leads to a well-defined end-state (win, loss or draw) that terminates the game. Associated with this state is a specified payoff, which is a real number and reflects the acceptability of a players outcome. Each player wants to maximise his own payoff. A crucial point is the precise specification of the rules of the game. In games like chess or other parlour games, the rules are given in a very precise way, but in many social interactions the rules are not given in such a precise way. Indeed, the kind of the precise specification of the rules of the games allow a roughly differentiation between two broad areas (Ritzberger, 2002): cooperative games (or coalitions) and non-cooperative (or strategic) games. In cooperative games players are able to make actionable contracts. This means that the players do not necessarily have to cooperate, but that any cooperation is actionable by an outside party such as a judge or the police. This thesis is focused on non-cooperative games, in which players are unable to make actionable contracts outside of those specifically modeled in the game. In non-cooperative game theory strategic choices have to be analysed. The choices of the player are crucial to determine the outcome of a game. This does not mean

that the players are not allowed to cooperate, but that cooperation must be self-enforced. In summary, crucial points in non-cooperative game theory are:

- The *rules* are completely given.
- Each individual *player* is the unit and fundament of the decision.
- Any kind of liabilities are not available (unless they are defined by the rules of the game).

Generally, each player has perfect knowledge of the game and of his opposition. This means, the player knows in full detail the rules of the game as well as the payoffs of all other players. A central assumption in most variants of classical game theory is that all players are rational. A player is said to be rational if, whenever a player can choose between two given alternatives, he will select the one that yields the greater payoff for him. Thus, during the game a rational player always aims to maximize his own payoff. In this manner, game theory will analyse how to play a game against rational opponents, or from a viewpoint of the player, which is the best way for a rational assumed agent to play the game. In non-cooperative game theory two different kinds of representation exist: the extensive form (also called game tree) and the normal form (also called strategic form). The extensive form (Gintis, 2000; Rieck, 2006) is a very common game form and contains a complete description of how the game is played over time. This includes for example the order, in which any finite number of players can make their actions, the information that players have at the time of their actions, and the set of payoffs. Nevertheless, this thesis focuses on the theory of normal-form games, which is the basic type of game studied in non-cooperative game theory.

A game of the normal-form type consists of a list of players L and their strategies, and the outcomes that result from each possible combination of choices. The outcome is associated with a certain payoff for each player. To be more precisely, a normal form game consists of a finite number of players, labeled with $i = 1, 2, \dots, I$. Each player i can choose between a certain strategy s_i from the pure-strategy space S_i available for him. A pure strategy is a specific action or move that a player has to do in every possible situation during the game. The chosen strategies all define the games strategy profile given by $s = (s_1, s_2, \dots, s_I)$. In this tuple s_i is the strategy of the player i . A strategy profile s is an element of the strategy space $S = S_1 \times S_2 \times \dots \times S_I$. Associated with each player is an utility function u_i , called payoff function, which depends on the strategy profile s . This payoff function has the form

$$\begin{aligned} u_i : S &\rightarrow \mathbb{R} \\ s &\mapsto u_i(s). \end{aligned} \tag{1.1}$$

Then the vector $u(s) = (u_1(s), u_2(s), \dots, u_I(s))$ contains the expected payoff for all players as a condition of the strategy profile s . The i -th component denote the payoff of the player i , thus, a game in normal form has the structure $(L, S, u(s))$ where $L = 1, 2, \dots, I$ is a set of players in a given strategy space S . This thesis is focused on normal-form games with mostly just two players ($I = 2, |S_1| = |S_2|$). Here, usually payoff matrices are used.

$$\begin{array}{c}
 \text{Player 2} \\
 \text{L } (s_{12}) \qquad \qquad \text{R } (s_{22}) \\
 \text{Player 1 } \begin{array}{l} \text{U } (s_{11}) \\ \text{D } (s_{21}) \end{array} \begin{pmatrix} u_1(s_{11}, s_{12}), u_2(s_{11}, s_{12}) & u_1(s_{11}, s_{22}), u_2(s_{11}, s_{22}) \\ u_1(s_{21}, s_{12}), u_2(s_{21}, s_{12}) & u_1(s_{21}, s_{22}), u_2(s_{21}, s_{22}) \end{pmatrix}
 \end{array} \quad (1.2)$$

The upper payoff matrix is a normal-form representation of a game in which each player can choose between two strategies. For example, if player 1, also called row player, plays U (up) and player 2, also called column player, plays L (left), player 1 receives $u_1(s_{11}, s_{12})$ and player 2 receives $u_2(s_{11}, s_{12})$. In each entry of the matrix the first number represents the payoff of the row player (in this case player 1) and the second number represents the payoff of the column player (in this case player 2). In a normal-form game the players move simultaneously or rather the players do not observe the move of the other player before making their own move and receive the payoffs as specified for the combinations of actions played (Fudenberg and Tirole, 1993; Luce and Raiffa, 1989; Osborne and Rubinstein, 1994). Even though in the previous explanation we exclude games, which have an infinite number of players or an infinite number of strategies for each player, there is no need to exclude such games. However, this thesis only deals with games with a finite number of strategies for each player. Usually, the players have the possibility to choose between two different strategy types called pure strategy and mixed strategy. A pure strategy defines a specific action that a player i will follow in every possible situation with probability 1 in a game. A mixed strategy of a player results of the probability distribution p_i over the pure strategies S_i . Here, a player i chooses not directly a pure strategy $s_i \in S_i$, but from a probability distribution p_i with the normalization $p_i = \sum p_i(s_i) = 1$. In this case $p_i(s_i)$ is the probability to choose strategy s_i . The payoff, e.g. of the column player using strategy j , can then be calculated from

$$u_j = \sum_k u_k(s_j, s_k) \cdot p_k(s_k), \quad (1.3)$$

where $p_k(s_k)$ is the probability that the row player chooses the strategy k .

Another important concept in game theory is a concept called Nash equilibrium³. In game theory the Nash equilibrium (Nash, 1950) is defined in the following way: Consider a game

³named after John Nash, who wrote, when he was 21 years old, his 27 page long dissertation, which earned him a Nobel Prize in economics in 1994

situation between two or more players, in which no player has anything to gain by changing only his own strategy. Thus, if each player has chosen a certain strategy and no player can increase his payoff by changing his chosen strategy, while the other players keep theirs unchanged, then the current set of strategy choices, with their corresponding payoffs, represent a Nash equilibrium. Let us consider a general payoff matrix between two players with two strategies (A and B) each.

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} (a, a) & (b, c) \\ (c, b) & (d, d) \end{pmatrix}. \end{array} \quad (1.4)$$

Then we have the following criteria:

1. A is a strict Nash equilibrium when $a > c$.
2. A is a Nash equilibrium when $a \geq c$.
3. B is a strict Nash equilibrium when $d > b$.
4. B is a Nash equilibrium when $d \geq b$.

Nash showed that in every finite normal-form game there exists at least one Nash equilibrium.

1.2.1.1 The Matching Pennies Game

Matching pennies is a zero-sum game with two players and with two strategies each. Each player has two options (± 1 or $\uparrow\downarrow$). Player one wins if both players chose the same option, otherwise player two wins. The players have to uncover their choices simultaneously. At first each player shows either head (H) or tail (T) from a coin. If both are heads or both are tails, player one wins, otherwise player two wins. The matching pennies game is quite similar to the three strategy version - rock, paper, scissors. The rock, paper, scissors (RPS) game is defined as follows: rock breaks scissors, scissors cut paper, and paper covers rock. If both strategies are the same, the game is in a tie. The optimal RPS strategy, which means one that is capable of competing with a perfect opponent, involves selecting rock, paper or scissors at random (Szolnoki and Szobo, 2004; Reichenbach, Mobilia and Frey, 2007). All in all two types of games are distinguished. In non-zero-sum games the total sum of all payoffs is variable, and so both players may win (or lose). On the other hand zero-sum games are games where the payoff is fixed. This means, whatever is gained by one player is lost by the other player. Hence, the sum of payoffs to all players is zero. The corresponding payoff

matrix for the matching pennies game is given by

$$\begin{array}{cc} & H & T \\ \begin{array}{c} H \\ T \end{array} & \begin{pmatrix} (-1, 1) & (1, -1) \\ (1, -1) & (-1, 1) \end{pmatrix} \end{array} \quad (1.5)$$

The matching pennies game has no Nash equilibrium in pure strategy, because there is no strategy set in which one of the players would want to switch if he knows the move of the other player. The diagram 1.6 shows the dynamic of the game, by drawing the best responses of the player in the given game matrix. The arrows show to the direction to which a player drifts, if he knows, that the other player chooses the strategy in the row (or column) where the arrow is placed.

$$\begin{array}{ccc} & H & T \\ \begin{array}{c} H \\ T \end{array} & \begin{array}{c} \xrightarrow{\text{Player 2}} \\ \xleftarrow{\text{Player 1}} \end{array} & \begin{array}{c} \\ \end{array} \\ & (-1, 1) & (1, -1) \\ & \uparrow & \downarrow \\ & T & (-1, 1) \end{array} \quad (1.6)$$

Only if an entry of the matrix is touched by the arrowhead of both players, we have a Nash equilibrium, because then no player has the need to switch from this strategy combination. Whenever one arrow comes in and the other comes out, we have no equilibrium point. So if player one chooses head, than player two will choose tail, which forces player one to choose tail and again makes player two choosing head, and so on.

Although, the game has no Nash equilibrium in pure strategy, there exists one equilibrium in mixed strategies. Assuming player one chooses head and player two also chooses head with the probability p , the expected payoff u for player one is given by

$$u_H = p \cdot (-1) + (1 - p) \cdot 1, \quad (1.7)$$

according to Eq. 1.3. If player one chooses instead the strategy tail, he can expect

$$u_T = p \cdot 1 + (1 - p) \cdot (-1). \quad (1.8)$$

To obtain the payment for player one of the entire game, we have to calculated the expected payoff.

$$\begin{aligned} u(q, p) &= q \cdot u_H + (1 - q) \cdot u_T \\ &= q \cdot [p \cdot (-1) + (1 - p) \cdot 1] + (1 - q) \cdot [p \cdot 1 + (1 - p) \cdot (-1)] \end{aligned} \quad (1.9)$$

Here we introduced the probability q that player one chooses the strategy “head”. To maximise the payoff $u(q, p)$, player one has only influence on the probability q . So we get the condition

$$\frac{\partial u(q, p)}{\partial q} = 1 - 2p \stackrel{!}{=} 0, \quad (1.10)$$

which yields $p = 1/2$. In the same way we get $q = 1/2$. The expected payoff is then calculated with $u(1/2, 1/2) = 1/2 \cdot u_H + 1/2 \cdot u_T = 0$. So we conclude the matching pennies game has only a Nash equilibrium in mixed strategies, in which each player chooses his strategy with the probability $p = q = 1/2$, which yields an expected payoff zero. In the published articles (Traulsen, Röhl and Schuster, 2004a; Röhl, Traulsen, Claussen, and Schuster, 2007) of this thesis we describe a way, using methods from evolutionary game theory, to win in this kind of “hopeless games” by exploiting stochastic fluctuations. The matching pennies game belongs to an interesting class of games called cyclic games.

1.2.1.2 The Prisoner’s Dilemma Game

The famous prisoner’s dilemma (PD, a non-zero-sum game) and the iterated prisoner’s dilemma (IPD) have been a rich source of research material since the last 50 years. The prisoner’s dilemma belongs to the class of social dilemma games, and the publication of Axelrod’s book “The Evolution of Cooperation” (Axelrod, 1984) in the 1980’s was mostly responsible for bringing this research to the attention to other areas outside of game theory including evolutionary game theory, evolutionary biology, networked computer systems, and facilitated cooperation between opposing countries (Fogel, 1993; Axelrod and D’Ambrosio, 1995). Currently, there exists a large literature base (see, for example, Boyd and Lorberbaum, 1987; Maynard Smith, 1982; Poundstone, 1992; Axelrod, 1997; Schuster, 2002; Nowak, 2006). Nevertheless, this is an on-going area of research. In this paragraph the prisoner’s dilemma game is presented in respect to classical game theory. In the article (Traulsen, Röhl and Schuster, 2004a) this game is addressed in the context of evolutionary game theory. The prisoner’s dilemma game is defined as a two-person-game, however, there exist also equivalent more-person social dilemmas such as “Tragedy of the commons” (Hardin, 1968).

The dilemma The classical prisoner’s dilemma is as follows: Two bandits are arrested by the police. The police has insufficient evidence for a criminal conviction. Thus, they separate both prisoners that they cannot exchange any information. Now, each prisoner (player) is offered the same deal: Each player can choose between two strategies called “cooperate” (C) and “defect” (D). “Cooperate” (C) means that he tells the police nothing (he cooperates with the other prisoner), whereas “defect” (D) means that the prisoner tells the police everything he knows. In this scenario we have then four possibilities:

- Player one chooses C and player two chooses C. If both player's plea of not guilty, they will ultimately set free after two years.
- Player one chooses C and player two chooses D. In this case player one has to go a long time, let us say five years, to prison, whereas player two is set free from prison.
- Player one chooses D and player two chooses C. Now player one is set free from prison, whereas player two has to stay in prison for five years.
- Player one chooses D and player two chooses D. If both players defect, then they have to stay in prison for a long time, say four years.

However, neither prisoner knows for sure what choice the other prisoner will make. So this dilemma rises the question: How should the prisoners act?

To obtain the payoff matrix we build for each matrix entry the difference between the maximal prison penalty (five years) and the value of the current penalty.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (3, 3) & (0, 5) \\ (5, 0) & (1, 1) \end{pmatrix} \end{array} = \begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (R, R) & (S, T) \\ (T, S) & (P, P) \end{pmatrix}. \end{array} \quad (1.11)$$

The second matrix describes the general payoff matrix with sucker's payoff S, punishment P, reward R and temptation T.

We assume, one player thinks that the other player will cooperate. If he himself also cooperates, he will receive a payoff of 3 for mutual cooperation. But if he chooses to defect, he will receive a payoff of 5 for the temptation to defect. Hence, if he thinks the other player will cooperate then the best decision is choosing to defect and, thus, to receive a payoff of 5. But what is the best choice if one player suspects that the other player will defect? If he cooperates he receives the sucker's payoff of zero. And if he defects both players would receive the punishment for mutual defection with the payoff of 1. Thus, if he thinks the other player will defect, the best decision for him would be to defect as well. Thus, all in all, the best decision for the player is to defect, no matter what option the opponent chooses (Nash equilibrium). Certainly, the same arguments hold also for the opponent. But, if both players choose defect, they receive just a payoff of 1 each. Whereas would both player choose mutual cooperation the outcome would be a payoff of 3 which is much more. Hence, there is the following scenario that two cooperating players earn more than one individual (rational) player, if both of them find a way to agree on mutual cooperation. This is the dilemma and the reason for research activities in the prisoner's dilemma game, is to find strategies that facilitate mutual cooperation. The values we have used above, to demonstrate the game, are not the only possible values, but they have to fulfill the conditions listed below.

$$\begin{aligned} S < P < R < T \\ 2R > S + T \end{aligned} \quad (1.12)$$

The condition in the first line guarantees that we actually have a social dilemma, whereas the second condition ensures that the players do not play the game in that way, that they end up with half the time being exploited and the other half of the time exploiting their opponent by playing the strategy combination (C, D) , or that one player cooperates and the other defects, so that they can divide the reward $(T + S)/2$ when the game is finished.

In the repeated prisoner's dilemma it was shown (Axelrod R. M. and Hamilton, W. D. 1981) that the deterministic strategy "Tit for Tat" is a highly successful strategy, compared to a wide range of other strategies. "Tit for Tat" is a relative simple strategy. An agent using this strategy will initially cooperate and then respond in such a way that he mimics the opponent's previous action. Nevertheless, "Tit for Tat" has the weakness that it is not fault-tolerant, e.i., a single error made by an agent (or noise) can destroy the "Tit for Tat" cooperation. A modified strategy called "Generous Tit for Tat" can correct mistakes. "Generous Tit for Tat" means, whenever the opponent has cooperated, the agent himself also cooperates and sometimes he even cooperates when the opponent has defected.

Another interesting strategy that may have long term advantages is "Pavlov", the most simple "win-stay-lose-shift strategy". A player using the Pavlov strategy begins by cooperating. Then he only cooperates if the opponent chooses the same strategy which he chose himself in the previous turn. Otherwise, the Pavlov player will switch to the other strategy (cooperation to defection and defection to cooperation). It was shown (Nowak and Sigmund, 1993) that Pavlov is a very robust strategy for the iterated prisoner's dilemma that even can outperform the "Tit for Tat" strategy in the presence of noise. Thus, the Pavlov strategy has the following advantages against the "Tit for Tat" strategy: a) it can correct occasional mistakes and b) it can exploit unconditional cooperators.

Whereas the prisoner's dilemma as a model to study also the phenomenon of cooperation has become something like a 'theoreticians's playground' in science, cooperation is also more and more observed in nature. For example, altruistic behavior has been reported to take place during the interaction of predator inspection in fishes (Milinski, 1987), food-sharing in vampire bats (Wilkinson, 1984), viruses infection of bacteria (Turner and Chao, 1999) or interaction of butterfly larvae with ants (Leimar and Axen, 1993). The butterfly larvae, e.g., secrete a nutritious liquid. The ants yield the liquid and in turn provide the larvae with protection against parasites and predators. The nutritious substance is costly to produce, thus the larvae would profit from obtaining the ant's safeguard without releasing the liquid. On the other hand, ants may profit from getting only the food rewards without of defending the larvae. So for both "players" at the first sight it seems to be better to defect. However, there are several differences to the prisoner's dilemma. For example, the rewards are asymmetric

and the moves the players make are not necessarily simultaneous. However, the underlying structure of interaction seems to be similar to the prisoner's dilemma, even though, it is presumably more complex.

1.2.2 From Classical Game Theory to Evolutionary Game Theory

Evolutionary game theory has its origin in the work of R.A. Fisher (The Genetic Theory of Natural Selection (1930)). It was, first of all, developed as an application of the mathematical theory of games based on Darwin's postulates to explore the social behavior of animals (Hofbauer and Sigmund, 1998; Nowak, 2006; Sigmund, 2005; Weibull, 1995). This primary work was mainly done by the biologist Maynard Smith⁴ (Maynard Smith and Price, 1973; Maynard Smith, 1982). Evolutionary game theory explains strategic aspects in the evolution of species due to the possibility that individual fitness may depend on population frequency. This includes the following aspects observed in nature, co-evolution, population genetics, speciation, extinction, diversity, procession, or the distribution and abundance of life. However, evolutionary game theory has also become of increasing interest to economists, sociologists, or anthropologists, based on the following facts:

- Evolution described by evolutionary game theory is a general concept not only related to biological evolution. In this manner, evolution can be also understood as cultural evolution, where evolution refers to changes in beliefs and norms over time.
- In classical game theory one assumes that players are rational. In contrast, in evolutionary game theory the rationality concept is not needed to model biological or social systems.
- In contrast to classical game theory evolutionary game theory is an explicitly dynamic theory and therefore provides an important element, which is missing in the traditional approach.

Presumably, the absence of rationality is the most important point between classical game theory and evolutionary game theory. In contrast to classical game theory, in evolutionary game theory trial and error processes rise strategies that can be selected by the evolutionary (biological, social or cultural) process. In biology, for example, species and populations represent strategy sets. Even a simple bacteria type can represent a certain strategy and would be eliminated if, e.g., the strategy results to be less successful with the underlying population dynamic. This is similar to the approach of solving "The Traveling Salesman" problem by using DNA computing methods instead of a complicated, artificial intelligence based,

⁴Originally he was an aeronautical engineer during the Second World War. However, after the war he became a second degree in genetics under the well-known biologist J.B.S. Haldane.

computer program. Just a heap of DNA is needed to represent lots of specific paths. The general assumption that players choose strategies which lead to a Nash equilibrium requires often high cognitive skills and rationality. Thus, in many situations these assumptions are unrealistic. Therefore, if evolutionary game theory demonstrates that evolutionary processes per se lead to this equilibrium in a played game, it would not be necessary to make such a more unrealistic assumption concerning the rationality of the agents. This equilibrium concepts are introduced by Maynard Smith and Price (1973) and are called “Evolutionary Stable Strategies” which are closely related to the Nash equilibrium used in classical game theory.

