

An Introduction to Evolutionary Game Theory

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Abstract

This introduction provides the reader with a basic knowledge about the fascinating field of evolutionary game theory. After presenting the mathematical notion of games, the two probably most important approaches to analyze a game are discussed. Each new concept is briefly discussed theoretically and then applied to the *Hawk-Dove-Game*.

1 Introduction

The phenomenon of cooperative interactions among animals has puzzled biologists since Darwin. Nevertheless, theoretical concepts to study cooperation appeared only a century later and originated in economics and political sciences rather than biology. The mathematicians John von Neumann and Oskar Morgenstern developed a framework called *Game Theory* that was able to describe the interaction between individuals. Important work in this field was done by John Nash who developed the concept of the so called Nash equilibria :

An equilibrium is reached as soon as no party can increase its profit by unilaterally deciding differently.[1]

Although there was great enthusiasm after the publication of Nash's work, a major obstacle remained. The outcome of a game in this time was interpreted as the only viable outcome of a careful reasoning by ideally rational players. Thus the justification of this rationality of the players comprised the main issue. The solution to this problem came from a complete different field: biology. John Maynard-Smith and George R. Price ingeniously related the economic concept of payoff functions with evolutionary fitness as the only relevant currency in evolution and laid of the corner stones for the field of evolutionary game theory[2]. In this work we try to give a first introduction to evolutionary game theory. Although this framework today is mostly used in economics and social sciences I concentrate on the biological interpretation. In the first section the general concept of a game is presented. Then the famous concept of evolutionary stable strategies that was developed by Maynard-Smith is given. The third part introduces a dynamical systems approach to games and connects it with the stable strategy concept. In the end a short outlook at the potential of evolutionary game theory is given.

2 Games from a Mathematical Point of View

Before we can make use of evolutionary game theory, we have to consider some important terms that are necessary to have a common vocabulary. The first thing we should define if talk about game theory is of course the term game.

Definition In mathematical terms a *game* consists of[3]

- a finite set of players $P = \{1, 2, \dots, I\}$ that interact in that game
- Strategy sets S_1, S_2, \dots, S_I which define for each possible situation in the game the reaction of the players
- Payoff functions $u_i : S_1 \times S_2 \times \dots \times S_I \mapsto \mathbb{R}$ that map a set of reactions (called strategy profile) to a certain number

In this short introduction I will concentrate on the simplest case where only two players at a time compete against each other. This situation is often termed pairwise competition and has the nice property that on can write the payoff function in matrix notation.

As a second simplification we only regard pure strategies, which means that these strategies are defined explicitly and do not depend on the other strategies. The opposite case would be a mixed strategy which could be defined as follows: with probability 0.1 play strategy A otherwise play strategy B.

With this basic knowledge about games we can look at a particular example which is called the Hawk-Dove-Game¹. In this game two animals compete against each other for a limited resource (e.g. food). Each of the players can choose either to play the strategy Hawk or Dove. The player with the strategy Hawk initiates aggressive behaviour and does not stop until he gets injured or the opponent backs down. The Dove strategy on the other hand lets the player immediately retreat if the opponent initiates aggressive behaviour. If we now define the value of the resource to be V and the cost of a conflict (e.g. getting injured) to be C , we can write down the payoff matrix for the Haw-Dove-Game:

	Hawk	Dove
Hawk	$\frac{1}{2}(V - C), \frac{1}{2}(V - C)$	$V, 0$
Dove	$0, V$	$\frac{V}{2}, \frac{V}{2}$

When a Hawk and a Dove meet clearly the Hawk gets the full resource whereas the Dove gets nothing. A little bit more interesting is the situation when two Doves meet each other in this case they share the resource and get both $\frac{V}{2}$ (if one wants to avoid the term “sharing” one could interpret that value even as average payoff). In the last possible case when two Hawks meet than there expected payoff is the probability of winning the fight times the value of the price (the resource V) minus the probability of losing times the cost of getting injured. If we now set assume that these probabilities are equal we get $\frac{1}{2}(V - C)$. [4]

¹There are several hundred different types of games. One of them, the famous *Prisoners-Dilemma* was presented in my presentation. To keep things simple I will concentrate here on the more biologically motivated *Hawk-Dove-Game* and use it to illustrate the basic concepts of evolutionary game theory.

