Game Theory

History:

First interest in game theory was started by **behavioral sciences** and **economics**. But even in economics, the approach was not very persuasive, mostly because of the lack of experimental foundation.

After a period of **mathematical 'purification**' of the approaches, game theory took of in the beginning of 1970, with the incorporation of **biological and evolutionary approaches**. In Biology, the fitness of the organism gave game theory a serious foundation.

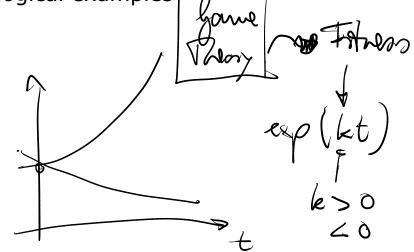
Books:

John Maynard Smith: Evolution and the Theory of Games. Ulrich Müller: Evolution und Spieltheorie, 1990 Rudolf Schüßler: Kooperation unter Egoisten, 1990 Michael Taylor: The possibility of cooperation, 1987 Richard Dawkins: the selfish gene. 1976, 2nd edition 1989. (dt: das egoistische Gen)

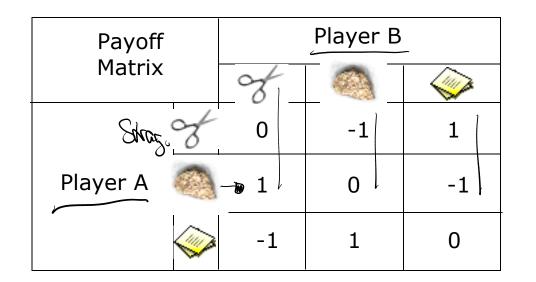
Matt Ridley: The origins of virtue: human instincts and the evolution of cooperation, 1996, pinguin paperback

Summary:

- Motivation: the selfish gene
- Simple games
- Matrix formulation of games
- Single vs. Multiple games: Prisoners dilemma
- Dynamic plotting
- Frequency dependent selection
- Stable bad solutions beat unstable good solutions in memory-less evolution.
- Biological examples



Matrix Games



$$V = \begin{bmatrix} 0 & -1 & 1 \\ 1 \not\sim & 0 & -1 \\ -1 & 1 & 0 \end{bmatrix}$$

e.g. Partner Game:

$$V_{ij} = -V_{ji}$$

A wide class of games can be described by a **payoff matrix**. They are called matrix games.

Let's look at **Knobeln** (engl: to toss). Each player can show **scissors, paper or stone**. Each of the player has profit matrix depending on what the other is playing.

The matrix has to be **read along the rows**. If I am player A, and play strategy scissors, then I have a payoff of 0 against scissors of player B, loose 1 against player B choosing stone and gain 1 if player B chooses paper.

Games where the payoff is distributed between partners are called **partner games or symmetric games** and yield a symmetric payoff matrix.

Here we also have the case of a **zero-sum game**: what is received is what is given, seen by the zero expectation value.

The Prisoner Dilemma

Another Matrix game is the **Prisoner Dilemma**. The scenario is as follows. **Two agents fight for a resource**. (In the original story, two prisoners are charged for the same criminal act). They first choose their strategy. Either they can be friendly and corporate with the other or they can be fierce and choose a competing strategy.

Payoff Matrix V		Player B		
		8	\odot	
Player A			5	3
	-> 😳	0	3	1.5

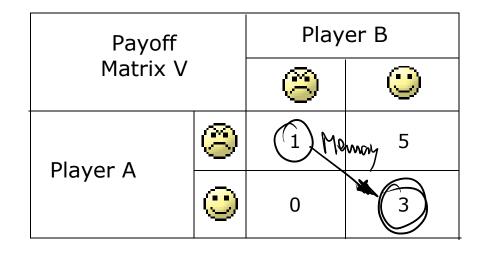
The interesting structure lays in the payoffs they obtain depending on the others strategy. If **both compete**, they obtain nothing. If both **cooperate**, they obtain 1. This is the symmetric part.

However, things become asymmetric, if competing meets cooperate: in that case the competing out wins the cooperating: competing gains 2, the cooperating looses 1.

What strategy should be played?