1.3 Evolutionary Dynamics

1.3.1 Introduction

Equilibrium concepts in evolutionary game dynamics are based on John Maynard Smith (Maynard Smith, 1982; Maynard Smith and Price, 1973) concept of an Evolutionary Stable Strategy (ESS) and are usually applied to evolutionary processes where players adopt a strategy and then learn from its comparative success. These concepts are also important in the study of the evolution of cooperation and altruism. As mentioned in the previous paragraph, evolutionary game theory does not depend on rational agents. A population of players interact in a game and each individual is associated with a fixed strategy. The player (individual) is randomly chosen and interacts with other individuals. The cumulated payoffs of the players are interpreted as (biological) fitness in this context. The population dynamics forms then a natural selection process: strategies which are better matched in the given environment (higher payoff) increase, otherwise (lower payoff) then decrease.

Let us consider a two-players game consisting of a population of X players. This means, the population represents the strategy X. Nevertheless, because of mutation, there is also a small quantity ϵ of invaders playing a different strategy Y.

$$\begin{array}{cc} & \begin{array}{cc} X & Y \end{array} \\ \begin{array}{c} X \\ Y \end{array} & \left(\begin{array}{cc} (a, a) & (b, c) \\ (c, b) & (d, d) \end{array} \right). \end{array} \quad (1.13)$$

The frequency⁵ of X is then $1 - \epsilon$. The payoff of X is greater than the one of Y if the following condition holds:

$$a(1 - \epsilon) + b\epsilon > c(1 - \epsilon) + d\epsilon \quad (1.14)$$

In the limit of $\epsilon \rightarrow 0$ we obtain $a > c$. In the case that we have $a = c$ we get $b > d$. Thus in a two-persons game the strategy X is an Evolutionary Stable Strategy (ESS)

1. if $a > c$ or
2. if $b > d$ (in the case of $a = c$).

This means a population X cannot be invaded by a small quantity of population Y invaders. The conditions only hold for infinite large population sizes. However, in this thesis we consider both infinite and finite population sizes. Furthermore, we also consider populations with more than two strategies. For an n-persons game the ESS is defined as follows (Hofbauer and Sigmund, 1998; Nowak, 2006). The notation, introduced in paragraph 1.2.1, is used.

⁵In the evolutionary context the term frequency refers to the relative abundance of a given population.

1. **Strict Nash equilibrium:** Strategy S_k is a strict Nash equilibrium if

$$u(s_k, s_k) > u(s_i, s_k) \quad \forall i \neq k. \quad (1.15)$$

2. **ESS:** Strategy S_k is an ESS if

$$u(s_k, s_k) > u(s_i, s_k) \quad \forall i \neq k \quad (1.16)$$

or

$$u(s_k, s_k) = u(s_i, s_k) \quad \text{and} \quad u(s_k, s_i) > u(s_i, s_i) \quad \forall i \neq k. \quad (1.17)$$

3. **Weak ESS:** Strategy S_k is a weak ESS if

$$u(s_k, s_k) > u(s_i, s_k) \quad \forall i \neq k \quad (1.18)$$

or

$$u(s_k, s_k) = u(s_i, s_k) \quad \text{and} \quad u(s_k, s_i) \geq u(s_i, s_i) \quad \forall i \neq k. \quad (1.19)$$

4. **Nash equilibrium:** Strategy S_k is a Nash equilibrium if

$$u(s_k, s_k) \geq u(s_i, s_k) \quad \forall i. \quad (1.20)$$

It follows, for example, that if we have a strict Nash equilibrium, we also have an ESS. Thus, all together the conditions imply the order: strict Nash equilibrium \Rightarrow ESS \Rightarrow weak ESS \Rightarrow Nash equilibrium. The concept of the evolutionarily stable strategy, or ESS, is an important part when studying evolutionary game dynamics. Maynard Smith and Price (Maynard Smith and Price, 1973) introduced fixed (genetically encoded) strategies, but the same logic can be applied to strategies, which are learned during the chronological sequence of an animals life. In most models of the prisoner's dilemma game the Tit for Tat strategy is profitable. Hence, if the entire population employs the Tit for Tat strategy, it cannot be invaded by individuals employing most other strategies. Therefore Tit for Tat is normally an ESS.

In evolutionary biology, fitness landscapes (Nowak and Sigmund, 2004; Nowak, 2006; Wright, 1932) play a role to describe and visualize the relationship between populations (genomes) and reproductive success. The fitness landscape is based upon two concepts, which are called the *height* and *distance*. The fitness of a specific gene sequence (\approx individual, as each genotype is mapped to a certain phenotype) is represented by the *height* in the landscape, whereas the similarity between genotypes corresponds to the *distance* in the landscape. This means that, e.g., genes (sequences) which are very similar are placed very close to each other. The fitness landscape is then formed by the set of all possible genotypic variants (Fig. 1.1). In the case of a constant fitness landscape environment, adaption

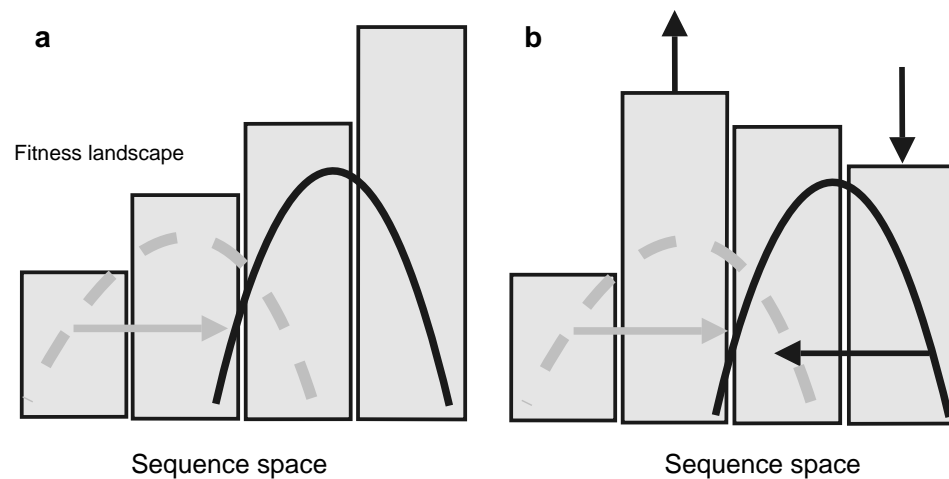


Figure 1.1: Evolution in changing environments is an important aspect of the theory of evolution. Evolution is an adaptive process of a population that occurs on the fitness landscape, here represented as bar charts. An adaptive process means that populations are able to find peaks in the fitness landscape. Here, dashed lines represent the initial population, whereas solid lines represent populations after the evolutionary process of mutation and selection. **(a)** The fitness landscape is constant, while the population moves through a sequence space. **(b)** The fitness landscape change, while the population moves through the sequence space. This is typical for evolutionary game dynamics or frequency depending selection.

can often be viewed as an evolutionary optimization problem. In this manner an evolving population usually climbs the hill upwards in the given fitness landscape. This is done by selection and mutation processes until a local maximum is reached. If a population has evolved to a local maximum it remains there until a new mutation opens a door to a higher fitness peak. However, if the mutation rate is too high a population might not be able to climb a peak or it happens that the population drifts away from a peak that it had already reached. This would result in a reduced fitness of the individuals. The optimization process can be described by mathematical methods (e.g. genetic algorithms) and it is often advantageous to introduce a scalar fitness function and to describe the dynamics with a potential function. In physics, this function corresponds to the potential energy of the system. While in physics an energy function is defined by minimizing the energy (potential function), in biology the fitness function is defined by maximizing the fitness. However, in reality this concept is often too simplified, because generally the fitness landscape changes as the population moves across. Therefore, evolutionary dynamics deals with dynamical fitness landscapes (Wilke

and Martinetz, 1999). This means that although the environment selects the adaptations, the adaptations themselves can shape the environment. This includes that new peaks and valleys might arise when a population moves through the fitness landscape. So far, we considered single populations. The situation becomes easier, if we consider co-evolutionary systems where several populations are involved, because each population can be a part of the other ones fitness landscape. Examples for co-evolution include the evolution of a host species and its parasites, predator-prey relationships, or the existence of mitochondria within eukaryotic cells (endosymbiotic theory).

In evolutionary game dynamics the simplex is a tool often used to describe and visualize evolutionary dynamics of frequency-depended selection (Fig. 1.2). A regular simplex S_{n+1} is a convex hull of a set from $n + 1$ points x_i in an n -dimensional Euclidian space \mathbb{R}^n .

$$S_n = \{\vec{x} \in \mathbb{R}^n \mid 0 \leq x_i \leq 1, x_1 + x_2 + \dots + x_n = 1\} \quad (1.21)$$

The simplex consists of the interior, the faces and the vertices. The interior of the simplex is defined by the set of all points x_i with $x_i > 0$ for all $i = 1, \dots, n$.

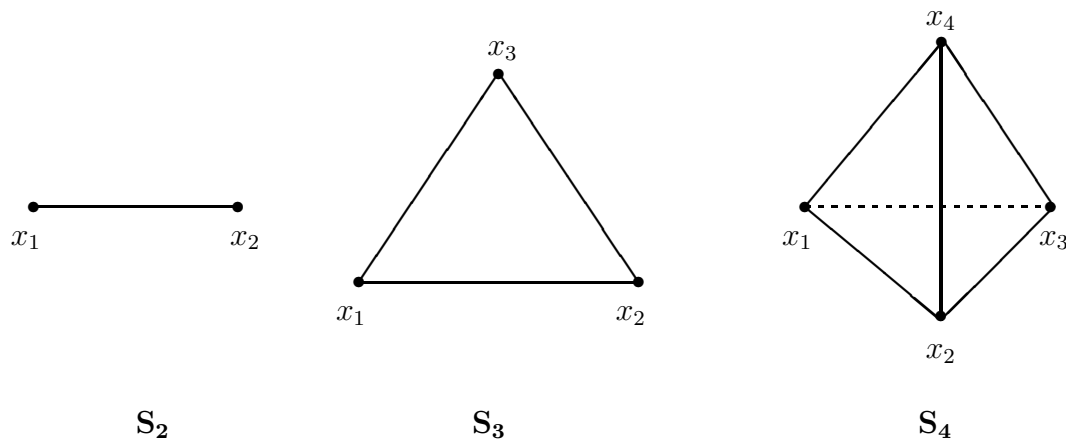


Figure 1.2: Selection dynamics takes places on the simplex, which is a convex hull of a set from $n + 1$ points x_i in an n -dimensional Euclidian space \mathbb{R}^n under the condition $\sum_{i=1}^n x_i = 1$. The componets of the simplex are called interior, faces and vertices.

The faces are given by the set of all points with the condition that there exists at least one point x_i with $x_i = 0$. The vertices are the set of all points x_i with $x_i = 1$ and $x_j = 0$ for all $j \neq i$. For example, the simplex S_2 is represented by the closed interval $[0, 1]$, whereas the interior is then the open interval $(0, 1)$ and the vertices a given by $x_i = \{0, 1\}$. A given population is, thus, represented by the vector $\vec{x} \in \mathbb{R}^n$ with each given x_i representing a

specific strategy. In this manner the vertices represent the situation, that there is only one strategy left, while all other strategies are extincted in the evolutionary process.

1.3.2 Replicator Dynamics

The replicator dynamics (Hofbauer and Sigmund, 1998; Nowak, 2006; Page and Nowak, 2002; Schuster and Sigmund, 1983; Zeeman, 1980) describes the evolution of the frequencies of strategies of populations and was first introduced for evolutionary game dynamics from Peter Taylor and Leo Jonker (1978). The replicator equation is a differential equation on the simplex S_n , and the population is assumed as infinitely large.

We assume a population consisting of n different types, i.e. strategies. We denote by x_i the frequency of the strategy i so that the structure of the population is given by the vector $\vec{x} = \{x_1, x_2, \dots, x_n\}$. We denote by f_i the fitness of type (strategy) i . The fitness is usually a non-negative real number and a function of the composition of the population, which describes the rate of reproduction. If the population is very large and if the individuals meet randomly, so that the generations merge and are mixed in a perfect way, we demand that the population $\vec{x}(t)$ is a time differentiable function. If we now consider a certain type i with fitness $f_i(\vec{x})$ and build the ratio \dot{x}_i/x_i , we obtain, if the ratio is greater than zero, that the specific type will increase in time. If the ratio is smaller than zero, the type will decrease in time. Thus, \dot{x}_i/x_i can be interpreted as a measure of evolutionary success of type i . With

$$\langle f(\vec{x}) \rangle = \sum_{i=1}^n x_i f_i(\vec{x}) \quad (1.22)$$

we define the average fitness (payoff) of the population. Because of the definition of the fitness we have $\dot{x}_i/x_i \propto f_i(\vec{x})$. Furthermore, it is plausible to assume that the average fitness can not be unaffected in the evolutionary process of type i . The simplest approach is to consider the difference between the fitness of type i and the average fitness $f_i(\vec{x}) - \langle f(\vec{x}) \rangle$. This leads to the replicator equation

$$\dot{x}_i = x_i(f_i(\vec{x}) - \langle f(\vec{x}) \rangle) \quad i = 1, \dots, n. \quad (1.23)$$

Obviously, the equation defines a frequency-dependent selection process, but it is important to note, that the dynamics is described without any mutation. The replicator dynamics is invariant of the simplex S_n that means, if $\vec{x}(t = t_0) \in S_n$ is given then $\vec{x}(t) \in S_n$ is also an element of the simplex for all $t \in \mathbb{R}$. If, for example, a trajectory starts in the interior, it will always stay there. It will reach the boundary just in the limit for $t \rightarrow \infty$. If the trajectory starts from the face of the simplex, those strategies which are not represented on the simplex will never appear. In consequence, the vertices of the simplex must be fixed points of the

replicator dynamics. Of course, there can also be fixed points in the interior or face of the simplex. Following Eq. 1.23 a population using strategy i will increase if the fitness (payoff) of type i is greater than the average fitness (payoff) of the population, whereas, if the fitness (payoff) of type i (strategy) is less than the average fitness, the strategy will decrease in time.

Often fitness functions f_i are linear. In this case there exists then an $n \times n$ payoff matrix $P = (p_{ij})$ such that $f_i(\vec{x}) = \sum_j p_{ij}x_j = (P\vec{x})_i$. The average payoff can then be written as $\vec{x} \cdot P\vec{x}$ which yields the following replicator equation

$$\dot{x}_i = x_i((P\vec{x})_i - \vec{x} \cdot P\vec{x}). \quad (1.24)$$

To illustrate the concept of the replicator dynamics, we will derive the replicator equation for the famous Hawk-Dove game (Maynard Smith and Price, 1973). In biology one interpretation of the game is that there exists a situation in which there is a competition for a shared resource and the contestants can choose either conciliation (strategy dove (D)) or conflict (strategy hawk (H)). The game is described by the following payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} \text{H} & \text{D} \end{array} \\ \begin{array}{c} \text{H} \\ \text{D} \end{array} & \begin{pmatrix} 0 & 6 \\ 2 & 4 \end{pmatrix} \end{array} \quad (1.25)$$

Let us assume a population divided into 2 types (strategies) H and D with the frequencies $x = x_1$ and $x_2 = 1 - x$ such that $x_1 + x_2 = 1$. In this context the vector $\vec{x} = (x, 1 - x)$ represents the population shares. With P_D (P_H) we denote the payoff of an individual (player) using strategy D (H) against the population \vec{x} . For the payoffs we obtain

$$\begin{aligned} P_H &= 0 \cdot x + 6 \cdot (1 - x) = 6 - 6x \\ P_D &= 2 \cdot x + 4 \cdot (1 - x) = 4 - 2x. \end{aligned} \quad (1.26)$$

Hence, the average payoff of the population is

$$\langle P \rangle = x \cdot (6 - 6x) + (1 - x) \cdot (4 - 2x) = 4 - 4x^2. \quad (1.27)$$

If we assume that the population shares develop over time, i.e., that x is a function of time t , and that the change in x , described by the time derivative $\dot{x} = dx(t)/dt$, is proportional to the difference with the average fitness, we obtain the following equation

$$\dot{x} = dx(t)/dt = x \cdot ((6 - 6x) - (4 - 4x^2)). \quad (1.28)$$

Equation (1.28) is the replicator dynamics for the Hawk-Dove game. The equation describes the population of ‘‘Hawks’’-players $[0, 1]$, which changes continuously (described by $dx(t)/dt$), and that this change is proportional to the difference of the fitness (payoff) at time

t and the average fitness of the population. The critical points (Schuster, 1995) are given from the condition $\dot{x} = 0$. We obtain

$$\dot{x} = 0 \quad \Longrightarrow \quad x_1 = 0, \quad x_2 = 1/2, \quad x_3 = 1. \quad (1.29)$$

The stability of these fixed points are then determined by the Jacobian J , which is in this one-dimensional case given by the derivation of \dot{x} and yields $\frac{d}{dx}\dot{x} = 2(1 - 6x + 6x^2)$. Because of

$$\left. \frac{d}{dx}\dot{x} \right|_{x=x_1} = \left. \frac{d}{dx}\dot{x} \right|_{x=x_3} = 2 > 1 \quad (1.30)$$

x_1 and x_3 are instable fixed points, whereas x_2 is a stable fixed point (Fig. 1.3).

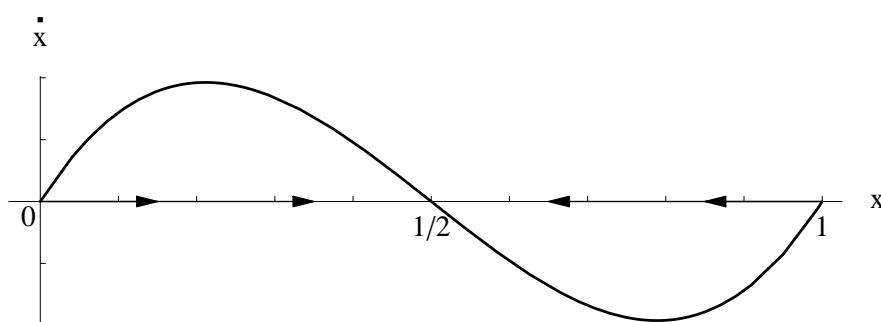


Figure 1.3: Phase diagram for the Hawk-Dove game. The dynamic shows three different fixed points $x_1 = 0$, $x_2 = 1/2$, and $x_3 = 1$. For these x values the derivative dx/dt is equal to zero, so that the population rates do not change in time.

In the case of $x = 0$ the whole population consists of hawk players. Their payoffs are equal to the average payoff and, thus, nothing changes. However, this fixed point is not stable and a slight agitation, e.g., a mutation resulting in a hawk player, increases the number of hawk players because dx/dt becomes positive. This increase will continue until the fixed point $x_2 = 1/2$ is reached. The same logic holds for the fixed point $x_3 = 1$, where the population consists of only dove players. If the system is at the fixed point $x = 1/2$ a small disturbance in either direction will bring the system back again to the state where half the population consists of dove players. Thus, among the three critical points, only $x = 1/2$ is a stable fixed point and the outcome is a stable coexistence of both types (hawk and dove players). Recalling from the previous paragraph 1.2.1.1, in mixed strategies in the matching pennies game $x = (1/2, 1/2)$ is also a Nash equilibrium. Because in both cases P is a 2×2 payoff-matrix, it follows that, first, P has at least one evolutionary stable strategy and, second, the $\vec{x} = (x, 1 - x)$ is an evolutionary stable strategy of P , if and only if x is a stable

fixed point of the replicator dynamics. Generally, every symmetric bi-matrix game has a symmetric Nash equilibrium.

Next we show that the mixed strategy $(1/2, 1/2)$ is also an evolutionary stable strategy. For this purpose we have to show that the condition

$$\vec{x} \cdot P\vec{x} = \vec{y} \cdot P\vec{x} \Rightarrow \vec{x} \cdot P\vec{y} > \vec{y} \cdot P\vec{y} \quad (1.31)$$

is always satisfied, whereas $\vec{y} = (y, 1 - y)$ is an arbitrary strategy opponent. If we calculate $\vec{x} \cdot P\vec{x} = \vec{y} \cdot P\vec{x}$ we obtain $3 = 3$ which is obviously always satisfied. Hence, we have to check if

$$\vec{x} \cdot P\vec{y} > \vec{y} \cdot P\vec{y} \quad (1.32)$$

for all $\vec{y} = (y, 1 - y) \neq \vec{x}$. We obtain the following inequality:

$$0 > -(1 - 2y)^2, \quad (1.33)$$

which is true for all $y \neq \frac{1}{2}$. Thus, $\vec{x} = (1/2, 1/2)$ is the unique evolutionary stable strategy.