3 Evolutionary Stable Strategies

There are two different approaches to analyze games in evolutionary game theory. In this section I want to address the approach derived from the work of Maynard Smith and Price which uses the concept of an evolutionary stable strategy. The other general approach will be presented in the next section.

In general what one tries to answer with this approach is the question, which of the possible strategies would be favoured by evolution. To do that Smith and Price introduced the idea of an evolutionary stable strategy which is defined as follows

Definition A strategy is called an evolutionary stable strategy (ESS) if it has the property that a population in which almost every member follows it no mutant can successfully invade.[5]

Now we try to derive mathematical relations from that literal definition. To do that we try to write down function that describes the fitness of a representative player for both strategies. For the player that follows the stable strategy σ we get the fitness function

$$W_\sigma = W_0 + (1 - p)\Delta W_{\sigma,\sigma} + p\Delta W_{\sigma,\mu}, \quad (1)$$

where W_0 is the baseline fitness, $\Delta W_{\sigma,\sigma}$ is the fitness gain the player receives when he plays against another one with the same strategy, $\Delta W_{\sigma,\mu}$ is the fitness gain the player gets when he plays against the mutant and p is the fraction of mutants in the population. The fitness function of the mutant can be written as

$$W_\mu = W_0 + (1 - p)\Delta W_{\mu,\sigma} + p\Delta W_{\mu,\mu}. \quad (2)$$

Here $\Delta W_{\mu,\sigma}$ is the increase in the fitness when the mutant meets a stable strategy player and $\Delta W_{\mu,\mu}$ is the payoff when two mutants meet. In order to be an ESS we expect that the fitness of the stable strategy player is higher than that of the mutant or in mathematical terms

$$W_\mu < W_\sigma \quad (3)$$

should hold. Since μ is an emerging mutant its fraction of the population should be much smaller than that of the stable strategy ($p \ll 1$). Thus we can in a first order ignore the last term in the equations (1) and (2) and get as the first relation for an ESS

$$\Delta W_{\sigma,\sigma} > \Delta W_{\mu,\sigma}. \quad (4)$$

The second relation for an ESS follows if in (4) equality holds and we can not ignore the last term in (1) and (2). In this case the ESS must fulfill

$$\Delta W_{\sigma,\sigma} = \Delta W_{\mu,\sigma} \text{ and } \Delta W_{\sigma,\mu} > \Delta W_{\mu,\mu}. \quad (5)$$

Altogether: a strategy σ is an ESS if it plays better against σ than a mutant does play against σ or the mutant μ and σ play equally well against σ but σ plays better against μ than μ does.

Fine, now let us try to apply the theoretical findings to our running example the Hawk-Dove-Game. First we ask the question: is the strategy Dove an ESS in the Hawk-Dove-Game? Thus we assume that our population consist mainly

of Doves and that a mutant appears that follows the strategy Hawk. With the use of the payoff matrix we defined in the previous section and the conditions for an ESS we immediately receive the following:

$$\Delta W_{\sigma,\sigma} \geq \Delta W_{\mu,\sigma} \quad (6)$$

$$\Delta W_{Dove,Dove} \geq \Delta W_{Hawk,Dove} \quad (7)$$

$$\frac{V}{2} \geq V \quad (8)$$

This condition can only be fulfilled if $V \leq 0$ in which case the game wouldn't make any sense at all. We therefore can conclude, that the strategy Dove is not an ESS.

Now we do the same calculations for the hawk, which yields

$$\Delta W_{\sigma,\sigma} \geq \Delta W_{\mu,\sigma} \quad (9)$$

$$\Delta W_{Hawk,Hawk} \geq \Delta W_{Dove,Hawk} \quad (10)$$

$$\frac{V - C}{2} \geq 0 \quad (11)$$

This relation is true iff $V \leq C$ or in biological interpretation if the value of the resource is larger than or equal to the cost of a conflict (the second condition (5) is true because of the symmetry of the Hawk-Dove-Game).