Interestingly, it depends on **the games history, i.e. on how often the game is played**. If the game is played once, the answer is quite clear. Without knowing the other, one will compete. In average, the gain will be (1+5)/2=2453 Cooperating is dangerous, the expectation value for this is (3+0)/2=1.5 and in average you will not gain anything. In average it is always better to compete. A boring game?

The Prisoner Dilemma



However the situation changes if the game is played multiple times between the same agents.

Axelrod has asked people to submit **computer programs** to compete in the game of multiple prisoner dilemma. After two tournaments of a wide variety of algorithms, it turned out that the **best strategy** was quite simple. It was called "**TIT for TAT**" ("wie du mir, so ich dir").

serendip.brynmawr.edu/playground/pd.html www.brembs.net/ipd/ipd.html Axelrod, R. (1981). Science, 211(4489):1390-6 TIT for TAT is very simple. **The first time** it takes the risk and **cooperates**. For all following games it **copies the strategy of the last move of the other agent**. This means the strategy "TIT for TAT" will cooperate if the other did cooperate last time, it will defect if the other did defect last time.

Axelrod argued that this strategy is "nice", "provokable" and "forgiving". It is "nice" since it starts with a cooperate move, can handle an always-defect strategy of the other well without loosing too much ("provokable"). But most importantly, it becomes immediately nice again if the other player cooperates ("forgiving").

So we see, there are games where it becomes crucial to **memorize both the agent** (did I play against him in the past?) and **what strategy the agent played** (did he compete last time?). A memory is a selection advantage since it allows to implement the optimal strategy.

Stability of Strategies: Frequency dependent Selection

Symmetry of the sexes.

We start with a commonly used example. For a farmer to have as many cows as possible, he might choose **one bull per 20 cows**. Why? The reproductive capability of the cow (k_{pi}) is much higher than for the bull $(k_{pi}=0)$ and the farmer will yield more animals for equal food resources.

But, how comes that such a solution is not found in nature? Simply: the **strategy is not stable** against random mutations. We start with a cow in average giving birth to 1 bull and 20 cows. **If one cow in the population gives birth with a ratio 1:1**, this phenotype has a large advantage over the others since **its many bulls** can exploit the existence of many cows.

Same is true for the opposite: starting with **1 cow and 20 bulls**, the phenotype with mutation for a 1:1 ratio will propagate better due to its **higher number of cows**.

We see that the frequency of species in the population determines the selection rules, termed **frequency dependent selection**. Technically speaking, the **Nash equilibrium** is not stable (20:1) and the inferior strategy of 1:1 is used.

As a result, nature uses the **inferior**, **but stable** strategy.

John Maynard Smith and George R. Price (1973). "The logic of animal conflict." Nature

 $(Female) \div (Male)$

 $20 \div 1$

Evolutionarily Stable Strategy (ESS)

Evolutionary stable strategy (ESS):

"A strategy such that if **all members** of the population adopt it, then **no mutant can invade the population** under the influence of selection."

Assume you have a population which is dominated by strategy p of the population and a mutation strategy m just developed. With the profit of the game V_{ij} of strategies i and j, the evolutionary stable strategy is given, if $V_{pp}>V_{mp}$, i.e. the majority strategy p yields more than a single minority m playing against the majority p.

In the case of equality we need a second condition of $V_{mp} > V_{mm}$.

$$V_{pp} > V_{mp}$$

or
$$V_{pp} = V_{mp} \text{ and } V_{pm} > V_{mm}$$

$$V_{pp} < V_{mm}$$

$$V_{pp} < V_{mm}$$

$$V_{mp} > V_{pp} \longrightarrow \rho \quad \text{Mar not a stable storategy}$$

Evolutionarily Stable Strategy (ESS)

As we have seen, such an evolutionary stable strategy does not need to be the best performing. It is well possible that V_{mm} is much better than V_{pp} , but it is not stable due to $V_{pp} > V_{mp}$.

We can see this for example in the Prisoner Dilemma. If the **majority population competes** at all times (**V=1**), a **coopera-tive mutation will loose** against it (**V=0**) and cannot grow. Strategy competition is stable.

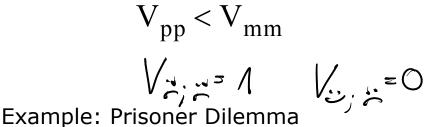
A globally better mutation m cannot supplant the worse, but stable strategy p with V_{pp} > V_{mm} .