1.3.3 Games in Finite Populations

Whereas a common method to study the evolutionary dynamics in games is through replicator equations, which requires infinite populations, continuous time and complete mixing of strategies, evolutionary dynamics in finite populations is no longer described by a deterministic differential equation (Fudenberg, Nowak, Taylor and Imhof, 2006; Nowak, Sasaki, Taylor and Fudenberg, 2004; Nowak, 2006; Taylor, Fudenberg, Sasaki and Nowak, 2004; Traulsen, Clausen and Hauert, 2005; Traulsen, Clausen and Hauert, 2006; Traulsen, Pacheco and Imhof, 2006). Evolutionary dynamics in finite populations, which means that the population size N is now given by an integer, requires a stochastic formulation, which is similar to the familiar replicator dynamics used for infinite populations. Often differential equations are easier to analyze. There exist a heap of analytical methods and also many numerical methods have been developed to determine solutions with a given degree of accuracy. However, many important biological effects occur only in a stochastic context.

One of the simplest stochastic processes is the so-called ‘‘Moran process’’ (Moran, 1958). This process was transferred to game theory by Martin Nowak (Nowak, Sasaki, Taylor and Fudenberg, 2004). The Moran process is defined as follows (Fig. 1.4): Consider a population with i individuals A and $k = N - i$ individuals B, such that $k + i = N$ is fixed. This determines then a state space $i = 0, 1, \dots, N$. The probability of choosing an A individual is given by i/N and the probability to choose a B individual is then $1 - i/N = (N - i)/N$. For the Moran process we can formulate then four different scenarios.

1. A is chosen for reproduction and A is chosen for elimination. After this event nothing has changed.
2. A is chosen for reproduction and B is chosen for elimination. After this event the variable i has increased to $i + 1$.
3. B is chosen for reproduction and B is chosen for elimination. After this event nothing has changed.
4. B is chosen for reproduction and A is chosen for elimination. After this event the variable i has decreased to $i - 1$.

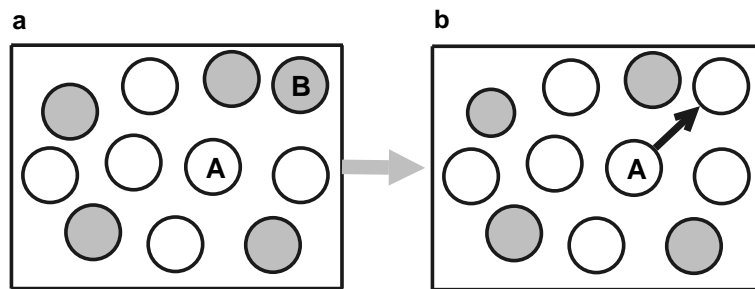


Figure 1.4: The Moran process describes the stochastic evolution in a finite population of constant size N . **(a)** Consider a homogeneous population of size N consisting of A (white) and B (grey) individuals. At each time step two individuals are chosen. Here, individual A is chosen for reproduction with a probability proportional to its fitness, and a randomly chosen individual B is picked for elimination. **(b)** The offspring A was replicated and has replaced the individual B. Therefore, the population size does not change in time.

The Moran process determines then a birth-death process. Which means that in every single time step (stochastic event), the state variable i can either increase by one, stay the same, or decrease by one. Thus, the stochastic transition matrix (Eq. 1.34), $P = (p_{ij})$ for this one-dimensional Markov process, is trigonal and of the type $(N + 1) \times (N + 1)$.

$$P = \begin{pmatrix} 1 & 0 & 0 & \dots & 0 & 0 & 0 \\ p_{1,0} & 1 - p_{1,0} - p_{1,2} & p_{1,2} & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{N-1,N-2} & 1 - p_{N-1,N-2} - p_{N-1,N} & p_{N-1,N} \\ 0 & 0 & 0 & \dots & 0 & 0 & 1 \end{pmatrix} \quad (1.34)$$

We denote by p_{ij} the probability of moving from state i to state j . The process has two absorbing states

$$\begin{aligned} p_{0,0} &= 1 & p_{0,i} &= 0 & \forall i > 0 \\ p_{N,N} &= 1 & p_{N,i} &= 0 & \forall i < N. \end{aligned} \quad (1.35)$$

The existence of these two absorbing states implies that no coexistence of A and B individuals is possible and that this happens, although there is no particular selection process. The occurrence that, although there is no selection, one individual will displace all other individuals and take over the whole population is called neutral drift. Besides these absorbing states all other states ($i = 1, 2, \dots, N - 1$) are transient. The process will remain in transient only for a certain limited time. Thus the question arises, what the fixation probability in this birth death process, i.e. the probability to reach an absorption in state N when starting in state i , could be. Let x_i be the probability to reach the absorption state N , when starting with i A individuals. This yields

$$\begin{aligned} x_0 &= 0 \\ x_i &= p_{i,i-1}x_{i-1} + p_{i,i}x_i + p_{i,i+1}x_{i+1} & i = 1, \dots, N - 1 \\ x_N &= 1. \end{aligned} \quad (1.36)$$

If we are in state 0, it is not possible, because of $x_0 = 0$, to reach state N . The probability to end up in state 0 when starting from state i is then given by $1 - x_i$. The solution of Eq. 1.36 is given by Karlin and Taylor (1975):

$$x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \gamma_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \gamma_k} \quad (1.37)$$

with $\gamma_i = p_{i,i+1}/p_{i,i-1}$. The fixation probability is valid for any birth death process, such as neutral drift, constant selection or frequency-dependent selection. For example, if we are interested in the probability that a single A individual will become the forefather of the whole population. Then Eq. 1.37 yields for state $i = 1$

$$\rho_A = x_1 = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \gamma_k}. \quad (1.38)$$

We denote by ρ_A the probability that a single A individual will spread over the whole population that contains $N - 1$ B individuals. In the same manner we obtain the probability that one single B individual will spread and reaches fixation in a population of A individuals by

$$\rho_B = 1 - x_{N-1} = \frac{\prod_{k=1}^{N-1} \gamma_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \gamma_k} = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=j}^{N-1} \gamma_k}. \quad (1.39)$$

As an example we consider now the fixation probabilities ρ_B and ρ_A for constant selection, in particular for neutral drift. Neutral drift comprised, that both A and B individuals shall have the same fitness. In the case that $p_{i,i-1} = p_{i,i+1}$, which means that A and B individuals have the same fitness, we have $\gamma_i = 1$. Therefore, all products are reduced to one and we obtain $\rho_A = \rho_B = x_1 = 1/N$. This leads to the result that in the case that there are i many A individuals

$$x_i = i/N \quad \forall i = 0, \dots, N. \quad (1.40)$$

Conversely, the probability that $N - i$ B individuals reach fixation and eliminate all A individuals is

$$1 - x_{N-i} = (N - i)/N \quad \forall i = 0, \dots, N. \quad (1.41)$$

If we calculate the ratio of the fixation probabilities we obtain

$$\frac{\rho_B}{\rho_A} = \prod_{k=1}^{N-1} \gamma_k. \quad (1.42)$$

It follows from Eq. 1.42 that if the product is smaller one, we have $\rho_B < \rho_A$ (otherwise we have $\rho_B > \rho_A$). This means, that a single A mutant becomes fixed in B population is more likely than vice versa.

1.4 Survey of the Publications

1.4.1 Stochastic Gain in Population Dynamics

The article “Stochastic gain in population dynamics” (Traulsen, Röhl and Schuster, 2004a) deals with an evolutionary game of two populations with different strategies and objectives analyzing the payoff in the context of a noisy environment. Whereas in the absence of noise the system evolves to a stable Nash equilibrium, in the presence of noise the system moves away from the Nash equilibrium. If one of the players in the game can adjust its adaptation rate relative to the opponents play, it is shown that this generates a constant benefit per time for the adaptive player.

To get a better insight we first discuss asymmetric conflicts. Then we introduce adaptive learning rates, which is one of the key ideas in this manuscript. We proceed then with the stochastic replicator dynamics and the “stochastic gain effect”.

Consider two players A and B. We assume that Player A wants to meet player B, while player B tries to avoid this meeting. If they choose the same way, they will meet and this is what A wants. Otherwise, they do not meet and this is good for B (Fig. 1.5). In this context, both players have different roles which can be mathematically described by different payoff matrices for the players. Nevertheless, this framework allows us to analyze the influence of different learning mechanisms in such systems.

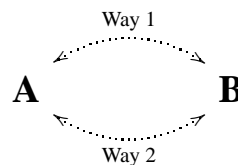


Figure 1.5: Asymmetric conflict. Player A wants to meet B, but player B do not like to meet A and therefore he tries to avoid this meeting. Which way (strategy) should A or B choose? Here A is anxious to synchronise, whereas B tries to do exactly the opposite of A.

The battle of the sexes, also called matching pennies game, is an example of an asymmetric conflict (Dawkins, 1976, Maynard Smith, 1982). The game gives some insight into the mating habits of certain animals. A thorough treatment of the game can be found in Hofbauer and Sigmund, 1998 and Schuster, 2002 (see also the paragraph 1.2.1.1). In the matching pennies game two players A and B place a penny on the table. If the pennies match, A wins B’s penny, otherwise B wins A’s penny. If we consider now two populations X and Y which

play this game against each other, we obtain the following replicator equations

$$\begin{aligned}\dot{x} &= \eta_x x(\pi_1(y) - \langle \pi_x(y, x) \rangle) \\ \dot{y} &= \eta_y y(\pi_1(x) - \langle \pi_y(x, y) \rangle).\end{aligned}\quad (1.43)$$

Here π_x (π_y) is the payoff of player X (Y). With $\langle \pi_x(y, x) \rangle$ ($\langle \pi_y(x, y) \rangle$) we denote the average payoff of population X (Y). For $\eta_x = \eta_y = 1$ we have a Hamiltonian system (Hofbauer and Sigmund, 1998) with the following constant of motion

$$H(x, y) = -2 \ln[x(1-x)] - 2 \ln[y(1-y)]. \quad (1.44)$$

In this case the trajectories oscillate around the Nash equilibrium at $(1/2, 1/2)$ yielding an average payoff of zero for each population. The key idea is then to introduce an adaptive learning rate (here denoted for the population X)

$$\eta_x = \eta_0 (1 - \tanh[\alpha_x(\langle \pi_x \rangle - \langle \pi_y \rangle)]) \quad (1.45)$$

with η_0 as the base selection rate, the perception ability α and the average payoff difference $\langle \pi_x \rangle - \langle \pi_y \rangle$ of both interacting populations. In the case of $\alpha \rightarrow 0$ we yield η_0 , which means that no adaptive learning occurs. For $\alpha \rightarrow \infty$ and $(\langle \pi_x \rangle - \langle \pi_y \rangle) > 0$ we obtain $2\eta_0$. However, for an intermediate α we have shown that such a learning mechanism can stabilize the mixed Nash equilibrium in the matching pennies game (Traulsen, Röhl and Schuster, 2004a). For that purpose we used a stochastic replicator dynamics (Fudenberg and Harris, 1992):

$$\dot{x}_i = x_i(\pi_i - \langle \pi \rangle) + \xi_i \quad (1.46)$$

by introducing an additive Gaussian noise term ξ_i with variance 1. Combining Eq. 1.43 with Eq. 1.46 we get

$$\begin{aligned}\dot{x} &= \eta_x(x, y) x(\pi_1(y) - \langle \pi_x(y, x) \rangle) + \xi_x \\ \dot{y} &= \eta_0 y(\pi_1(x) - \langle \pi_y(x, y) \rangle) + \xi_y.\end{aligned}\quad (1.47)$$

This is a stochastic replication equation with an adaptive learning rate. Here, disturbances can drive the system away from the Nash equilibrium. We have shown that the fluctuations ruled by small amplitudes of Gaussian noise increase the capability of learning of one population and therefore increase the payoff beyond the Nash equilibrium. This is an interesting extension of the replicator dynamics to adaptive learning rates and the fundamental role of the noise in the dynamics. We demonstrated this effect, called ‘‘stochastic gain effect’’ also in non-cyclic games, in particular for the noise in the prisoner’s dilemma game with adaptive selection rate.

1.4.2 Stochastic Gain in Finite Populations

Evolutionary game theory describes population dynamics under frequency dependent selection. Frequency dependent selection means, that the fitness of an individual (phenotype⁶) is dependent on the relative frequency of other individuals (phenotypes) in the population. Frequency dependent selection can be subdivided in positive and negative frequency dependent selection. Whereas in the first case the fitness of an individual increases as it becomes more common, in the latter one the fitness of an individual decreases as it becomes more common, i.e., less frequent individuals have a higher fitness than common ones (Sigmund and Nowak, 1999; Maynard Smith, 1982; Nowak, 2006; Nowak and Sigmund, 2004). Usually, such systems are described by deterministic replicator equations (Hofbauer and Sigmund, 1998; Taylor and Jonker, 1978), which are defined for infinite large population sizes. However, this article addresses the problem of finite populations. Using methods from statistical physics, a connection between replicator equations and related microscopic processes can be established (Helbing, 1993; Helbing, 1996; Traulsen, Clausen and Hauert, 2005; Traulsen, Clausen and Hauert, 2006). Nevertheless, for bi-matrix games details of the microscopic process can affect macroscopic properties, and, furthermore, the finiteness of a population can lead to further important effects (Traulsen, Clausen and Hauert, 2005).

We will now explain the model and the underlying selection dynamics, used in the published articles, by giving detailed background information. At first, we discuss the Moran process in the context of “weak selection”. Then, we show that for large populations the dynamics of the system can be approximated by a Fokker-Planck equation. Finally, we show that in the limit for infinite population sizes both microscopic processes (the Moran process as well as the “local update rule”) lead to replicator equations.

The Moran process from population genetics (Moran, 1958) can be used to describe frequency-dependent selection dynamics in finite populations. In 1.3.3 we stressed the dynamics with one evolving population as usually done in evolutionary game theory. Nevertheless, we consider two interacting populations X and Y , both of size N . The two populations play then the matching pennies game against each other, i.e., an X individual interacts with an Y individual. At this juncture each individual can choose between two strategies 0 and 1. For example an X_0 individual can play against an Y_0 or Y_1 individual. We denote by X_i that an individual from population X chooses the strategy $i = \{0, 1\}$. The Nash equilibrium only evolves, if both populations play the mixed strategy $(1/2, 1/2)$ (see paragraph 1.2.1.1

⁶The phenotype is the set of all observable physical or biochemical characteristics of an organism, as determined by both, genetic makeup and environmental influences. For our purpose, it is sufficient to identify this term with an individual.

and 1.3.2). The payoff matrix is then given by

$$\begin{array}{cc} & Y_0 & Y_1 \\ \begin{array}{c} X_0 \\ X_1 \end{array} & \begin{pmatrix} +1, -1 & -1, +1 \\ -1, +1 & +1, -1 \end{pmatrix} \end{array} \quad (1.48)$$

The average payoff π_0^X of each of the X_0 individuals depends on the number of Y_0 individuals, j_0 , and on the number of Y_1 individuals, $j_1 = N - j_0$. We obtain

$$\begin{aligned} \pi_0^X &= 1 \cdot \frac{j_0}{N} - 1 \cdot \frac{N-j_0}{N} \\ \pi_1^X &= -1 \cdot \frac{j_0}{N} + 1 \cdot \frac{N-j_0}{N}. \end{aligned} \quad (1.49)$$

The expression $\frac{j_0}{N}$ is the probability to play with a j_0 opponent, whereas $\frac{N-j_0}{N}$ refers to the probability to play against a j_1 opponent. Conversely, the payoffs of the Y population depend on the number of X_0 and X_1 individuals, i_0 and $i_1 = N - i_0$, which yield

$$\begin{aligned} \pi_0^Y &= -1 \cdot \frac{i_0}{N} + 1 \cdot \frac{N-i_0}{N} \\ \pi_1^Y &= 1 \cdot \frac{i_0}{N} - 1 \cdot \frac{N-i_0}{N}. \end{aligned} \quad (1.50)$$

The fitness of X and Y is a combination of background fitness and the payoff and is given by

$$\begin{aligned} f_i^X &= 1 - w + w\pi_i^X & i \in \{0, 1\} \\ f_i^Y &= 1 - w + w\pi_i^Y & i \in \{0, 1\}. \end{aligned} \quad (1.51)$$

Here, $w \in [0, 1]$ is a parameter that measures the intensity of selection and specifies the contribution of the game to the fitness (Nowak, 2006). The limit $w \rightarrow 0$ is called “weak selection”. For example, if $w = 0$, the game plays no rule for the fitness. The case $w = 1$ is called “strong selection”, which means that in this case the fitness is totally determined by the expected payoffs, because the fitness of an individual is then identical to its payoff. Note, that in the selection dynamics of the Moran process an individual is chosen proportional to its fitness for reproduction. Here, we have to distinguish between payoff and fitness.

The transition probabilities in the X population (similarly for the Y population) are, thus, given by

$$T_X^{i \rightarrow i+1} = \frac{\eta_x}{2} \frac{f_0^X i}{f_0^X i + f_1^X (N-i)} \frac{N-i}{N} \quad (1.52)$$

$$T_X^{i \rightarrow i-1} = \frac{\eta_x}{2} \frac{f_1^X (N-i)}{f_0^X i + f_1^X (N-i)} \frac{i}{N} \quad (1.53)$$

$$T_X^{i \rightarrow i} = 1 - T_X^{i \rightarrow i+1} - T_X^{i \rightarrow i-1}. \quad (1.54)$$

Here η_x is the adaptive learning rate, which is given by

$$\eta_x = \eta_0(1 - \tanh(\alpha_x \cdot \Delta\pi)). \quad (1.55)$$

With $\Delta\pi = \langle \pi^X \rangle - \langle \pi^Y \rangle$ we denote the difference between the average payoffs. The adaptive learning rate plays a crucial role. If, for example, the average payoff of population X is greater than the one of the Y population, the adaptation of the strategies becomes slower. Why should the X population learn so fast, when everything goes well? On the other side, when the X population has a smaller average payoff than the Y population, it is useful to adapt in a speedy manner. This principle is similar to the so-called “win stay, lose-shift” rule. We found, that an adaptive population under the influence of internal noise (which arises naturally from the finiteness of a population) can gain an increased average payoff in transient phases.

Besides of the Moran process we also stressed a different microscopic update mechanism, which is based on the pairwise comparison of individuals called “local update rule”. The main difference between the local update rule and the Moran process is, that the former one is based only on local information, i.e. the payoff difference between the interacting individuals, whereas the Moran process is not defined in a local way. We showed then that if one population using the local update rule plays against a population using the Moran process, the latter wins. In an information theoretical point of view these results are understandable.