In this section we learned that an evolutionary stable strategy is resistant against emerging mutants. We derived the mathematical consequences of being an ESS and we applied our new knowledge to the Hawk-Dove-Game and learned that only the strategy Hawk is evolutionary stable.

4 The Evolutionary Dynamics Approach

In this section we will present the second concept to analyze a game in evolutionary game theory. The general question of that approach is: How will a population of individuals that repeatedly plays a certain game evolve? The answer to that question is largely determined by the conditions under which the individuals interact. First we concentrate on a very simple setting of an infinitely large population of players with two different strategies that randomly encounter each other. In order to get not too deep into theoretical analyses we introduce the concept by applying it on our running example the Hawk-Dove-Game.

First we have to determine all quantities and their relation with each other that are necessary to describe the dynamics of the population. Since our population is infinitely large it is sufficient to keep track of the fractions of individuals that follow a certain strategy. With p_H and p_D we denote the fractions of Hawks or Doves respectively. To model a real dynamical system we have to include some kind of reproduction. The reproduction rate should be proportional to fitness of an individual, which we denote with w_H and w_D respectively, in relation to the mean fitness \bar{w} . With these five quantities we can now write down the equations that relate the number of individuals in the current generation with the number

of individuals in the next generation:

$$p'_H = p_H \frac{w_H}{\bar{w}} \quad (12)$$

$$p'_D = p_D \frac{w_D}{\bar{w}} \quad (13)$$

These equations are called *replicator equations* and were offered by Taylor and Jonker (1978) and Zeeman (1979)[5]. The only thing that is missing is an equation that describes the fitness of an individual. To derive that we use the assumption that the individuals meet each other randomly. If we now pick an arbitrary Hawk we can conclude that a fraction of p_H of his encounters in the current generation were encounters with other Hawks, whereas a fraction of p_D where encounters with Doves. If we now use the well known payoffs, we get

$$w_H = p_H \Delta W_{Hawk,Hawk} + p_D \Delta W_{Hawk,Dove} \quad (14)$$

as expression for the fitness of a randomly chosen hawk. The same considerations hold for the Doves and we can immediately write down the fitness term

$$w_D = p_H \Delta W_{Dove,Hawk} + p_D \Delta W_{Dove,Dove}. \quad (15)$$

The mean fitness \bar{w} can finally be calculated by

$$\bar{w} = p_H w_H + p_D w_D. \quad (16)$$

To get the dynamics of the resulting system one can either perform a computer simulation or analyze the system analytically. Since our system is quite simple we do the latter.

One of the most common tasks in the analysis of a dynamical system is the detection of fixed points. A fixed point constitutes a state of the system, where it does not change any more. To find these points we look at the reproduction equations (12) and (13). Since the sum of p_H and p_D is always equal to 1, we can concentrate on one of these equations. To find the fixed point p_H^* we make the ansatz

$$p_H^* = p_H^* \frac{w_H}{\bar{w}} \quad (17)$$

and easily see the two possibilities: a trivial one with $p_H^* = 0$ and another one when $w_H = \bar{w}$. The latter implies that either $p_D = 0$ or $w_H = w_D$. Thus we have up to 3 fixed points. Fine, but what does that mean from a biological point of view? Biologically this implies that the population is stable if either one species (Hawks or Doves) became extinct or the fitness of both is the same. Since we now know the fixed points of our system we can check whether they are stable or not. It should be obvious that $p_H = 1$ is stable iff $w_H > \bar{w} > w_D$ and $p_H = 0$ is stable iff $w_H < \bar{w} < w_D$. To decide in which case one of the three situations ($>$, $<$, $=$) occurs we look at the equality case. Therefore we consider

the fitness equations (14) and (15), plug-in the payoff values and equate them.