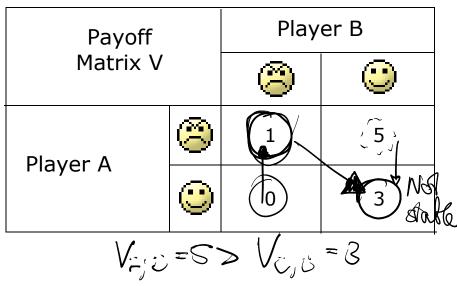
On the other side, if the **cooperative strategy** would be adopted by everyone, it would be **advantageous** (V=3). However any **mutation which competes** gains more (V=5) and will grow, eventually overtaking the population.

But as we have seen, dynamic, memory based strategies (**TIT for TAT**) can compete against all other strategies and in many situations lead to an **average yield** of **V=3**.

$$V_{pp} > V_{mp}$$

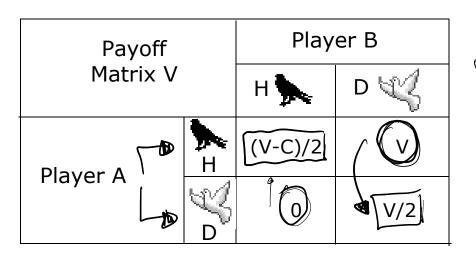
or
$$V_{pp} = V_{mp} \text{ and } V_{pm} > V_{mm}$$





Vorlesung Biophysik Braun - Evolution

Example: The Hawk-Dove Game (Chicken Game)



$$V_{pp} > V_{mp}$$

(vpp = V_mp and Vpm > V_mm)

Davis, Spieltheorie für Nichtmathematiker [#] population dyn en.wikipedia.org/wiki/Hawk-dove_game Maynard Smith, J. (1982) Evolution and the Theory of Games.

When **fighting for a resource**, opponents can use **two** typical **strategies**. The

- O o Hawk strategy escalates and continues until injured or until the opponent retreats
- 60 **Dove strategy retreats** if opponent escalates.

We parametrize the payoff. **V for winning the fight** and **C for the cost of an injury**, we find the payoff matrix to the left.

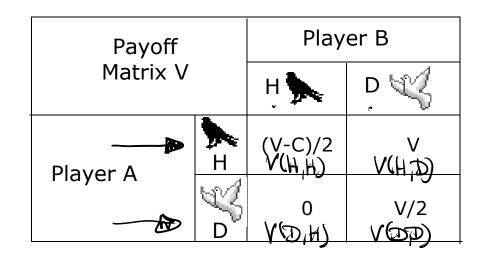
We recall the condition for an evolutionarily stable strategy (ESS) on the left.

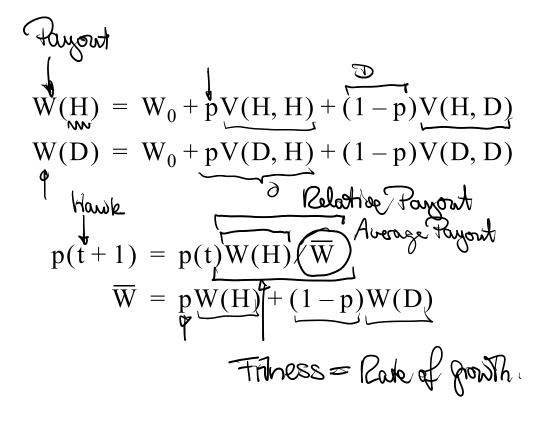
If **all were doves**, each gaining V/2, a hawk can always invade with V (V being positive). We again have frequency dependent selection.

All being hawks is evolutionarily stable strategy, if (V-C)/2>0. Otherwise a dove which gains 0 can compete initially. In other words, hawks are ESS if it is worth risking injury (C<V) to get the resource.

The case becomes interesting, when C>V, i.e. the injury C is not worth taking for the resource V. To study this we switch to population dynamics.