Next, we show that in the case for large population sizes N , the dynamics of the system can be approximated by a Fokker-Planck equation (Gardiner, 2003; Schuster, 2002; Traulsen, Clausen and Hauert, 2005). For this purpose we start from the master equation

$$P^{\tau+1}(j) - P^\tau(j) = P^\tau(j-1)T_{j-1}^+ + P^\tau(j+1)T_{j+1}^- - P^\tau(j)T_j^- - P^\tau(j)T_j^+. \quad (1.56)$$

We denote with $P^\tau(j)$ the probability to be in state j and time τ . By introducing the system size parameter N and the van Kampen’s notation (Gardiner, 2003) $x = j/N$, $t = \tau/N$ and $T_j^\pm \rightarrow T^\pm(x)$ we can rewrite the probability density as

$$\rho(x, t) = NP^\tau(j). \quad (1.57)$$

Together with equation 1.56 this yields

$$\begin{aligned} \rho(x, t + N^{-1}) - \rho(x, t) &= \rho(x - N^{-1}, t)T^+(x - N^{-1}) + \rho(x + N^{-1}, t)T^-(x + N^{-1}) \\ &\quad - \rho(x, t)T^-(x) - \rho(x, t)T^+(x). \end{aligned} \quad (1.58)$$

Because the limit for large N is of interest, we now make a Taylor expansion at x and t . For the probability density we obtain

$$\begin{aligned} \rho(x, t + N^{-1}) &\approx \rho(x, t) + \frac{\partial}{\partial t}\rho(x, t)\frac{1}{N} \\ \rho(x \pm N^{-1}, t) &\approx \rho(x, t) \pm \frac{\partial}{\partial x}\rho(x, t)\frac{1}{N} + \frac{\partial^2}{\partial x^2}\rho(x, t)\frac{1}{2N^2} \end{aligned} \quad (1.59)$$

and for the transition probabilities we get

$$\begin{aligned} T^+(x - N^{-1}) &\approx T^+(x) - \frac{\partial}{\partial x} T^+(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} T^+(x) \frac{1}{2N^2} \\ T^-(x - N^{-1}) &\approx T^-(x) + \frac{\partial}{\partial x} T^-(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} T^-(x) \frac{1}{2N^2}. \end{aligned} \quad (1.60)$$

The terms in Eq. 1.58 which are independent of $1/N$ are canceled. We now rearrange the terms depending on their order of $1/N$, whereas we will neglect terms that are higher in the order of $O(N^2)$. Starting with the terms of order $1/N$ we find for the left hand side the term $\frac{\partial}{\partial t} \rho(x, t)$. On the right hand side, we obtain

$$\begin{aligned} &-\rho(x, t) \frac{\partial}{\partial x} T^+(x) + \rho(x, t) \frac{\partial}{\partial x} T^-(x) - T^+(x) \frac{\partial}{\partial x} \rho(x, t) + T^-(x) \frac{\partial}{\partial x} \rho(x, t) \\ &= -\frac{\partial}{\partial x} [T^+(x) - T^-(x)] \rho(x, t). \end{aligned} \quad (1.61)$$

We now select the terms of order $1/N^2$. On the right hand side we get then

$$\begin{aligned} &\left(\frac{\partial}{\partial x} \rho(x, t) \right) \left(\frac{\partial}{\partial x} T^+(x) \right) + \frac{1}{2} \rho(x, t) \frac{\partial^2}{\partial x^2} T^+(x) + \frac{1}{2} T^+(x) \frac{\partial^2}{\partial x^2} \rho(x, t) \\ &+ \left(\frac{\partial}{\partial x} \rho(x, t) \right) \left(\frac{\partial}{\partial x} T^-(x) \right) + \frac{1}{2} \rho(x, t) \frac{\partial^2}{\partial x^2} T^-(x) + \frac{1}{2} T^-(x) \frac{\partial^2}{\partial x^2} \rho(x, t) \\ &= \frac{1}{2} \frac{\partial^2}{\partial x^2} [T^+(x) + T^-(x)] \rho(x, t). \end{aligned} \quad (1.62)$$

Bringing all together, the equation now becomes

$$\frac{\partial}{\partial t} \rho(x, t) = -\frac{\partial}{\partial x} [T^+(x) - T^-(x)] \rho(x, t) + \frac{1}{2} \frac{\partial^2}{\partial x^2} \frac{T^+(x) + T^-(x)}{N} \rho(x, t). \quad (1.63)$$

By using the notation $a(x) = T^+(x) - T^-(x)$ and $b(x) = \sqrt{1/N [T^+(x) + T^-(x)]}$ we can write the equation as

$$\frac{\partial}{\partial t} \rho(x, t) = -\frac{\partial}{\partial x} a(x) \rho(x, t) + \frac{1}{2} \frac{\partial^2}{\partial x^2} b^2(x) \rho(x, t). \quad (1.64)$$

Equation 1.64 (1.63) is a Fokker-Planck equation with the drift term $a(x)$ and the diffusion term $b(x)$, which describes the deterministic time evolution of the nonequilibrium probability distribution.

Now, the Itô-calculus (Gardiner, 2003; Schuster, 2002; Traulsen, Clausen and Hauert, 2005) can be applied to obtain a stochastic differential equation, called Langevin equation. In this scope the Fokker-Planck equation mentioned above corresponds to the stochastic differential equation given by

$$\dot{x} = a(x) + b(x)\xi. \quad (1.65)$$

Here ξ is uncorrelated Gaussian noise. In the limit of $N \rightarrow \infty$ the diffusion term $b(x) \propto \sqrt{1/N}$ vanishes and a deterministic differential equation

$$\dot{x} = T^+(x) - T^-(x), \quad (1.66)$$

which is the replicator equation of the system, is found. For the Moran process (Traulsen, Clausen and Hauert, 2005) we get, here for the X population, by setting the adaptive learning rate $\eta = 1$,

$$\dot{x} = \alpha x \cdot (\pi_0(x) - \langle \pi(x) \rangle), \quad (1.67)$$

with $\alpha = 1/(\frac{1-w}{w} + \langle \pi(x) \rangle)$. Equation 1.67 is the adjusted replicator dynamics (Maynard Smith, 1982). Note, that α depends on the average payoff of the population. For the local update rule we obtain for the X population

$$\dot{x} = \beta x \cdot (\pi_0(x) - \langle \pi(x) \rangle), \quad (1.68)$$

with $\beta = w/\Delta\pi_{\max} = \text{const.}$ In contrast to the adjusted replicator dynamics β affects the timescale only.

In summary, both processes converge in the limit for $N \rightarrow \infty$ to replicator equations. The local update mechanism leads to the standard replicator dynamics, whereas the Moran process leads to the adjusted replicator dynamics.

1.4.3 Impact of Fraud on the Mean-Field Dynamics of Cooperative Social Systems

The question of cooperation is crucial for understanding evolution. For example, genomes, cells, multicellular organisms, social insects and presumably any arbitrary group of interacting individuals, this includes the human society, are all based on cooperation (Axelrod, 1984; Nowak, 2006b; Nowak and Sigmund, 2005). Cooperation means that an individual must dismiss their selfish behavior by helping another individual. Darwin's principle says that evolution is a constant struggle for survival and this implies that individuals should not support others at a cost to themselves (Maynard Smith, 1982). Nevertheless, in reality individuals are often willing to forgo some of their reproductive potential and support others, even if such an action reduces fitness in the short run. However, it might be possible that such behavior increases the survival chances in the long run.

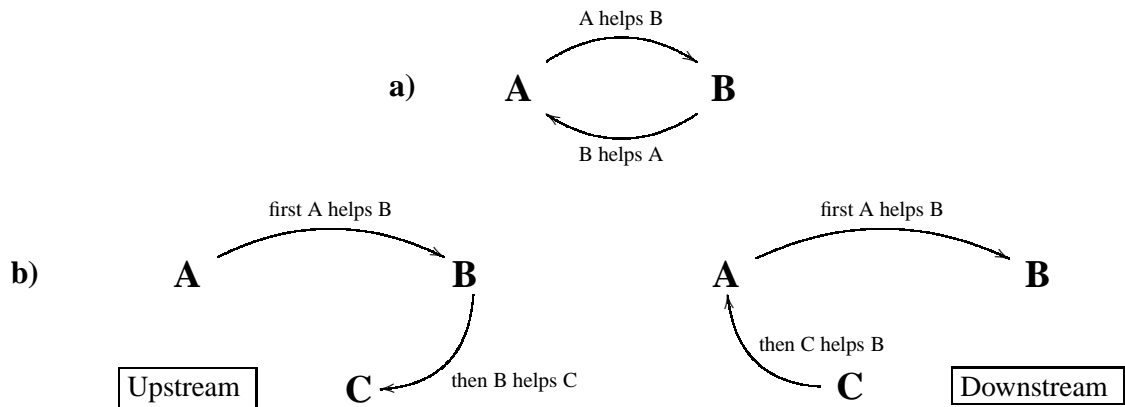


Figure 1.6: Cooperation can be based on direct reciprocity or on indirect reciprocity. **(a)** Cooperation can be based on repeated interactions with the same individual, which is called direct reciprocity, and means that an individual A helps B and (for same reason) B is then also willing to help A. **(b)** Two different strategies called “upstream” and “downstream”, which are both based on their reputation, are examples for indirect reciprocity. Upstream reciprocity means that a person (B) is getting help from one person (A), and then helps another person (C). In this case the first recipient B thanks another person C for what A did. Downstream reciprocity means, that an individual, here A, helps another individual B and receives than, because of this action, help from a third person, here C. In this case the person A is thanked by someone, here C, who observes and approves the action.

In this context, one of the main questions is, how natural selection encourages unselfish behavior. One approach towards the understanding of this phenomenon has been made in terms of mechanisms for the evolution of cooperation, which includes kin selection (Hamilton, 1963; Frank, 1998), i.e., if the donor and the recipient of an altruistic act are genetic relatives, group selection (Maynard Smith, 1976; Wilson, 1975; Traulsen and Nowak, 2006), which means that competition is also between groups and not only between individuals, and network reciprocity (Herz, 1994; Ohtsuki, Hauert, Lieberman and Nowak, 2006; Lindgren and Nordahl, 1994; Perc, 2006; Schweitzer, Behera and Mühlenbein, 2002; Szabó and Tóke, 1998; Szabó and Hauert, 2002; Santos, Rodrigues and Pacheco, 2005; Santos and Pacheco, 2005), which means that clusters of cooperators outcompete defectors. However, for the purpose of the thesis two mechanisms called direct reciprocity (Trivers, 1971; Axelrod, 1984; Hauert and Schuster, 1997) and indirect reciprocity (Brandt and Sigmund, 2004; Brandt and Sigmund, 2005; Brandt and Sigmund, 2006) are of special interest. The latter one is quite interesting, because this mechanism distinguishes humans from all other living species on earth (Alexander, 1987).

Direct reciprocity (Fig. 1.6 a) treats the following problem. Assuming an evolutionary game in which are repeated encounters between the same two individuals, whereas each of them can choose between the strategies cooperate or defect. Now it is possible that under certain conditions a strategy of mutual cooperation may be favored by both players even if it pays each player in the short term (see prisoner's dilemma game in paragraph 1.2.1.2). In this manner, direct reciprocity can lead to the evolution of cooperation if the probability p of another encounter between the same two individuals exceeds the cost c to benefit b ratio of the altruistic act $p > c/b$. Indirect reciprocity (Fig. 1.6 b), which can be subdivided in upstream reciprocity and downstream reciprocity, is defined as act, where the return for a favor comes from someone different than the recipient of the benefaction. This is a typical phenomenon in human societies. Indirect reciprocity is complex. For example, consider an individual B (see Fig. 1.7) which has defected in the previous round of an evolutionary game. What should individual A do now? In general, individual A has two possibilities. First, he can punish individual B for his behaviour. Second he can help B as an altruistic act. In the article "Evolution of indirect reciprocity by image scoring" M. Nowak and K. Sigmund (1998) introduced a theoretical framework to model indirect reciprocity, which does not require that the same two individuals ever meet again, by a mechanism, which they called image scoring to stress this kind of problems.

The article "Impact of fraud on the mean-field dynamics of cooperative social systems" is based on the image scoring model, which works as follows: Consider an evolutionary game with two types of individuals (strategies) called discriminators and defectors. In this population each individual has the option to help one another or not. Random pairs of individuals are chosen, of which one is the donor of some altruistic act, whereas the other is



Figure 1.7: Indirect reciprocity has to address the following problems. Assuming that individual B has defected in a previous action and as a result of his action he now has a lower reputation. Then, the question is, if A should help B and what should be done in this case with the reputation of individual A. **(a)** Individual A does not help B. Thus, B is punished for previous defections. Why should the reputation of A then be reduced? **(b)** Individual A helps B, but helping defectors can destabilize cooperation. So, why should the reputation of A increase, although B is a defector?

the recipient. The donor can cooperate and help the recipient, but he has to pay for this act a cost c . Then the recipient receives a benefit of value b (with $b > c$). If the donor does not help, he can save the cost, so that both individuals receive nothing (zero payoff). Now, each player is labeled with a flag called image score. In a simple case the image score has only the two values 0 or 1. A player with the image score 1 is labeled as good, whereas a player with an image score 0 is labeled as bad. It is essential that all other players can see the image score and can use this information for future decisions. A defector never helps, whereas discriminators help only players with the image score 1. The question arises, how a player can get or lose his good reputation. An individual can only change his reputation status, if he was chosen as a donor. If he then cooperates, his image score becomes 1. Otherwise, if he defects, the image score becomes 0. Thus, the image score depends only on the last move of a player as a donor. For a defector the information about the image score does not matter, because he always defects. If he was chosen as a donor his image score becomes bad. However, at the beginning all players are labeled as good, in this case the defector has the possibility to increase his payoff, if he is chosen as a recipient. Then it was shown (Nowak and Sigmund, 1998) that individual selection can favour cooperative strategies, targeted to recipients who have helped others in the past. Furthermore, they showed that the probability q of knowing the image score of the recipient must exceed the cost to benefit ratio of the altruistic act $q > c/b$ to fulfill the emergence of evolution of cooperation.

In this manner, the discriminators behavior can lead to cooperation, which is of more benefit for the individuals than in the case, that they act as independent individuals. However,

this can only occur for $q > c/b$ which is a very important corollary to generate cooperation. Otherwise, the population can always be exploited by selfish individuals (defectors) who benefit even more by not taking part to the community and just earning its benefits. Nevertheless, it is important to note that both, cooperators as well as defectors, are fair players and, thus, are respectable “people”, because there is no specific rule that says, e.g., that defectors have to help. Selfish behavior is not criminal and defectors are no cheaters.

This is the starting point to introduce a new type of player, which we will call scammer (or fraud). A “scammer strategy” is defined as follows: If a scammer is chosen as a donor, his behaviour is the same as that of a discriminator, i.e., he helps other individuals with image score 1 and denies help for those who are labeled as bad (0). In the latter case his reputation becomes also bad. However, scammers bluff by manipulation of their own reputation in the way that they always seem to have a good reputation for other players. In this manner he always yields the benefit b if he is chosen as a recipient and the donor is not a defector. Furthermore, a scammer, if he is chosen as a donor, does not pay the cost for cooperation. We then analysed this extended model by introducing a detection probability α . In the case that the scammer is detected, he has to pay a high penalty ρ . We analysed both, a constant detection probability and an adaptive detection probability. In the case of a constant detection probability we show that below a certain value of $\alpha = \alpha_1$ the dynamics is determined by scammers. And, furthermore we showed that above a certain value of $\alpha = \alpha_2$ scammers become extinct. In this case the dynamics is then determined by discriminators and defectors only. However, in the intermediate parameter region for the detection probability $\alpha_1 < \alpha < \alpha_2$ we observed, that fraud can even enhance cooperation. Nevertheless, for a lower detection probability α real systems would break down. One possibility to avoid the breakdown of the system is given by using a high detection probability. However, for an adaptive detection probability, we observe, because of the existence of a nontrivial fixed point in the interior of the simplex, that the dynamics can lead to the coexistence of discriminators, defectors and scammers.

Our model offers two interesting prospects. On the one side, it allows to study evolution of cooperation in the context of fraud, which delivers a new insight in cooperative systems. On the other side, we have now for the first time the possibility to analyse and describe the rule of cheating in such reputation systems. We note that classical evolutionary game theory does not sufficiently model this ‘living on the expense of others’, which is typically feasible during a limited amount of time only.

The evolution of cooperation does not seem to be a logical consequence of Darwin’s principles that favour the strong and selfish individuals. But also, several mechanisms exist that can maintain cooperation. Nevertheless, if these mechanisms are too costly they are only maintained, if there is a way for scammers to persist. In this case, it is the cheating that ultimately stabilizes the evolution of cooperation.

In conclusion, our results show that in indirect reciprocity discriminators might benefit from coexistent scammers that fake their reputation, depending on their detection probability and on the cost to benefit ratio. When the probability to detect scammers vanishes with the fraction of scammers (in the case of adaptive detection probability), a certain amount of fraud is always found in the system. Thus, a limited presence of scammers in the population can increase cooperative behavior in our model. We show, that complex cooperative systems become vulnerable to self-interested scammers when a critical number is exceeded or when they cannot be detected at low abundance.

2 Publications

This chapter contains the following publications:

- Arne Traulsen, **Torsten Röhl** and Heinz Georg Schuster,
Stochastic gain in population dynamics,
Physical Review Letters **93**, 028701 (2004)
(selected for the Virtual Journal of Biological Physics Research **8** (2), 2004)
- **Torsten Röhl**, Arne Taulsen, Jens Christian Claussen and Heinz Georg Schuster,
Stochastic gain in finite populations,
Physical Review E, submitted
- **Torsten Röhl**, Claudia Röhl, Heinz Georg Schuster and Arne Taulsen.
Impact of fraud on the mean-field dynamics of cooperative social systems,
Physical Review E **76**, 026114 (2007)

2.1 Stochastic gain in population dynamics

Stochastic Gain in Population Dynamics

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We introduce an extension of the usual replicator dynamics to adaptive learning rates. We show that a population with a dynamic learning rate can gain an increased average payoff in transient phases and can also exploit external noise, leading the system away from the Nash equilibrium, in a resonancelike fashion. The payoff versus noise curve resembles the signal to noise ratio curve in stochastic resonance. Seen in this broad context, we introduce another mechanism that exploits fluctuations in order to improve properties of the system. Such a mechanism could be of particular interest in economic systems.

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Game theory [1] describes situations in which the success or payoff of an individual depends on its own action as well as on the actions of others. This paradigm can be applied to biological systems, as evolution through natural selection can be viewed as an optimization process in which the fitness landscape changes with the state of the adaptive populations [2]. Evolutionary game theory focuses mainly on systems with a single fitness function for all individuals, which is identified with the payoff function of a game [3–5]. In nature, often different populations with different ambitions interact with each other, as shoppers and sellers [6], attackers and defenders [6], or males and females [5]. Here the payoff functions are different for the interacting populations. A mean-field description of such asymmetric conflicts is given by the coupled replicator equations [4,5,7]. These equations have a very rich dynamical behavior and can even display Hamiltonian chaos [8,9]. In previous work [3–5] it has been tacitly assumed that both populations have the same adaptation mechanisms. But it seems to be natural that different mechanisms are applied by the interacting populations, e.g., different adaptation rates. Here we analyze such systems for the case that both populations have slightly different adaptation mechanisms. We assume that one population can control its own adaptation rate. This alters the velocity when the system is approaching the stable Nash equilibria [10] in strategy space, leading to an increased average payoff.

In real systems, fluctuations disturbing the system are to be expected. Such disturbances can arise from a variety of effects, e.g., errors of the players [11], deviations from a perfectly mixed population, or immigration of individuals with different strategy distributions. So far, stochastic extensions to the replicator dynamics have mainly been analyzed in the context of equilibrium selection [12,13]. Here we show that a population with an adaptive learning rate can obtain an increased payoff if these fluctuations are present. For small noise intensities the average payoff increases, while very large fluctuations can no longer be exploited, leading to a decrease of the average payoff.

This recalls the stochastic resonance effect [14–17], where the signal to noise ratio of a system is improved for intermediate noise intensities. In contrast to the usual stochastic resonance, a periodic force is not involved here, making the mechanism more similar to coherence resonance [18]. Seen in this broader context, we introduce another mechanism that exploits fluctuations in order to improve the performance of the system.

We consider two adaptive species X and Y —each with different strategies—that are involved in a repeated game. Both populations have different objectives described by payoff matrices P_x and P_y . The fraction of individuals x_i that adopt a certain strategy i grows proportional to the relative payoff of the strategy i ; the same holds for Y . In the presence of noise, this coevolution can be described by the coupled replicator equations

$$\begin{aligned}\dot{x}_i &= x_i \eta_x [\Pi_i^x - \langle \Pi^x \rangle] + \xi_i^x, \\ \dot{y}_i &= y_i \eta_y [\Pi_i^y - \langle \Pi^y \rangle] + \xi_i^y,\end{aligned}\quad (1)$$

where η_x and η_y are the learning rates of the populations. We assume for simplicity that the noise ξ_i is Gaussian with autocorrelation $\langle \xi_i^k(t) \xi_j^l(s) \rangle = \sigma^2 \delta_{ij} \delta_{kl} \delta(t-s)$ as in Ref. [12]. We also follow Ref. [12] in choosing reflecting boundaries. The payoffs are defined as $\Pi_i^x = (P_x \cdot \mathbf{y})_i$, $\langle \Pi^x \rangle = \mathbf{x}^T \cdot P_x \cdot \mathbf{y}$, and similarly for y .

We extend the usual replicator dynamics by introducing adaptive learning rates as

$$\eta_x = 1 - \tanh(\alpha_x \Delta \Pi), \quad (2)$$

where $\Delta \Pi = \langle \Pi^x \rangle - \langle \Pi^y \rangle$ is the time dependent difference between the average payoffs of the populations and $\alpha_x \geq 0$ is a “perception ability” of the population. In order to maintain the basic features of the replicator dynamics, the learning rate must be a positive function with $\langle \eta \rangle = 1$, which is ensured by Eq. (2). For $\alpha_x > 0$ the population X learns slower if it is currently in a good position; otherwise, it learns faster. The value of α_x determines how well a population can assess its current state. The adaptive learning rate leads to a faster escape

from unfavorable states, while on the other hand the population tends to remain in preferable states. Other choices for η_x which ensure these properties mentioned above will not alter our results. In the following, we focus on a setting where only one population has an adaptive learning rate η_x as in Eq. (2).

The noise introduced above drives the system away from the Nash equilibrium and leads for small amplitude to a positive gain of the population with an adaptive learning rate, whereas for large noise amplitudes the fluctuations smear out the trajectories in phase space so strongly that they can no longer be exploited. Hence, we expect an optimal noise effect for intermediate values of σ . In order to be able to compare the payoffs of both populations, we assume that the dynamics starts from the Nash equilibrium.