$$w_H = w_D \quad (18)$$

$$p_H \frac{1}{2}(V - C) + p_D = p_H 0 + p_D \frac{V}{2} \quad (19)$$

$$p_H \frac{1}{2}(V - C) + (1 - p_H)V = (1 - p_H) \frac{V}{2} \quad (20)$$

$$V - \frac{V}{2} + p_H \left(\frac{V}{2} - \frac{C}{2} - V + \frac{V}{2} \right) = 0 \quad (21)$$

$$\frac{V}{2} = p_H \frac{C}{2} \quad (22)$$

$$p_H = \frac{V}{C} \quad (23)$$

Finally we derived a clear characterisation of our system, which we can directly interpret biologically: The fitness of the strategy Hawk is always larger than or equal to the fitness of the strategy dove (this can be seen in equation (20) remembering that $V, C \geq 0$). Thus the state were all individuals in a population follow the strategy Hawk is a stable fixed point, whereas the state were all individuals follow the strategy Dove is always an unstable fixed point. A third stable fixed point (coexistence) occurs if the two strategies have the same fitness. This happens if the frequency of the Hawks equals $\frac{V}{C}$. Since p_H has to be in the range of 0 and 1 this is only possible if $C > V$ (the cost of a conflict is higher than the value of the resource). Figure 1 summarizes the behaviour of the dynamical system with help of a bifurcation diagram.

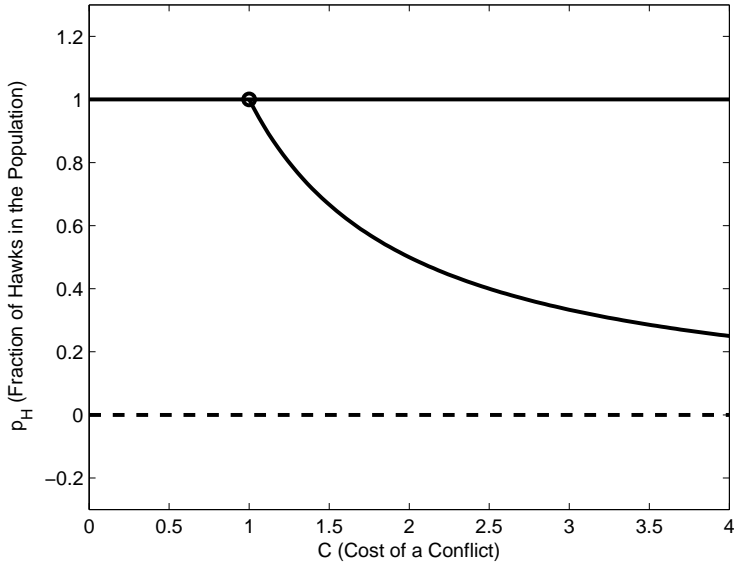


Figure 1: Bifurcation diagram for varying conflict costs and fixed resource value of the dynamical Hawk-Dove-Game system

The fact that the strategy Hawk is an ESS and a stable fixed point in the setting

of a dynamical system is no coincidence. De facto the definition of an ESS states that the system resists slight perturbations from the state were all individuals follow that strategy, which is the definition of stable fixed point.

In this section we presented the second possibility that one can use to examine games in the framework of evolutionary game theory. A description of a dynamical system was developed by joining the well known replicator equation and a fitness term. In the last paragraph we saw that there is a clear connection between the ESS concept and the dynamical systems approach. This connection is weakened if we change the definition of the population and for example use a finite population size and non-random encounters between the two strategies. This setting would be of course a little bit more realistic, but would also render the analysis even more complicated and one would have to use numerical simulations instead. For the interested reader I have written a small application that performs numerical simulations of the Hawk-Dove-Game in a 15x15 grid world. It can be found under <http://page.mi.fu-berlin.de/ueckert>.

5 Evolutionary Questions

In this introduction we showed some concepts to analyze a game but did not handle real world problems. In fact the framework of evolutionary game theory was not developed as university amusement but as tool to solve problems. Some biological questions that can be handled with this framework are: Why is the ratio of the sexes in most of the species 1:1? How could cooperativity develop during evolution? Do mitochondria hate males since they are only passed from females to the next generation? Why are mostly females taking care of the offspring? Why do female waterstriders perform a certain number of back flips before they accept a male as mating partner? etc.

Although evolutionary game theory has provided numerous insights to particular evolutionary questions, a growing number of social scientists have become interested in evolutionary game theory in hopes that it will provide tools for addressing a number of deficiencies in the traditional theory of games. Especially in economics evolutionary game theory is getting more and more important. Covering this topic would require some more work ...

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