As a first example, we consider the zero-sum game “matching pennies” [3,19]. Here both players can choose between two options ± 1 . Player one wins if both players select the same option and player two wins otherwise. The game is described by the payoff matrices

$$P_x = \begin{pmatrix} +1 & -1 \\ -1 & +1 \end{pmatrix} = -P_y. \quad (3)$$

The replicator equations follow from Eqs. (1) and (3) as

$$\begin{aligned} \dot{x} &= -2\eta_x x(2y-1)(x-1) + \xi_x, \\ \dot{y} &= +2\eta_y y(2x-1)(y-1) + \xi_y, \end{aligned} \quad (4)$$

where $x = x_0$ and $y = y_0$. Let us first consider the zero noise limit in the case $\eta_x = \eta_y = 1$. As for all zero-sum games, i.e., $P_x = -P_y^T$, the system (1) without noise becomes Hamiltonian and has a constant of motion [20]. Here the constant is given by $H(x, y) = -2\ln[x(1-x)] - 2\ln[y(1-y)]$. The trajectories oscillate around the Nash equilibrium at $x = y = 1/2$. $H(x, y)$ is connected to the temporal integral of the average payoff $\langle \Pi_x \rangle = (\mathbf{x}^t)^T \cdot P_x \cdot \mathbf{y}^t$ during a period with $\langle \Pi^x \rangle > 0$,

$$\int_{t_0}^{t_1} \langle \Pi^x \rangle dt = -\frac{H(x_0, \frac{1}{2}) - H(\frac{1}{2}, \frac{1}{2})}{4}, \quad (5)$$

where $(x, y) = (x_0, \frac{1}{2})$ at t_0 and $(x, y) = (\frac{1}{2}, x_0)$ at t_1 .

If we include adaptive learning rates (2) into the system, we find $\dot{H}(x, y) = -2 \tanh(\alpha_x \Delta \Pi) \Delta \Pi \leq 0$, vanishing for $\alpha_x = 0$. Hence, adaptive learning rates dampen the oscillations around the Nash equilibrium, and the trajectories in the $x-y$ plane spiral towards the Nash equilibrium where $\langle \Pi_x \rangle = \langle \Pi_y \rangle = 0$ (see Fig. 1). In addition, this leads to an increased payoff of one population. As the matrices (3) describe a zero-sum game, it is sufficient for a population if it knows its own current average payoff $\langle \Delta \Pi \rangle = 2\langle \Pi_x \rangle$.

Numerical simulations for $\alpha_x > 0$ show that the temporal integral of the payoff becomes

$$\left\langle \int_{t_0}^{t_1} \langle \Pi_x \rangle dt \right\rangle_{(x_0, y_0)} = -\frac{1}{8} [H(x_1, y_1) - H(x_0, y_0)]. \quad (6)$$

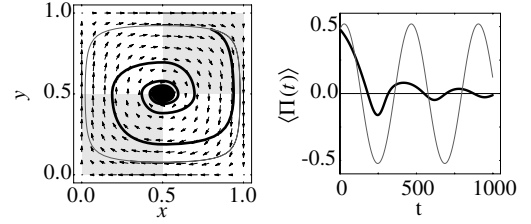


FIG. 1. Matching pennies: Comparison between the behavior of a population with a constant learning rate [i.e., $\alpha_x = 0$ (thin lines)] and a population with an adaptive learning rate [perception ability $\alpha_x = 10$ (thick lines)]. The opponent has in both cases a constant learning rate $\eta_y = 1$. Left: Trajectories in strategy space. Arrows show the vector field of the replicator dynamics. Population X has positive (negative) average payoff in gray (white) areas. Right: Time development of the average payoff of the population X. The adaptive learning rate increases the time intervals in which the corresponding population has a positive payoff, dampening the oscillations around the Nash equilibrium [21].

The averaged initial value $H(x_0, y_0)$ can be calculated as $\int_0^1 dx_0 dy_0 H(x_0, y_0) = 8$. For $t \rightarrow \infty$ the system relaxes to the Nash equilibrium where $H = 8 \ln 2$. Hence, we find for the average cumulated payoff with $\langle \int_{t_0}^{\infty} \langle \Pi_x \rangle dt \rangle_{(x_0, y_0)} \leq -\frac{1}{8}(8 \ln 2 - 8) \approx 0.307$. Numerical simulations yield 0.308 ± 0.005 independent of α . We conclude that a population can increase its average payoff if it has an adaptive learning rate $\alpha_x > 0$ and if the game does not start in the Nash equilibrium. The adaptation parameter α influences only the time scale on which the Nash equilibrium is approached.

Small noise intensities drive the system away from the fixed point and the population with the adaptive learning rate gains an increased payoff. If the noise amplitude σ becomes too large, the trajectories will be smeared out homogeneously over the positive (gray) and negative (white) payoff regions in phase space (Fig. 1). This implies that the average gain of population one decreases to zero; cf. Fig. 2. Although the average payoff is very small even for the optimal noise intensity, the cumulated payoff increases linearly in time. This means that for long times the gained payoff accumulates to a profitable value.

As a second application we analyze the effect of adaptive learning rates and noise on the prisoner’s dilemma. We use the standard payoff matrix [22]

$$P_x = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} = P_y, \quad (7)$$

where rows and columns are placed in the order “cooperate” and “defect.” As this game is not a zero-sum game, the population with the adaptive learning rate must be able to compare its own average payoff with the opponent’s average payoff. The replicator dynamics of this system is determined by Eqs. (1) and (7),

$$\begin{aligned} \dot{x} &= x\eta_x(x-1)(1+y) + \xi_x, \\ \dot{y} &= y\eta_y(y-1)(1+x) + \xi_y. \end{aligned} \quad (8)$$

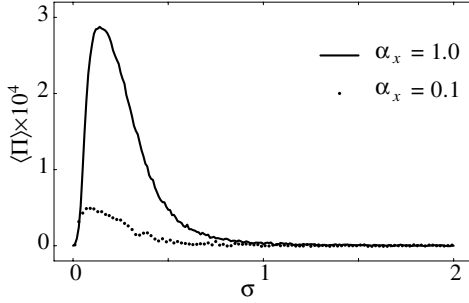


FIG. 2. Matching pennies: Average payoff of a population with an adaptive learning rate against a population with a constant learning rate under the influence of noise for different noise intensities ($\alpha_y = 0$, averages over 2×10^4 initial conditions and 2×10^4 time steps; see [21] for further details).

There is a stable fixed point in the Nash equilibrium $x = y = 0$ where both players defect and an unstable fixed point for mutual cooperation, i.e., $x = y = 1$.

The average payoff difference under the influence of noise is similar as in matching pennies. Small fluctuations lead the system slowly away from the Nash equilibrium and tend to increase the payoff. If the fluctuations are too large, they disturb the population with adaptive learning rates and the payoff decreases again (see Fig. 3). Interestingly enough, here too much noise even leads to a decreasing payoff difference.

In order to describe the “stochastic gain” effect analytically, we introduce a simplified model. A linearization of Eq. (8) around the stable Nash equilibrium leads for constant learning rates to $\dot{x} = -\eta_x x + \xi_x$ and $\dot{y} = -\eta_y y + \xi_y$. We now analyze a game in which the replicator dynamics is given by these linear equations and include adaptive learning rates based on the payoffs for the prisoner’s dilemma. With $\Delta\Pi = -5(x - y)$ the adaptive learning rate η_x becomes $\eta_x = 1 + \tanh[5\alpha(x - y)] \approx 1 + 5\alpha(x - y)$ for $\alpha, x, y \ll 1$. The simplified system can be viewed as a small noise expansion of the prisoner’s dilemma, where the trajectory stays close to the Nash equilibrium. For $\eta_y = 1$ the simplified noisy replicator equations read

$$\dot{x} = -x - \alpha'x(x - y) + \xi_x, \quad (9a)$$

$$\dot{y} = -y + \xi_y, \quad (9b)$$

where $\alpha' = 5\alpha$. The effect of different constant learning rates is discussed in Ref. [23]. The mechanism we introduce here is more intricate, as the adaptive learning rate leads to a dynamical adjustment of the learning rate, and the average of $\eta_x = 1 + \alpha'(x - y)$ over all possible strategies is $\eta_x = 1$.

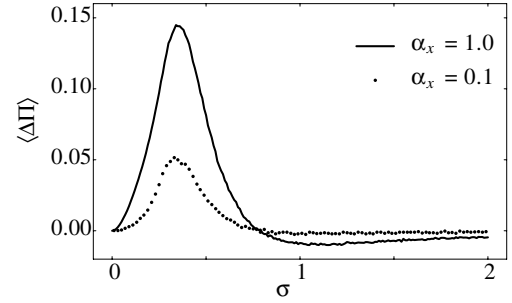


FIG. 3. Prisoner’s dilemma: Average payoff difference of a population with an adaptive learning rate against a population with a constant learning rate for different noise intensities. The negative payoffs arise from the fact that we have $\eta_x < \eta_y$ for $x < y$ ($\Delta t = 0.01$, $\alpha_y = 0$, averages over 2×10^4 initial conditions and 2×10^4 time steps).

Equation (9b) describes an Ornstein-Uhlenbeck process [24]; here the dynamics is restricted to $0 \leq y \leq 1$. The Fokker-Planck equation [25] for $p_y = p_y(y, t|y_0, t_0)$,

$$\dot{p}_y = \frac{d}{dy} \left(y p_y + \frac{\sigma^2}{2} \frac{d}{dy} p_y \right), \quad (10)$$

has the stationary solution $p_y^s = \mathcal{N}_y e^{-y^2/\sigma^2}$, where $\mathcal{N}_y^{-1} = \int_0^1 e^{-y^2/\sigma^2} dy$. We find the mean value $\langle y(\sigma) \rangle$ as

$$\langle y \rangle = \int_0^1 dy y p_y = \frac{\sigma(1 - e^{-\sigma^{-2}})}{\sqrt{\pi} \operatorname{erf}(\frac{1}{\sigma})}. \quad (11)$$

y is a correlated stochastic process which appears in Eq. (9a) as a multiplicative noise. Numerical simulations indicate that we may neglect the stochastic nature of y and replace it by $\langle y \rangle$ for small α . This leads to an approximated Fokker-Planck equation for $p_x = p_x(x, t|x_0, 0)$,

$$\dot{p}_x = \frac{d}{dx} \left[-a(x)p_x + \frac{\sigma^2}{2} \frac{d}{dx} p_x \right], \quad (12)$$

where $a(x) = -x - x\alpha'(x - \langle y \rangle)$. Since x is (similarly to y) also restricted to $0 \leq x \leq 1$, we find the stationary solution

$$p_x^s = \mathcal{N}_x \exp \left[-\frac{x^2}{\sigma^2} - \frac{2\alpha'x^3}{3\sigma^2} + \frac{\alpha'\langle y \rangle x^2}{\sigma^2} \right] \quad (13)$$

with the normalization constant \mathcal{N}_x . Since x is typically of the order of σ for $\sigma \ll 1$, the term x^2/σ^2 is finite. Therefore, we can expand Eq. (13) for $\alpha' \ll 1$ and obtain by expanding $\langle x \rangle$ again an analytical expression for $\langle \Delta\Pi \rangle = -5(\langle x \rangle - \langle y \rangle)$,

$$\langle \Delta\Pi \rangle = -5\alpha' \frac{d}{d\alpha'} \langle x \rangle = 5\alpha' \left\{ \frac{\sigma^2}{2} - \delta^3 \sigma \gamma (1 - \gamma)^2 + \delta^2 (1 - \gamma) \left[\frac{5}{3} \gamma - \frac{7}{6} \sigma^2 (1 - \gamma) \right] - \delta \gamma \left(\frac{2}{3\sigma} + \sigma \right) \right\}, \quad (14)$$

where $\delta = \frac{1}{\sqrt{\pi} \operatorname{erf}(1/\sigma)}$ and $\gamma = e^{-1/\sigma^2}$. The asymptotics of Eq. (14) can be computed as $\langle \Delta\Pi \rangle = \alpha'/(24\sigma^2)$ for $\sigma \gg 1$ and

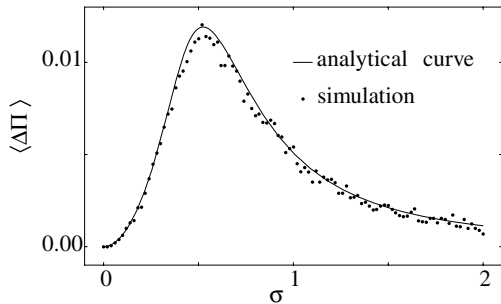


FIG. 4. Simplified model: Comparison of the average payoff difference $\langle \Delta \Pi \rangle$ from a simulation of Eqs. (9a) and (9b) and the analytical function Eq. (14) ($\Delta t = 0.01$, $\alpha' = 5\alpha = 0.1$, averages over 4×10^4 time steps and 4×10^4 realizations).

$\langle \Delta \Pi \rangle = \alpha' \left(\frac{5}{2} - \frac{35}{6\pi} \right) \sigma^2$ for $\sigma \ll 1$. We stress that this simplified system which consists of a stable fixed point with a linear adaptive learning rate in the presence of noise is the simplest possible model that describes the stochastic gain effect. Figure 4 shows a comparison between the analytical payoff difference Eq. (14) and a simulation of Eqs. (9a),(9b).

To summarize, we have introduced an extension to the usual replicator dynamics that modifies the learning rates using a simple “win stay–lose shift” rule. In this way, a population optimizes the payoff difference to a competing population. This simple rule leads to a convergence towards the mixed Nash equilibrium for the game of matching pennies [26]. Even in games with stable Nash equilibria as the prisoner’s dilemma, transient phases can be exploited, although the basins of attraction are not altered, as, e.g., in Ref. [23]. Weak external noise drives the system into the transient regime and leads to an increased gain for one adaptive population.

In conclusion, we have found a learning process which improves the gain of the population with an adaptive learning rate under the influence of external noise. Fluctuations lead to an increased payoff for intermediate noise intensities in a resonancelike fashion. This phenomenon could be of particular interest in economics, where interactions are always subject to external disturbances [6,13,27].

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- [21] To ensure the conservation of $H(x, y)$ after a discretization of Eq. (4), symplectic algorithms have to be applied. The algorithm proposed by Hofbauer [20] can be written as

$$\begin{aligned} x_i^{t+1} &= x_i^t + x_i^t [\Pi_i^x - \langle \Pi^x \rangle] \frac{1}{C/\eta_x + \langle \Pi^x \rangle}, \\ y_i^{t+1} &= y_i^t + y_i^t [(\Pi_i^y)^+ - \langle \Pi^y \rangle^+] \frac{1}{C/\eta_y + \langle \Pi^y \rangle^+}, \end{aligned} \quad (15)$$

with $C \gg 1$ and where $(\Pi_i^y)^+ = (P_y \cdot \mathbf{x}^{t+1})_i$, $\langle \Pi^y \rangle^+ = (\mathbf{y}^t)^T \cdot P_y \cdot \mathbf{x}^{t+1}$. Here we choose $C = 100$.

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2.2 Stochastic gain in finite populations

Stochastic Gain in Finite Populations

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Flexible learning rates can lead to increased payoffs under the influence of noise. In [A. Traulsen, T. Röhl, and H.G. Schuster, Phys. Rev. Lett. **93**, 028701 (2004)], we have demonstrated this effect based on a replicator dynamics model which is subject to external noise. Here, we utilize recent advances on finite population dynamics and their connection to the replicator equation to extend our findings and demonstrate the stochastic gain effect in finite population systems. Finite population dynamics is inherently stochastic, depending on the population size and the intensity of selection, which measures the balance between the deterministic and the stochastic parts of the dynamics. This internal noise can be exploited by a population using an appropriate microscopic update process, even if learning rates are constant.

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I. INTRODUCTION

Evolutionary biology considers the dynamics of systems in which the potential to produce offspring differs among the individuals in a population. Individuals with higher fitness produce more offspring and spread in the population. In the simplest cast, different types of individuals have different fitness and one expects that the fittest type spreads fastest. Evolutionary game theory describes population dynamics under frequency dependent selection, i.e. when the fitness depends on the types and frequencies of other types in the population [1–4]. Traditionally, such systems are described by deterministic replicator equations [5–7], which corresponds to a mean field approximation in physics. Using techniques from statistical physics, a connection between replicator equations and related microscopic processes can be established [8–12].

Usually, evolutionary game theory addresses the dynamics within a single population and describes how different types spread in this population [13–17]. In structured populations, the microscopic update rule that determines how individual players switch strategies can significantly change the macroscopic dynamics [17–19]. Well mixed populations without any structure can be described by the replicator equation. Different microscopic dynamics lead to different forms of the replicator equation in the limit of infinite populations. However, usually this affects timescales and does not alter the stability of fixed points and the qualitative dynamics.

Bi-matrix games (or asymmetric conflicts) address situations in which two different populations with different preferences interact, which is the generic case in economics. In biology, the two populations can be males and females or defenders and attackers of a territory [1]. In social and economic systems, one could think of employees and employers or shoppers and sellers [20]. Usually, evolutionary game theory considers the competition between different individuals within a population (e.g. between timid and aggressive males). But one can also compare the average success of one population to the average success of the second population. In these systems, slight changes in the details of the replicator dynamics can change the qualitative dynamics and the stabil-

ity of fixed points [1]. In a previous paper, we have shown that one population that changes its adaptation or learning rate according to its current situation can in the long run outperform a population with a constant learning rate in the presence of external additive noise [21].

Here, we investigate this “stochastic gain” effect in interacting finite populations and show that even internal noise that naturally arises from the finiteness of a population can be exploited in this way. We start by showing that the effect can be found in finite populations not subject to external noise and demonstrate that our results are valid with different microscopic update mechanisms. Subsequently, we show examples that an adaptive learning rate (which forms the basis of the “stochastic gain” in Ref. [21]) is not necessary at all if both populations employ different microscopic update mechanisms. In this case, specific microscopic update rules are more successful.

II. THE BASIC MODEL

To address the stochastic gain effect in finite populations, we consider two interacting populations X and Y , both of size N . Each individual can choose between two strategies 0 and 1. The payoff in the X population depends on the number of different strategic types in the Y population and vice versa. The payoffs for a single interaction can be written as

$$\begin{array}{c} X_0 \\ X_1 \end{array} \begin{array}{cc} Y_0 & Y_1 \\ \left(\begin{array}{cc} a_{00}, b_{00} & a_{01}, b_{01} \\ a_{10}, b_{10} & a_{11}, b_{11} \end{array} \right) \end{array}. \quad (1)$$

Thus, a X_0 individual interacting with an Y_0 individual obtains the payoff a_{00} whereas its interaction partner obtains b_{00} . The average payoff π_0^X of each of the X_0 individuals depends on the number of Y_0 individuals, j_0 , and on the number of Y_1 individuals, $j_1 = N - j_0$. It is given by $\pi_0^X = a_{00}j_0/N + a_{01}(N - j_0)/N$. Similarly, we have $\pi_1^X = a_{10}j_0/N + a_{11}(N - j_0)/N$. In the Y population, the payoffs depend on the number of X_0 and X_1 individuals, i_0 and $i_1 = N - i_0$, which leads to $\pi_0^Y = b_{00}i_0/N + b_{10}(N - i_0)/N$

and $\pi_1^Y = b_{01}i_0/N + b_{11}(N - i_0)/N$. The payoffs now determine the probability that a new strategy is adopted. Different ways to incorporate this strategy dynamics are possible [22–24].

Here, we follow [10] and use a microscopic update mechanism based on the pairwise comparison of individuals we call “local update rule”: One focal individual is selected at random and compares its payoff to a randomly selected role model from the same population. It adopts the strategy of the role model with a probability proportional to the payoff difference. Thus, the probabilities to change the number of X_0 individuals from i to $i \pm 1$ are given by

$$T_X^{i \rightarrow i \pm 1} = \eta_x \left(\frac{1}{2} \pm \frac{w}{2} \frac{\pi_0^X - \pi_1^X}{\Delta\pi_{\max}} \right) \frac{i}{N} \frac{N - i}{N}. \quad (2)$$

Since the payoffs depend on y , these transition probabilities depend on the number of different types of the Y -population. The learning rate η_x determines how likely it is to change a strategy in the X population. For $\eta_x \ll 1$, it is very unlikely that an individual switches the strategy. In the extreme case of $\eta_x = 0$, the population does not evolve. For the maximum value $\eta_x = 1$, evolution within the X population proceeds fastest. The intensity of selection w controls how likely it is to adapt to a better (or worse) strategy [10, 16]. For $w \ll 1$, selection is weak and the probability to switch to a better strategy is only slightly higher than the probability to switch to a worse strategy. For $w = 1$, the probability to adopt a better strategy reaches one if the payoff difference $\pi_0^X - \pi_1^X$ reaches the maximum possible payoff difference $\Delta\pi_{\max}$. With probability $T_X^{i \rightarrow i} = 1 - T_X^{i \rightarrow i+1} - T_X^{i \rightarrow i-1}$, the number of X_0 and X_1 individuals remains constant. In an equivalent way, we obtain

$$T_Y^{j \rightarrow j \pm 1} = \eta_y \left(\frac{1}{2} \pm \frac{w}{2} \frac{\pi_0^Y - \pi_1^Y}{\Delta\pi_{\max}} \right) \frac{j}{N} \frac{N - j}{N}. \quad (3)$$

The transition probabilities Eqs. (2) and (3) define a birth-death process in each of the two populations on the state space $\{i, j\} = \{0, 1, \dots, N\}$. For large populations, the dynamics of the system can be approximated by a Fokker-Planck equation with the drift term $T^{i \rightarrow i+1} - T^{i \rightarrow i-1}$ and the diffusion term $\sqrt{[T^{i \rightarrow i+1} + T^{i \rightarrow i-1}]/N}$ [10]. Applying the Itô calculus [25–27], this description is equivalent to a stochastic differential equation for the fraction of X_0 individuals in the X population, $x = i/N$, and the fraction of Y_0 players in the Y population, $y = j/N$,

$$\begin{aligned} \dot{x} &= \eta_x \frac{w}{\Delta\pi_{\max}} (\pi_0^X - \pi_1^X) x(1-x) + \sqrt{\eta_x \frac{x(1-x)}{N}} \xi \\ \dot{y} &= \eta_y \frac{w}{\Delta\pi_{\max}} (\pi_0^Y - \pi_1^Y) y(1-y) + \sqrt{\eta_y \frac{y(1-y)}{N}} \xi. \end{aligned} \quad (4)$$

Here, ξ is white Gaussian noise with the variance 1. The multiplicative noise term vanishes for $N \rightarrow \infty$ and at the boundaries.

Having introduced a specific microscopic update mechanism, we now concentrate on a particular game for which the

stochastic gain effect is most striking. We consider the payoff matrix

$$\begin{array}{cc} & Y_0 & Y_1 \\ X_0 & (+1, -1) & (-1, +1) \\ X_1 & (-1, +1) & (+1, -1) \end{array}. \quad (5)$$

This game is known as “matching pennies” (in economics) or “battle of the sexes” (in biology), see [1, 10, 28] for a biological motivation of this game. The X population is better off if it uses the same strategy as the Y population, i.e. a X_0 player obtains the highest payoff when matched with a Y_0 player and a X_1 player obtains the highest payoff when matched with a Y_1 player. Individuals from the Y population obtain the highest payoff when paired with a different strategy in the X population, i.e. Y_0 with X_1 and Y_1 with X_0 . In the limit $N \rightarrow \infty$, we obtain from Eq. (4) the usual replicator equation. In this case, the system cycles on closed trajectories around a neutral fixed point at $(x, y) = (1/2, 1/2)$. Due to the symmetry of the game, both populations obtain the same average payoff. The same holds under the influence of external noise [21]. In the case of a finite population, the microscopic update mechanism is a natural source of internal noise. Considering the symmetry between Eqs. (2) and (3), both populations have the same average payoff even in this case.

III. ADAPTIVE LEARNING RATE

Usually, the learning rates η_x and η_y have the same fixed value. Szolnoki and Szabó have analyzed a system in which different players have different, but fixed values of η [29]. Here, we assume that the rate with which a population adapts to a new situation is different depending on the average success of a population. If the overall success is unsatisfactory, one is more likely to try something new. In biology, a population with small average fitness might decrease in size, leading to a smaller population that adapts faster. We follow our previous work based on the replicator equation [21] and introduce an adaptive learning rate η_x for the X population. This rate η_x increases above a base value η_0 when the average payoff difference to the Y population is negative. It decreases below η_0 when the payoff difference is positive. In our case, the adaptive learning rate is given by

$$\eta_x = \eta_0 (1 - \tanh(\alpha_x \cdot \Delta\pi)). \quad (6)$$

Here, $\Delta\pi = \langle \pi^X \rangle - \langle \pi^Y \rangle$ is the difference between the average payoffs, which are defined by $\langle \pi_X \rangle = (\pi_0^X \cdot i + \pi_1^X \cdot (N - i))/N$ and $\langle \pi_Y \rangle = (\pi_0^Y \cdot j + \pi_1^Y \cdot (N - j))/N$. The parameter η_0 is set to $\frac{1}{2}$ and α_x determines how sensitive this change in the learning rate is. If the X population has a larger average payoff than the Y population, adaptation of strategies becomes slower. If the X population has a smaller average payoff than the Y population, adaptation of strategies becomes faster. Thus, we introduce an adaptive learning rate that follows the “win stay — lose shift” paradigm in the comparison between the two populations.

Our system is reduced to the one analyzed in [21] in the limit of $N \rightarrow \infty$. However, the nature of the noise is very

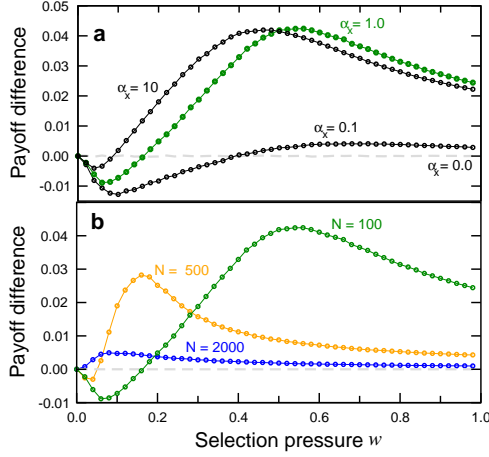


FIG. 1: (Color online) Average payoff difference of a population with an adaptive learning rate $\eta_x = 0.5 - 0.5 \tanh(\alpha_x \cdot \Delta\pi)$ compared to a population with a constant learning rate of $\eta_y = 0.5$ in the matching pennies game using the local update rule, see text. **(a)** Payoff differences are shown for a constant population size of $N = 100$ and for different α . The average payoff difference is small if the intensity of selection w is small otherwise the population with an adaptive learning rate has a higher average payoff. The stochastic gain effect becomes more pronounced with increasing α . (averages over $R = 2 \cdot 10^4$ random initial conditions in the interior until the maximum time $T = 10^5$ or until the absorbing boundaries of the system are reached). **(b)** Payoff differences for three different population sizes for fixed $\alpha = 1.0$. The total payoff decreases with higher population size N because the noise intensity decreases. In the limit of $N \rightarrow \infty$ we obtain the equation for the stochastic replicator dynamic without external noise. Thus the payoff difference converges to zero. Averages over $R = 7000$ random initial conditions until the absorbing boundaries are reached or until the maximum time $T = N \cdot 10^3$.

different: In [21], the noise is additive and arises from an external source. Here, the noise is multiplicative and arises internally from the system. In Fig. 1, we demonstrate that for finite populations, the stochastic gain effect can still be found with the additional twist that now internal noise is exploited. The noise intensity is controlled by w : A small w implies that the system is close to neutral selection where all individuals have the same fitness. In this case, it is difficult to increase payoffs solely by changing the rate of adaption. A large w means that the system is very unlikely to leave the area close to the point $(x, y) = (0.5, 0.5)$ where both populations have the same payoff. Thus, there exists an optimal w for which the payoff difference becomes highest. For $N \rightarrow \infty$, the internal noise vanishes and the effect is not longer present. We have started with a random initial condition and simulated the system until one strategy in one population has reached extinction. Fig. 1 shows the mean payoff difference averaged over a large number of such runs.

Next, we show that this result does not depend on the details of the microscopic update mechanism. A standard approach

for game dynamics in finite populations is the frequency dependent Moran process [22, 30–32]. In each of the two populations, the following update process takes place: One individual is selected at random, but proportional to fitness. We define fitness f as a convex combination of a background fitness set to 1 and the payoff, e.g. $f_0^X = 1 - w + w\pi_0^X$. Since our payoffs vary between -1 and 1, the intensity of selection w has an upper limit ($w < 0.5$) to ensure that fitness is positive. The selected individual produces identical offspring, which replaces a randomly chosen individual. The transition probabilities in the X population are thus given by

$$T_X^{i \rightarrow i+1} = \frac{\eta_x}{2} \frac{f_0^X i}{f_0^X i + f_1^X (N-i)} \frac{N-i}{N} \quad (7)$$

$$T_X^{i \rightarrow i-1} = \frac{\eta_x}{2} \frac{f_1^X (N-i)}{f_0^X i + f_1^X (N-i)} \frac{i}{N}, \quad (8)$$

where we have introduced a factor 1/2 to make both considered processes identical for $w \rightarrow 0$. Similar equations hold for the Y populations.

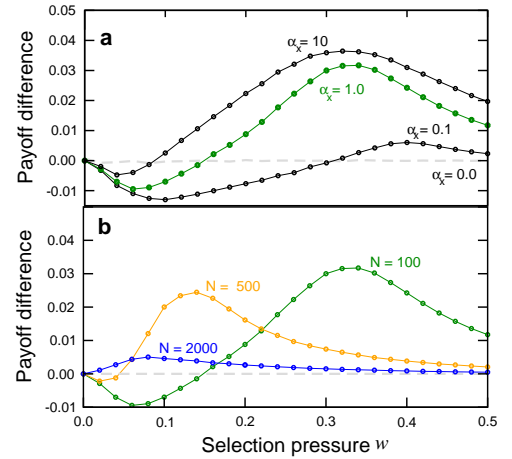


FIG. 2: (Color online) Average payoff difference of a population with an adaptive learning rate $\eta_x = 0.5 - 0.5 \tanh(\alpha_x \cdot \Delta\pi)$ against a population with a constant learning rate of $\eta = 0.5$ in the matching pennies game using the frequency dependent Moran process in both populations. The parameter values in **(a)** and **(b)** are identical to Fig. 1, but in the Moran process shown here, the maximum intensity of selection is given by $w = 0.5$. Qualitatively, the stochastic gain effect does not depend on the details of the update mechanism in finite populations: With α increasing from $\alpha = 0.0$ the payoff advantage of the adaptive population increases. However, there is an optimal α for which the stochastic gain effect is most pronounced (see text). With increasing N the system approaches a deterministic replicator system and the intrinsic noise vanishes. Thus, increasing N leads to smaller payoff differences. Moreover, the finite size effect of a negative payoff difference for low intensity of selection vanishes.

In the Moran process strategies with higher fitness are more likely to be selected for reproduction, whereas selection at

death is the same for all strategies. Thus, the average abundance of fitter strategies increases over time. The frequency dependent Moran process is reduced to the adjusted replicator dynamics in the limit $N \rightarrow \infty$ [10]. For the adjusted replicator dynamics it is known that the game defined by the payoff matrix Eq. (5) has an asymptotically stable fixed point at $(x, y) = (0.5, 0.5)$ [1]. Thus, it is not a priori clear that the stochastic gain effect can be observed even in the frequency dependent Moran process. However, Fig. 2 shows that a variable rate of adaptation also leads to an increased payoff in this process.

To illustrate the effect further, we consider the probability density for the different states of the system. Fig. 3 shows that for $\alpha_x = 0$, this probability density is symmetric in the state space $(i, j) \in (\{0, \dots, N\}, \{0, \dots, N\})$ leading to a vanishing average payoff difference. With increasing α_x the time the system spends in states in which the X population has the higher average payoff, increases. However, if α_x becomes too large, then adaptation of the X population is so strong that random fluctuations no longer take the system to states in which the payoff difference is large. Thus, there exists an optimal α_x for which the payoff difference becomes highest for any given w .

IV. COMPETITION OF UPDATE MECHANISMS

So far, we have assumed that both populations use the same update mechanism and that only the adaptive learning in one population is different. However, one can also consider two different update mechanisms in the two populations. This is motivated by the following observation [10]: The local update mechanism leads to the standard replicator dynamics $\dot{x} = x(\pi_x - \langle \pi \rangle)$ in the limit $N \rightarrow \infty$. The frequency dependent Moran process leads to the adjusted replicator dynamics $\dot{x} = x(\pi_x - \langle \pi \rangle) / \langle \pi \rangle$ in this limit. The only difference is that the right hand side is divided by the average payoff. However, this can be interpreted as a change in the learning rate, as a large average payoff leads to slow dynamics and a small average payoff to fast dynamics. Thus, we expect that when a population using the frequency dependent Moran process competes with a population using the local update mechanism, the former will perform better without any external change in the rate of adaption. Fig. 4 shows that this is actually the case. This result becomes more pronounced for higher intensities of selection. However, in the processes discussed here, there is an upper limit in the intensity of selection. To address this issue, one has to resort to different microscopic update mechanisms [24, 33].

This shows that an increased average payoff can be obtained from a different microscopic update mechanism. In principle, this could lead to higher level selection: If competition does not only occur within populations, but also between groups of individuals [32], then groups using a more successful update mechanism will perform better. In this way, a more successful update mechanism might be selected in the long run.

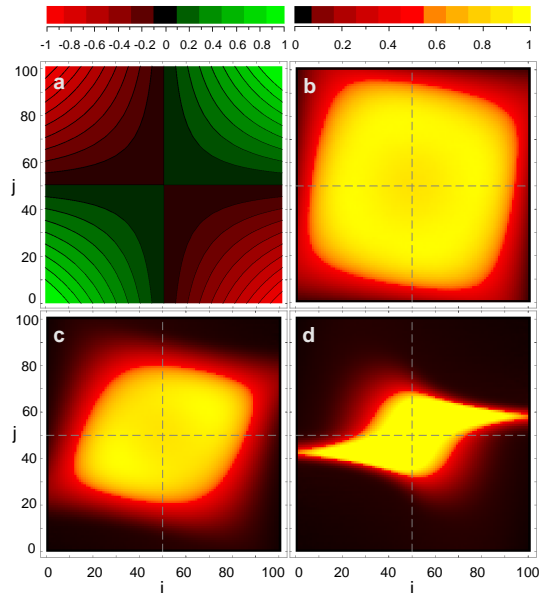


FIG. 3: (Color online) Payoff distribution and stationary distribution for the Moran process in the strategy space spanned by the state space for a constant population size of $N = 100$ are shown encoded by a color scale where bright colors indicate high values. (a) The average payoffs $\langle \pi_X \rangle = (\pi_0^X \cdot i + \pi_1^X \cdot (N - i)) / N$ of the adaptive populations (X) are shown. In the bottom left and top right areas (green) the payoffs of the adaptive population (X) are positive, whereas in the bottom right and top left areas (red) the payoffs are negative. The adaptive population can obtain a higher stationary probability density in the bottom left and top right areas, leading to the stochastic gain effect. (b) The stationary distribution for $\alpha = 0.0$ is symmetric. The population dynamics drives the system around the fixed point of the replicator dynamics at $(x, y) = (0.5, 0.5)$. (c) With increasing $\alpha = 1.0$ the system is driven to the interior. Now the areas where the average payoff for the adaptive population is higher shows a larger stationary probability density. (d) Same as in (c) but the stationary distribution for $\alpha = 10.0$ is shown. Increasing α further leads to a smaller probability density in the areas where the payoff difference is high and, thus, the payoff difference decreases again for large α . For all figures, parameter values are $N = 100$, $R = 5 \cdot 10^5$, $w = 0.35$, $T = N \cdot 10^3$.

V. DISCUSSION

We have demonstrated that the stochastic gain effect first discussed in [21] can also be found in finite populations. In this case, the internal noise arising from the finiteness of the population can be exploited. The intensity of this noise can be controlled by the intensity of selection, which determines how likely it is that individuals adopt better (or worse) strategies.

Recently, there has been an increased interest in stochastic effects in evolutionary games. Perc *et al.* have shown that in spatial games, coherence resonance can be observed [34, 35].

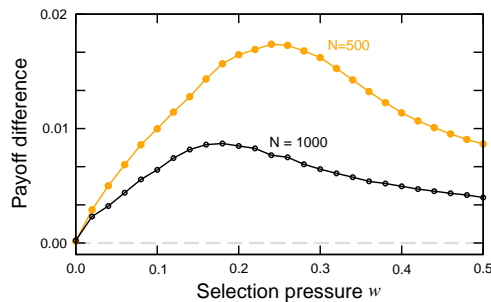


FIG. 4: (Color online) Average payoff difference of a population using the Moran process against a population using the local update rule for two different sizes of population N . Both populations are nonadaptive with a constant learning rate of $\eta_0 = 0.5$. Independent of the selection pressure w the population using the Moran process obtains a higher payoff. Thus, the stochastic gain effect can also be observed in the absence of variable learning rates. The total payoff decreases with higher population size N . In the limit of $N \rightarrow \infty$ both dynamics result in the equation for the deterministic replicator dynamic, without external noise, thus, the payoff difference tends to zero. Parameter values are $N = 500, 1000$, $T = N \cdot 10^3$, $R = 15000$.

It has been shown that noise can even enhance cooperation in many circumstances [36–38]. Internal as well as external noise have been considered in these systems and it has been shown that the nature of these disturbances can be very different [39, 40].

The existence of the stochastic gain effect without any adaptive learning rates ($\eta_x = \eta_y = 0.5$) is based on the application of different microscopic update rules. This effect could have potential applications for economy where traders try to improve their payoff by exploiting fluctuations. A finite number of interacting agents can be a source of noise in these systems. Clever local update rules that use more and more information about the market and other traders can be advantageous in these systems. Our results highlight the importance of the detailed consideration of microscopic update mechanisms, as they can significantly alter the macroscopic dynamics of a system.

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2.3 Impact of fraud on the mean-field dynamics of cooperative social systems

PHYSICAL REVIEW E **76**, 026114 (2007)**Impact of fraud on the mean-field dynamics of cooperative social systems**Torsten Röhl,¹ Claudia Röhl,² Heinz Georg Schuster,¹ and Arne Traulsen³¹*Institute of Theoretical Physics and Astrophysics, University of Kiel, Leibnizstraße 15, D-24098 Kiel, Germany*²*Institute of Anatomy, University of Kiel, Olshausenstrasse 40, D-24098 Kiel, Germany*³*Program for Evolutionary Dynamics, Harvard University, Cambridge, Massachusetts 02138, USA*

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The evolution of costly cooperation between selfish individuals seems to contradict Darwinian selection, as it reduces the fitness of a cooperating individual. However, several mechanisms such as repeated interactions or spatial structure can lead to the evolution of cooperation. One such mechanism for the evolution of cooperation, in particular among humans, is indirect reciprocity, in which individuals base their decision to cooperate on the reputation of the potential receiver, which has been established in previous interactions. Cooperation can evolve in these systems if individuals preferably cooperate with those that have shown to be cooperative in the past. We analyze the impact of fake reputations or fraud on the dynamics of reputation and on the success of the reputation system itself, using a mean-field description for evolutionary games given by the replicator equation. This allows us to classify the qualitative dynamics of our model analytically. Our results show that cooperation based on indirect reciprocity is robust with respect to fake reputations and can even be enhanced by them. We conclude that fraud *per se* does not necessarily have a detrimental effect on social systems.

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I. INTRODUCTION

Evolution is a constant struggle for survival. Individuals compete continuously. Natural selection implies that individuals should not support others at a cost to themselves. Thus, it is surprising that individuals are often willing to forgo some of their reproductive potential and support others instead. While such an action reduces fitness in the short run, it might increase the survival chances in the long run. This phenomenon has been explained in terms of mechanisms for the evolution of cooperation, which include kin selection [1,2], group selection [3–5], network reciprocity [6–16], direct reciprocity [17–19], and indirect reciprocity [20–28]; see [29] for a recent review. Among humans, a particularly interesting mechanism is indirect reciprocity, which “presumably may distinguish us humans from all other living species on earth” [30].

Here, we model indirect reciprocity, where cooperation is based on a status or reputation that individuals obtained in previous interactions. Indirect reciprocity is frequently applied to improve trade on online platforms [31–33]. Recently, it has been shown that it is also a potential mechanism that can help to address such global cooperation problems as climate preservation [34]. Theoretical work on reputation systems has considered the influence of unintended errors [27,28]: A “trembling hand” can lead to the wrong action and a “fuzzy mind” might lead to a wrong assessment and hence a wrong reputation. However, a possible manipulation of reputation by the players is usually not taken into account. Furthermore, these models do not involve any time delays and typically assume that an action is immediately assessed [20,35]. In reality, this is not always the case: We discover that we have been ripped off when it is too late, read the fine print of a contract when we have already signed, or discover that public funds are missing when it is not longer possible to backtrack the scammers. Although their behavior is “bad,”

these scammers can maintain a “good” reputation for some time. Indeed, in human social systems generally a small fraction of people exist who break the rules for their own advantage and are sanctioned by the community [36]. As this kind of “fraud” is fake cooperation, it is different from public defection and also the effect of punishing this action can deviate from the conventional ones [37,38]. So far, it is unclear why sanctions by the community have not eliminated fraud from social systems. Also the impact of fraud on the evolution of cooperation has not been analyzed yet. We address these questions by extending the image scoring framework described by Nowak and Sigmund [20]. Image scoring is a particular simple moral system assigning a reputation to an action and determining the choice of an action based on such reputation. As image scoring bases reputation only on actions and is independent of previous reputations, it is especially robust if information on previous encounters is not reliable. Theoreticians have criticized this framework, as more sophisticated moral systems avoid the problem that a good individual who refuses to cooperate with a bad individual immediately becomes bad [36,39,40]. Moreover, image scoring is not evolutionarily stable and does not belong to the “leading eight” moral systems of Ohtsuki and Iwasa, who analyzed 4096 moral systems and identified the eight most cooperative of them [21]. However, behavioral experiments have shown that image scoring is a plausible mechanism for cooperation among humans and is preferred under many circumstances over more sophisticated moral systems [41–43]. It also requires only minimal information. Thus, image scoring seems to be a reasonable starting point to address the problem of fraud. We base our model on the replicator equation, which provides a mean-field description of the dynamics of game-theoretic systems [44,45]. This allows us to classify the different dynamical regimes of the system analytically.

II. THE MODEL

Here, we first recall the image scoring framework and discuss the intuitive meaning of the parameters. The detailed mathematical implementation of the process is described in Secs. II A and II B. In the image scoring framework, two individuals are chosen at random, one as a potential donor and one as a recipient. The donor has the possibility to pay the cost c to support the recipient, who then obtains the benefit $b > c$. A pair of individuals only meets once. Therefore, the donor does not expect a return from the recipient himself, but hopes that through establishing a good reputation, the cost for his cooperation will be compensated by the benefit from an altruistic act of someone else in future encounters. We assume that the donor does not support the recipient directly, but invests in a public good and allows the recipient to take advantage of this good. Discriminators aim to improve their payoff by investing the cost c in their reputation and thus attract help from others, because the reputation, which is initially good for all individuals, only stays good if they help others and keep public confidence in this way. If they deny help, their reputation becomes bad. Defectors avoid the risk of investments in their reputation and do not support others. Thus, their good reputation from the beginning of each round remains good only until they are chosen as potential donors and deny help. Whereas in the short run nondonors yield the higher payoff by saving the costs for cooperation, in the long run cooperators increase the chance of obtaining a benefit based on their good reputation, and cooperation might thus yield the higher payoff.

This reputation-based cooperation can be exploited by “scammers” who manipulate their own reputation [23], especially if these do not need to fear imminent punishment. Therefore, we introduce an additional strategy, namely, fraud. Scammers only pretend to invest in the public good and encourage others to use the common good. While this allows them to maintain a good reputation, it undermines the system in the long run, since the common resource is overused. In reality, this can happen if transfers are made via anonymous public funds, if checks bounce, or if credit cards are misused. If the society is unable to detect and prevent such fraud, it will quickly spread and destroy the system. However, if there is a certain probability α ($0 \leq \alpha \leq 1$) that fraud is discovered, the situation becomes more interesting. For $\alpha=0$, fraud is never discovered and will spread in the population. For $\alpha=1$, reputation can never be faked successfully. Whenever a scammer is discovered, he has to pay a penalty proportional to the number of potential donors, $\rho(x+z)$, but does not change his behavior. The constant ρ can take any real value, but it seems to be reasonable that it is of the same order of magnitude as the benefit from cooperation, b . This leads to a new kind of dynamics between discriminators, defectors, and scammers. We follow Nowak and Sigmund [20] and model the dynamics with two different stages. On a fast time scale of interactions, reputations change and payoffs are accumulated. It is assumed that the information on the new reputation is available to all individuals before the next round occurs. On a slower time scale, the differences between the accumulated payoffs leads to a change of strategies. In this process, the numbers of discriminators, defectors, and scammers change.

A. Change of reputation and payoff accumulation

We consider three different types of individuals: discriminators, defectors, and scammers. All three types can have good or bad reputation (or image score). At the beginning of each generation, the image score is set to good for all individuals. Individuals interact for several rounds. The frequency of players with bad and good reputations, i.e., image score $i=0,1$, is denoted as x_i (discriminators), y_i (unconditional defectors), and z_i (scammers).

The frequency of individuals with image scores 0 or 1 changes from round to round, since a donation can change the reputation. An upper index denotes the round; e.g., x_1^2 is the frequency of discriminators with a good reputation in round 2. In the first round, all individuals have image score 1. Thus, the initial condition of each generation is given by $x_0^1=y_0^1=z_0^1=0$. The frequencies x_1^1 , y_1^1 , and z_1^1 (which sum up to 1) reflect the composition of the population. This composition changes based on the success of the strategies on a slower time scale (see below). In round 1, individuals obtain payoffs based on the initial reputation, which is always positive. Consequently, the reputation in round j depends on the actions in round $j-1$. Thus, actions in round j determine the future payoff obtained in round $j+1$.

For example, consider a discriminator with a good reputation. If he is chosen as a potential donor (which happens with probability $1/2$), his image score changes. If he is paired with an individual in good reputation, he cooperates and his reputation remains good. If he is paired with an individual in bad reputation, he does not cooperate. Then, his reputation becomes bad. The frequency of discriminators with a good reputation decreases due to this process from round j to round $j+1$. However, it increases when discriminators with a bad reputation cooperate again with others. Thus, x_1 changes from round j to round $j+1$ as

$$x_1^{j+1} = x_1^j + [x_0^j \varphi^j - x_1^j (1 - \varphi^j)]/2. \quad (1)$$

Here $\varphi^j = x_1^j + y_1^j + z_1^j$ is the fraction of all players who obtain help in round j . In an equivalent similar way, we obtain

$$x_0^{j+1} = x_0^j + [x_1^j (1 - \varphi^j) - x_0^j \varphi^j]/2,$$

$$y_0^{j+1} = y_0^j + y_1^j/2, \quad y_1^{j+1} = y_1^j - y_1^j/2,$$

$$z_0^{j+1} = z_0^j + [z_1^j (1 - \varphi^j) - z_0^j \varphi^j]/2,$$

$$z_1^{j+1} = z_1^j + [z_0^j \varphi^j - z_1^j (1 - \varphi^j)]/2. \quad (2)$$

The total numbers of discriminators $x = x_0^j + x_1^j$ remains constant during a generation. Equivalently, also $y = y_0^j + y_1^j$ and $z = z_0^j + z_1^j$ remain constant. Note that the real reputation of scammers changes despite the fact that their fake reputation is always good. We note that the reputation dynamics depends only on the fraction of players with different reputation and strategies. It is independent of the parameters of the underlying game, i.e., the cost c , the benefit b , the penalty ρ , and the detection probability α .

Based on the fractions of players in good and in bad reputation, we now calculate the average payoffs P_C , P_D , and P_S of cooperative discriminators, defectors, and scammers, respectively. We denote the payoff of a discriminator with good reputation as $P_{C,1}$ and the payoff of a discriminator with bad reputation as $P_{C,0}$. Equivalent notation is used for defectors and scammers. When an individual is chosen as a donor (which happens with probability $1/2$) and cooperates, then the cost of cooperation c is subtracted from its payoff. For example, a discriminator with a bad reputation cooperates with probability φ^j in round j . Thus, its payoff changes on average by $-\varphi^j c/2$ in that round. Cooperation leads to the benefit b . For example, an unconditional defector in good reputation increases his payoff by b whenever he interacts with a cooperater or a scammer and is chosen as a recipient. Thus, its payoff changes by $+b(x+z)/2$. For scammers, we have to distinguish two cases. With probability $1-\alpha$, they are viewed as individuals with a good reputation, but never pay the cost for cooperation. With probability α , they are punished for their fraud. The average payoffs for all players obtained in round j are

$$\begin{aligned} P_{C,0}^j &= -\varphi^j c/2, \\ P_{C,1}^j &= [-\varphi^j c + b(x+z)]/2, \\ P_{D,0}^j &= 0, \quad P_{D,1}^j = b(x+z)/2, \\ P_{S,0}^j &= P_{S,1}^j = (1-\alpha)b(x+z)/2 - \alpha\rho(x+z)/2, \end{aligned} \quad (3)$$

where c is the cost, b the benefit, α the detection probability, and ρ the penalty for fraud. Figure 1 shows examples of the dynamics of reputations and payoffs during a generation.

Equations (1) and (2) indicate that there are always some players of a certain strategy that are in good reputation and others that are in bad reputation. The success of a strategy depends on the accumulated payoffs averaged over these two reputations. After n rounds, discriminators have accumulated the average payoff

$$\mathcal{P}_C = \sum_{j=1}^n \frac{P_{C,0}^j x_0^j + P_{C,1}^j x_1^j}{x_0^j + x_1^j}. \quad (4)$$

The sums for defectors and scammers simplify to closed analytical expressions; defectors accumulate the payoff

$$\mathcal{P}_D = \sum_{j=1}^n \frac{P_{D,0}^j y_0^j + P_{D,1}^j y_1^j}{y_0^j + y_1^j} = b(x+z)(1-2^{-n}) \quad (5)$$

and scammers obtain

$$\mathcal{P}_S = \sum_{j=1}^n \frac{P_{S,0}^j z_0^j + P_{S,1}^j z_1^j}{z_0^j + z_1^j} = \frac{(1-\alpha)b - \alpha\rho}{2}(x+z)n. \quad (6)$$

For $n=0$, no interactions take place and all payoffs are zero. For a single interaction, $n=1$, defectors have always the highest payoff among the three strategies. Discriminators pay the cost of cooperation, but cannot take advantage of their

reputation. Scammers avoid paying the cost, but with probability α they are discovered and have to pay the punishment ρ . Thus defectors are more successful than scammers and fraud does not pay for a single interaction (cf. Fig. 1). Whether scammers or discriminators obtain a higher payoff depends on the parameters and on the initial condition. From $\mathcal{P}_C > \mathcal{P}_S$ we obtain with $n=1$ the condition $\alpha(x+z) > c/(b+\rho)$. In this case, discriminators are more successful than scammers. For $n \geq 2$, the dynamics becomes more complex.

Based on these accumulated payoffs for the short-term dynamics, we can now address the long-term dynamics that changes the fraction of discriminators, defectors, and scammers.

B. Change of strategies

The average payoffs that are accumulated over n rounds determine how successful a strategy is. As usual in evolutionary game theory, we equate payoff and fitness and players produce offspring proportional to their payoff. Note that each strategy consists of players with good reputation and of players with bad reputation. The accumulated payoffs considered here are the averages over the two reputations. We use the replicator dynamics to identify strategies that are successful in the long run based on their payoffs [45]. There are different microscopic processes that lead to slightly different differential equations [46–49]. As they do not change the stability of fixed points, we do not have to consider these alternative descriptions here. In the replicator equation, the fraction of the three strategies changes as

$$\begin{aligned} \dot{x} &= x(\mathcal{P}_C - \langle \mathcal{P} \rangle), \\ \dot{y} &= y(\mathcal{P}_D - \langle \mathcal{P} \rangle), \\ \dot{z} &= z(\mathcal{P}_S - \langle \mathcal{P} \rangle), \end{aligned} \quad (7)$$

where $\langle \mathcal{P} \rangle = x\mathcal{P}_C + y\mathcal{P}_D + z\mathcal{P}_S$ is the average payoff in the population. The replicator dynamics does not change the normalization, $x+y+z=1$. Due to the way that payoffs are calculated in Eqs. (3)–(5), the system is highly nonlinear. Note that the payoffs and hence the dynamics depends for a given initial condition on the number of rounds n , the cost c , the benefit b , the punishment ρ , and the detection probability α .

III. RESULTS

The global dynamics of the system is qualitatively determined by the dynamics between two strategies. As a starting point for our analysis, we assume that the detection probability α is independent of the number of scammers.

A. Constant detection probability

First, we consider the case of discriminators and scammers only. In this case, there are no individuals that do not receive help, $\varphi = x_1 + z = 1$. Hence, we have $\mathcal{P}_C = \mathcal{P}_S$ for detection probability

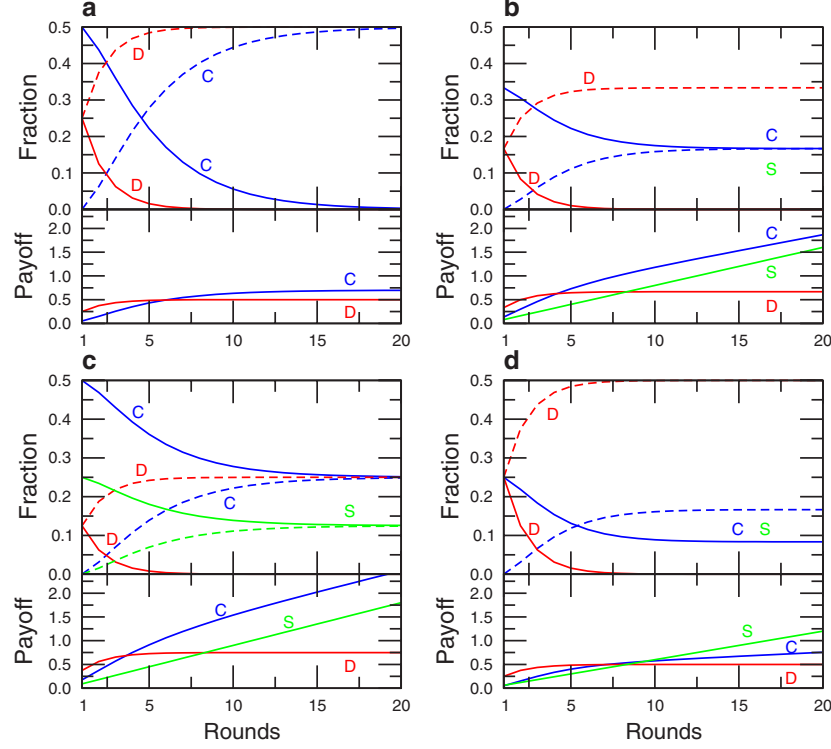


FIG. 1. (Color online) Time evolution of reputation and payoffs for the three different types (discriminating cooperators C with fraction x , defectors D with fraction y , scammers S with fraction z) for four different initial conditions. Initially, all individuals are in good reputation. Full lines show the dynamics of the fraction of individuals with good reputation, dashed lines show the fraction of individuals with bad reputation. (a) Without scammers, the reputation of both discriminating cooperators and defectors becomes bad after a few rounds. If the number of rounds is high enough, the accumulated payoff of discriminators becomes higher, which would in the long-term dynamics lead to an increase of their fraction (initial condition $x=0.5$, $y=0.5$). (b) Dynamics starting from a symmetric mixture of all three strategies, $x=y=z=1/3$. Because of the same initial values for discriminators and scammers, both have the same distribution, but different payoffs [cf. Eq. (2)]. Here, the payoff of discriminators is highest for more than four rounds, which leads to an initial increase of the fraction of discriminators in the replicator dynamics. (c) Starting from $x=0.5$, $y=0.25$, and $z=0.25$, the number of discriminators and defectors with bad reputation reaches $x_0^\infty=0.25$ in the long run. Cooperators again obtain the highest payoff if the number of rounds is sufficiently high. (d) If the initial condition is $x=0.25$, $y=0.5$, and $z=0.25$, the number of rounds determines the winning strategy: For only one round, defectors are most successful. If the number of rounds n satisfies $1 < n < 8$, then cooperators are most successful. Finally, scammers have the highest payoff for $n > 8$ (in all panels, the parameter values are $\alpha=0.38$, $b=1.0$, $c=0.4$, $\rho=1.0$).

$$\alpha_1 = \frac{c}{b + \rho}, \quad (8)$$

$$\alpha_2 = \frac{b}{b + \rho} \left(1 - \frac{2}{n} + \frac{2^{1-n}}{n} \right). \quad (9)$$

independent of n . An α larger than α_1 leads to a drift toward discriminators, a smaller α to a drift toward scammers. However, a society dominated by scammers is not possible, as this would produce benefits at no costs. Hence, reputation loses its meaning before fraud takes over. In reality, there are additional constraints, e.g., a maximum fraction of scammers. In order to tackle fraud, one should aim for a low cost to benefit ratio c/b and a high penalty to benefit ratio ρ/b if it is not possible to increase the detection probability α .

Without discriminators, $x=0$, the critical detection probability can be computed from $\mathcal{P}_D = \mathcal{P}_S$, which yields

For $\alpha > \alpha_2$, defectors are better off than scammers in the absence of discriminators and fraud vanishes ultimately as illustrated in Fig. 2(b). Note that, for large n , the ratio α_1/α_2 reduces to the cost to benefit ratio of cooperation c/b , which appears to be a crucial parameter for all mechanisms of cooperation [29].

The dynamics between discriminators and defectors depends only on the cost to benefit ratio and on the number of rounds in which the reputation of individuals changes [20,50]. If the number of rounds is sufficiently high, the dynamics is bistable. The position of the unstable equilibrium is given by the numerical solution of $\mathcal{P}_C = \mathcal{P}_D$.

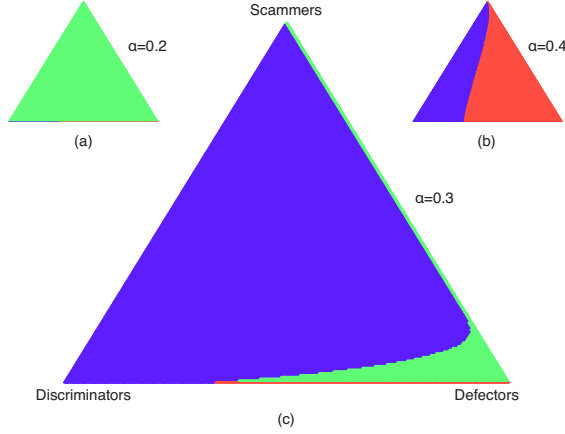


FIG. 2. (Color online) Simplices representing the evolutionary dynamics of the discriminator, defector, and scammer strategies for different detection probabilities α . Each point in the given area is colored depending on the fixed point of the dynamic. The corners represent the pure strategies. The sides represent competition between two strategies. For all diagrams the same parameter values are taken except for the probability α that a scammer is detected. (a) If the probability that a scammer is detected is below $\alpha_1=0.25$, scammers can take over the population ($\alpha=0.2$). Discriminators and defectors survive only if no scammers are initially present. (b) For $\alpha > \alpha_2 \approx 0.336$, scammers go extinct since they are discovered too frequently. Depending on the initial condition, cooperators or defectors prevail ($\alpha=0.4$). (c) For intermediate detection probabilities, $\alpha_1 < \alpha < \alpha_2$, the dynamics leads from defectors to scammers, but from scammers to discriminators ($\alpha=0.3$). The basin of attraction of the discriminators is significantly larger than in situations with high α [$b=1.0, \rho=1.0, c=0.5, n=6$, blue (dark gray) are discriminators, red (medium gray) are defectors, green (light gray) are scammers].

Let us now return to the full dynamics of all three strategies (see Fig. 2). As described above, for $\alpha < \alpha_1$, scammers dominate the system. For $\alpha > \alpha_2$, scammers have no influence on the dynamics. The replicator dynamics of the system has two stable fixed points, unconditional defection and discriminating cooperation. A very different situation is observed for intermediate detection probability $\alpha_1 < \alpha < \alpha_2$ [Fig. 2(c)]. The size of this region increases with the number of rounds n , since α_2 is an increasing function of n . For large n , it is given by $\alpha_2 - \alpha_1 \approx (b-c)/(b+\rho)$ and increases with larger $b-c$, but decreases with larger $b+\rho$.

Qualitatively, the situation is the same for all parameters within this region: While discriminators prevail compared to scammers, the scammers can still outperform defectors. The fixed point of unconditional defection is unstable and the dynamics leads to scammers. Errors on the trajectory toward scammer dominance will inevitably lead to the revival of discriminating cooperators. Similar, mutations in the strategies or stochasticity arising from a finite population size can also lead from the very narrow path from defectors toward scammers (cf. Fig. 2) into the basin of attraction of discriminators. These will finally take over the system and cannot be outperformed by the other two strategies. Hence, fraud has a

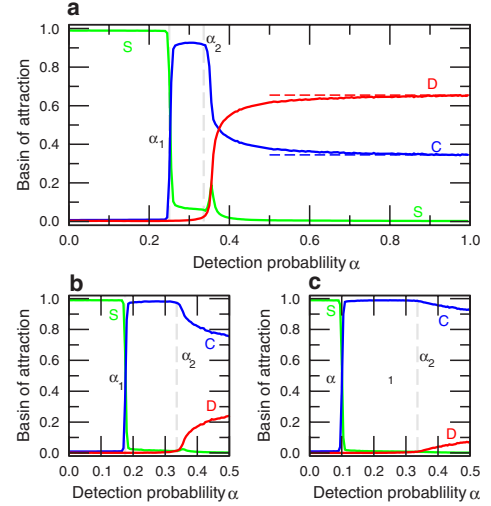


FIG. 3. (Color online) Size of the basin of attraction (cf. Fig. 2) of the different stable fixed points in dependence on the detection probability α . As in Fig. 1, C denotes cooperating discriminators, D unconditional defectors, and S scammers. (a) In a system with high cost ($c=0.5$), scammers dominate the system for $\alpha < \alpha_1=0.25$. For $\alpha_1 < \alpha < \alpha_2=0.336$, the basin of attraction of discriminators is greatly enlarged, but scammers still dominate over defectors. If $\alpha > \alpha_2$, then defectors and discriminators dominate. Compared to the analytical result for the situation without any scammers (horizontal dashed lines), discriminators have a larger basin of attraction. (b) For smaller costs of cooperation, $c=0.35$, the value of α_1 is reduced to 0.175, whereas α_2 remains constant. Without scammers, discriminators have a larger basin of attraction than defectors, but in our case it is further enlarged due to the initial presence of scammers. (c) If we decrease the cost to $c=0.2$, the value of α_1 is reduced to 0.1. In all three panels, each data point is an average over 10^5 initial conditions. For each initial condition, we solved the replicator equations (6) numerically using a Euler discretization with $\Delta t=0.01$. After $T=10^5$ time steps, we determined the strategy with the highest abundance. The small peaks of the scammer curve in (a) and (b) for values of $\alpha > \alpha_2$ indicate a very slow dynamics, in which the trajectory is after T time steps still close to the unstable scammer fixed point. For $\Delta t \rightarrow 0$ and $T \rightarrow \infty$, no scammers are present for $\alpha > \alpha_2$ (in all panels, the parameter values are $b=1.0, \rho=1.0, n=6$ rounds).

counterintuitive positive effect on the evolution of cooperation, as it considerably enlarges the basin of attraction of discriminators and destabilizes the situation in which only defectors are present. Interestingly, when few scammers are present, discriminators benefit from this when competing with defectors, as their basin of attraction is increased.

To demonstrate the positive effect of scammers and the increase of the $\alpha_1 < \alpha < \alpha_2$ region with decreasing cost of cooperation c , we have numerically calculated the basin of attraction (see Fig. 3) for three different costs of cooperation. The numerical results are in very good accordance with the analytical results. For high α the proportion of discriminators and defectors are determined by the ratio c/b . For $c=0.5$ and $\alpha < \alpha_2$, the discriminators can even have a larger basin

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than defectors, in contrast to the situation without scammers. For small c , discriminators are advantageous compared to defectors in the absence of scammers. Nonetheless, in the presence of scammers their basin of attraction increases.

For $n=3$ rounds, one can analytically show that fraud enhances cooperation. In a system without fraud, $z=0$, and $n=3$ rounds, there is an unstable fixed point x^* for the dynamics between discriminators and defectors if $0 < 5c < 12b$ given by

$$x^* = -2 + \frac{\sqrt{4b^2 - bc - 3c^2}}{b - c}. \quad (10)$$

If we add a small fraction of scammers near this fixed point, we can ask whether the difference between discriminator and defector payoff becomes positive or negative. For $z \ll 1$, we find

$$\mathcal{P}_C - \mathcal{P}_D \approx \left(\frac{2b - c}{8} x^* + \frac{4b - 5c}{8} \right) z > 0. \quad (11)$$

Since this payoff difference is always positive for $c < b$, discriminators are always better off when few scammers are present compared to situations without scammers. For $n=2$, the reasoning is similar: For $0 < 4c < b$, the unstable fixed point is given by $x^* = 3c/(b-c)$. For small z we find near the fixed point $\mathcal{P}_C - \mathcal{P}_D \approx (b-c)z/4$, which is positive if $c < b$. Thus, for $n=2$ and $n=3$ the basin of attraction of discriminators grows due to the presence of scammers, regardless of which strategy ultimately prevails.

B. Adaptive detection probability

The analysis in the previous paragraph is a necessary prerequisite to tackle the more realistic case in which the probability to detect scammers increases with their presence. If only a small fraction of the population steals from public funds, this is unlikely to have a detrimental effect on the system and will not be detected. However, if this fraction grows to larger values, such fraud endangers the common enterprise and the detection probability grows. The simplest approach to such a dynamic detection rate is to make it proportional to the number of scammers, i.e., $\alpha = \beta z$. In this way, it is hard to detect a small number of scammers, while it becomes significantly easier to detect them if their number increases. With this extension, the fixed points at the pure strategies are destabilized (see Fig. 4). The ultimate outcome of the dynamics is given by stable fixed points where a certain fraction of scammers is present. If discriminators and scammers coexist this fraction is given by α_1/β [see Eq. (8)]. If defectors and scammers coexist, it is given by α_2/β [see Eq. (9)].

However, we do not have to restrict ourselves to a linear function for the detection probability: Our results hold for any strictly increasing function $f(z)$. A steeper increase leads to a smaller fraction of scammers, which is given by the solution of $f(z) = \alpha_1$ (absence of defectors) or $f(z) = \alpha_2$ (absence of discriminators). Thus, the stable fixed points of the system can be calculated analytically for any strictly increasing function $f(z)$. Besides the three trivial unstable fixed

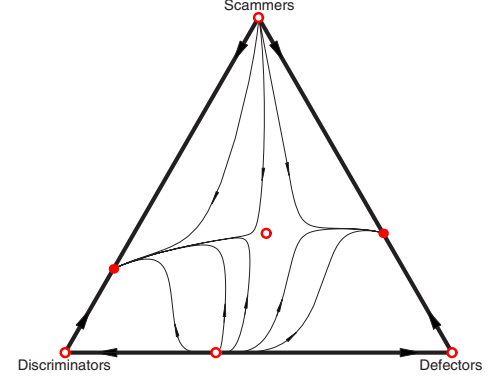


FIG. 4. (Color online) Dynamics between discriminators, defectors, and scammers with a scammer detection probability α proportional to their abundance z in the system $\alpha(z) = \beta z$. Since scammers are very successful when their abundance is low, situations without scammers become unstable. However, since high abundance of scammers implicates a high detection probability, the fixed point with scammers only is destabilized. Depending on the initial condition, the system ends up in one of two fixed points. (i) For a coexistence of discriminators and scammers, the fraction of scammers is given by $\alpha_1/\beta = 0.3$. (ii) For coexistence of defectors and scammers, the fraction of the latter is given by $\alpha_2/\beta = 0.358$ ($b = 1.0$, $c = 0.5$, $\rho = 1.0$, $n = 7$, $\beta = 1$).

points at $x=1$, $y=1$, and $z=1$, the system also has two non-trivial unstable equilibria. The fixed point between discriminators and defectors has been calculated from $\mathcal{P}_C = \mathcal{P}_D$ in Eq. (9) for the special case of $n=3$. In general, it can only be determined numerically. The fixed point in the interior that appears only for adaptive detection probability has to be determined numerically from $\mathcal{P}_C = \mathcal{P}_D = \mathcal{P}_S$ for a given set of parameters.

IV. DISCUSSION

Here, we have introduced a framework for reputation mechanisms that takes into account fake reputations. Many social, political, and economical systems show characteristics that emerge from differences in real and fake reputations. For example, think of political scandals where individuals act at the expense of the community, not paying any costs until they are detected or, in the worst case, the system breaks down. This living at the expense of others is typically feasible during a limited amount of time only. The simplicity of our model allows a future comparison with behavioral experiments, which have successfully corroborated several theoretical results in game theory [41–43, 51]. By concentrating on the mean-field dynamics of the system, we are able to obtain an analytical classification of the dynamics of the system.

In a finite population, stochastic effects would change this prediction. Without errors or mutations that lead to strategies that are not present, the system will ultimately reach one of the corners of the simplex. For small error rates, the new strategy is lost again or adapted by the whole population

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before a second error arises [52–54]. Thus, the stationary distribution is determined by the transition rates between the corners of the simplex. In this case, one would expect that discriminators dominate. However, this analytical approach involves at least a temporary dominance of scammers, which might not be feasible in real systems. For higher error rates, errors in the scammer corner of the simplex or on the trajectories from defectors to scammers in the parameter region $\alpha_1 < \alpha < \alpha_2$ will lead into the basin of attraction of discriminators. Even with high error rates, the system will spend most of the time in the adjacency of the discriminator corner. Thus, the possibility of faking image scores together with a small probability for errors can lead to cooperation based on reputation in this system. A possible extension of this model is to consider interactions on social networks. However, only the simplest cases of fixed [6–14,55–62] or evolving networks [63–68] allow tackling these problems analytically. In our case, additional complications occur due to the nonlinearity in the calculation of payoffs, which makes most analytical approaches unfeasible.

In conclusion, our results show that in indirect reciprocity discriminators might benefit from coexistent scammers that

fake their reputation, depending on their detection probability and on the cost to benefit ratio. If scammers dominate over defectors, they can help discriminators to initiate cooperation, as the presence of scammers allows discriminators to obtain a good reputation. Once defectors are rare, scammers are displaced by discriminators. When the probability to detect scammers vanishes with the fraction of scammers, a certain amount of fraud is always found in the system. Thus, a limited presence of scammers in the population can increase cooperative behavior. Complex cooperative systems become vulnerable to self-interested scammers when a critical number is exceeded or if they cannot be detected at low abundance. This could explain why evolution did not eliminate fraud from social systems.

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3 Discussion

3.1 Conclusions and Outlook

Evolutionary game dynamics developed into a growing field of mathematics with interesting connections to evolutionary biology and received growing influence on economical and social research (Aumann and Hart, 2002; Hofbauer and Sigmund, 1998; Weibull, 1995). One reason for this success is that evolutionary dynamics and concepts of evolutionary game theory can be formulated in terms of exact mathematical equations describing mutation and selection of replicating individuals (Nowak, 2006). There exist fruitful connections between game theoretical investigations and theoretical physics, namely, the methods of the theory of dynamical systems or of statistical mechanics (Hauert and Szabo, 2005; Schuster, 2002; Sella and Hirsch, 2005). In this thesis, asymmetric conflicts have been analysed and discussed. We developed a framework, in which two populations with different selection mechanisms interact within a repeated game. Naturally, when individuals interact, their success depends not only on their own actions, but also on the decisions of others. For example, many problems in biology, economics, sociology and politics involve decision making in complex situations, in which the result of an action does not only depend on this action itself but also on the simultaneous actions of others. Furthermore, a basic principle is that agents optimize their behavior with respect to their success (Darwin, 1859; Maynard Smith, 1982). Here, games were analysed in which, as a new element, i.e. the possibility that the rate of this adaptation process depends on the overall success of agents compared to their competitors, was introduced. It was found that agents with a flexible, time dependent adaptation rate can increase their payoff under the influence of external noise, which is present in all real systems in a natural way. Since noise plays an important role in such systems the obtained results do not depend of any certain kind of noise, whereas in infinite population the stochastic gain effect was found by adding a Langevin term of Gaussian distributed noise to the replicator equations (Fudenberg and Harris, 1992). Nevertheless, external fluctuations can influence the system in the same way like internal noise can do. Internal noise can arise from “noisy decision making” individuals making errors with a certain probability when interacting with other individuals. It is crucial that this kind of noise can generate deviations, which lead the system away from the equilibrium. In this way a population with an adaptive selection rate can increase its average payoff during the transient phase, i.e., beyond the Nash equilib-

rium. In this manner, evolution can be seen as the process leading from a certain status quo in a certain time, driven to the next state by the natural (=noisy) environment. We proceed by utilizing recent advances of evolutionary game dynamics in finite populations to address the stochastic gain effect in finite populations, where fluctuations arise naturally from microscopic dynamics. In contrast to infinite population, in finite populations the evolutionary dynamics is no longer described by differential equations (e.g. replicator equations). Here the dynamics is inherently stochastic, depending on the population size and the intensity of selection (Fudenberg, Nowak, Taylor and Imhof, 2006; Nowak, 2006; Traulsen, Clausen and Hauert, 2005; Traulsen, Clausen and Hauert, 2006). The demonstration of the stochastic gain effect in infinite as well as in finite populations is an important point, because most evolutionary game dynamics have been studied in infinite, rather than in finite populations. The field of evolutionary game theory, which deals with finite populations, still has many challenges for the future. For example, a resemblance between the Moran process in finite population and the adjusted replicator dynamics (Maynard Smith, 1982) in infinite populations was shown. Or, in the same manner, the local update rule in finite populations corresponds to the standard replicator dynamics (Hofbauer and Sigmund, 1998) in infinite populations.

Different microscopic update mechanisms, namely the Moran process and the local update rule were analysed. It was shown that the stochastic gain effect can be found in both populations when using this different microscopic update rules. Furthermore, the existence of the stochastic gain effect without any variable adaptation rates, solely based on the application of different microscopic update rules was demonstrated. Even though, it is not the purpose of this thesis to test the applicability of these methods to real biological systems, it might be of interest to find these results confirmed in real dynamical biological systems. For example, think of interacting different populations using different microscopic mechanisms: In this case, the behavior of the individuals of each population, which might be partially genetically determined in a natural way, could correspond with the microscopic update mechanism. However, the result which demonstrates that agents can exploit noisy disturbances in a resonance like fashion has not only potentially important consequences for biological systems. Especially in economic systems, the possibility of exploiting market fluctuations via flexible adaptation rates of agents can have interesting practical applications, because the presented mechanism delivers new insight to benefit also from fluctuations which are usually considered as negative (Traulsen, Röhl and Schuster, 2004b). Thus, the results of this thesis stress the importance of the detailed consideration of different microscopic update mechanisms in finite populations, because they can significantly affect the macroscopic dynamics of a system.

The second part of this thesis, proceeded with studying the evolution of cooperation by indirect reciprocity (Nowak and Sigmund, 1998b; Nowak and Sigmund, 2005; Nowak, 2006b) in the context of fraud. Or, more precisely, the impact of fraud in such systems was anal-

ysed. Usually natural selection is assumed to promote the selfish individuals at the expense of others (Darwin, 1859; Nowak and Sigmund, 2005). On the other side many biological systems, which include the human societies, are organized to work in a cooperative context. A standard framework to study indirect reciprocity is a mechanism called image scoring (Nowak and Sigmund, 1998). We extended this framework for reputation mechanisms by introducing fake reputations. Fake reputations are quite interesting. Though, so far it is unclear, whether intentional fraud occurs in biological systems (Lunau, 2002), the role of fraud in humans opens a door for investigations reaching from evolution of cooperation to consciousness (Schuster, 2007). Different kinds of fraud could be observed in many biological (Brännström and Dieckmann, 2005; Lunau, 2002) systems and in particular in the human society (Schiller, 2003; Roberds, 1998). For example, recently it was shown that the size of the neocortex in a certain primate species is a measure for which individuals of that species use deceptive tactics for social manipulation (Byrne and Corp, 2004). Often fraud is seen as a victimless crime, but it affects everyone not only banks or financial institutions. Anyone who has been a victim of fraud knows the inconvenience and distress it causes. For example, fraud all together costs the British economy an enormous amount of money, estimated as at least £13.9 billion in 2005 (ACPO, 2007). The costs of fraud impact throughout the economy as fraud drives up costs for consumers (for example by increased insurance premiums) and reduces the amount of money available for public services (because fraudsters claim benefits that they are not entitled to, which leaves less available for public spending). Up to the present, it is unclear why sanctions by the community have not eliminated fraud from social systems and also the impact of fraud on the evolution of cooperation has not been analyzed yet. In other words, what is the role of fraud in biological or social systems? Obviously, it is difficult to come up with a meaningful answer. However, modelling evolution of indirect reciprocity by image scoring seems to be an ideal platform to study the influence of fraud. Another interesting point is that the simplicity of our model allows further comparison with behavioral experiments, which have already successfully corroborated several theoretical results in game theory (Bernhard, Fischbacher and Fehr, 2006; Knoch, Pascual-Leone, Meyer, Treyer and Fehr, 2006; Milinski, Semann, Bakker and Krambeck, 2001; Milinski, Semmann and Krambeck, 2002; Semmann, Krambeck and Milinski, 2003; Wedekind and Milinski, 2000). Our model opened a platform for biological experiments as well as for economic ones, whereas for the latter one it is presumable easier to start with (Camerer, 2003). A crucial parameter in our model is the detection probability, which gives us the possibility to model the frequency of scammers. For example, a high detection probability corresponds to a low frequency of scammers. Naturally, scammers who are detected, as in real systems, are punished from the community, i.e., have to pay a high penalty. Recently, it was shown experimentally (Rockenbach and Milinski, 2006) that even in the presence of effective reputation mechanisms, people do not entirely cease punishing those that put self-interest ahead

of the collective interest. Furthermore, when given a choice, subjects even prefer a society with the option of both, maintaining their own reputation on the one side and the possibility of punishing scammers on the other side (Rockenbach and Milinski, 2006). In consequence, the introduction of the detection probability seems to be rational. It was shown in this thesis that for a low detection probability the cheaters also eliminate the discriminators and their basin of attraction fills in almost the whole simplex area. From the game-theoretical point of view the system is "crashed", because now cheaters would cooperate mutually and thus could augment their payoff from nothing. On the other side, it is well known that many complex systems (e.g. social, political, economical) seem to show this characteristics that cannot be described by conventional methods. Think off, for example, political scandals where 'cheaters' act so long at the expense of the community (cheaters never pay their costs) until they are detected or, in the worst case, the system crashes. It is worth to note that classical game theory, for example, like zero-sum games (matrix games) are not able to model sufficiently this 'living on the expense of others'. However, a possibility to avoid the breakdown of the system due to a low detection probability is to introduce an adaptive detection probability or using a high detection probability. In real systems both mechanisms are applied with more or less success.

Taken together, the results show, that in our extended image scoring model for indirect reciprocity discriminators indeed might benefit from coexisting cheaters depending on their detection probability and the cost/benefit ratio. It was shown for the first time analytically that a defined presence of cheaters in the population increases cooperative behavior, i.e., that cooperation is robust with respect to fake reputations and can even be enhanced by them. For example, if scammers dominate over defectors, they can help discriminators to initiate cooperation, as the presence of scammers allows discriminators to obtain a good reputation. This means that in rainy days, cooperation based systems can benefit from cheaters.

Taken together, the results of my thesis yield new insight in the role of fraud in social systems, as we showed that fraud per se does not necessarily have an only detrimental effect on such systems. Complex cooperative systems only become assailable to selfish cheaters, if a critical number is exceeded. This could be an answer, why evolution did not eliminate cheating behavior from biological or social systems.

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Selbständigkeitserklärung

Ich erkläre, dass ich die vorgelegte Arbeit – abgesehen von der Beratung durch meinen Betreuer Prof. Dr. Heinz Georg Schuster – selbständig und nur unter Benutzung der angegebenen Literatur angefertigt habe.

Die den Veröffentlichungen zugrunde liegende Forschungsarbeit wurde – abgesehen von der Beratung durch Prof. Dr. Heinz Georg Schuster – ausschließlich von mir selbst durchgeführt. Ausnahmen sind die folgenden Veröffentlichungen:

- Der Artikel „Stochastic gain in population dynamics“ ist in Kooperation mit Dr. Arne Traulsen entstanden, der an der quantitativen Analyse und Modellbildung beteiligt war. (siehe Dissertation von Arne Traulsen: „Statistical Mechanics of Groups Interacting in Coevolutionary Games“).
- Bei dem Artikel „Stochastic gain in finite populations“ hat Dr. Arne Traulsen und PD Dr. habil. Jens Christian Claussen zur Modellbildung beigetragen.
- Bei dem Artikel „Impact of fraud on the mean-field dynamics of cooperative social systems“ haben Dr. Arne Traulsen und Dr. Claudia Röhl zur Modellbildung beigetragen.

Bis auf die genannte Ausnahme versichere ich, dass die vorliegende Dissertation weder ganz noch zum Teil bei einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt worden ist.

Ich habe keine früheren Promotionsversuche unternommen.

Kiel, den 7.12.2007