Example: The Hawk-Dove Game (Chicken Game)





From Game Theory to Population Dynamics

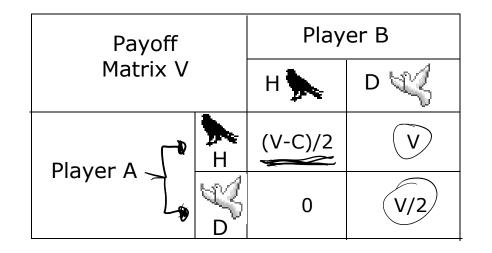
We now allow the **population** to be split into the two strategies with **p the frequency of strategy hawk (H)**.

And we **add a dynamics** to the matrix game by determining the **fitness W** by the **payoff matrix V(i,j)**. W(H) is the fitness of strategy hawk, W(D) the fitness of strategy dove. We linearly **link the fitness to the payoff matrix V(i,j)** and add a constant fitness W₀.

Consider the **fitness of the hawk W(H)**. With probability p it meets another hawk, gaining in fitness by V(H,H), with probability (1-p) the hawk meets a dove, gaining in fitness by V(H,D). The same for the Dove (left).

Additionally, we **add a dynamics** by using the fitness as determinant for the propagation of the strategy. The result is a finite time differential equation. Thus one might want to **reinterpret population dynamics with game theory**.

Stable Strategies in Hawk-Dove Game



$$V(H, I) = V(D, I)$$

$$pV(H, H) + (1-p)V(H, D)$$

$$= pV(D, H) + (1-p)V(D, D)$$

$$p(V-C)/2 + (1-p)V = (1-p)V/2$$

$$p = V/C$$

•
$$V(\mathbf{1}, \mathbf{D}) = pV + (1-p)V/2 = (p+1)V/2$$

> $V/2 = V(D, D)$

• V(I, H) = p(V - C)/2> (V - C)/2 = V(H, H) Now we can **study the case V<C** (injury is more severe than gain from resource) with **population dynamics**.

As discussed before, **neither all Hawks nor all Doves are an ESS**. Hawks invade Doves with V>V/2 and Doves can invade Hawks with (V-C)/2<0. But now we can analyze **mixtures in the population** with p the probability for playing strategy hawk.

One can incorporate mixtures of populations also by introducing a **genotype I which randomly chooses hawk strategy** with probability p. It can be proved that if I is an ESS, then the following holds: V(H,I)=V(D,I). On the left side it is evaluated leading to the **probability of p=V/C**. If the resource is low in value, less hawks are played, otherwise the mostly hawk is chosen.

We still have to prove the **stability criterion**: V(I,D)>V(D,D) and V(I,H)>V(H,H). As seen on the left, for V<C the mixed strategy is indeed an ESS.

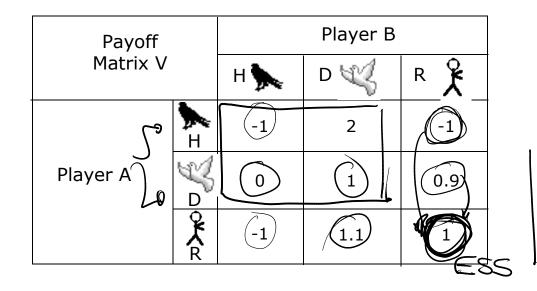
Extensions to Hawk-Dove Game

Payoff Matrix V		Player B	
		н	D 🍕
Player A	Η	(V-C)/2	V
Flayer A	σÆ	0	V/2

We go one step further. Suppose that in a population of frogs, males fight to the death over breeding ponds. This would be an ESS if any one cowardly **frog** that does not fight to the death always fares worse (in fitness terms, of course). A more likely scenario is one where fighting to the death is not an ESS because a frog might arise that will stop fighting if it realizes that it is going to lose. This frog would then reap the benefits of fighting, but not the ultimate cost. Hence, fighting to the death would easily be invaded by a mutation that causes this sort of "informed fighting."

From: en.wikipedia.org

Hawk-Dove-Retaliator Game



R is ESS V(R, R) > V(D, R)V(R, R) > V(H, R)

I is ESS $I = 0.5H + 0.5D^{-1}$

Another extension to the game of dove and hawks is the **Retaliator strategy**. To keep it simple, we set the game to fixed payoffs: V=2, C=4, therefore the mixed strategy I with P=0.5 is an ESS.

The **Retaliator (R) behaves like a dove** against another dove, but **if the opponent escalates like a hawk**, R escalates also and becomes a hawk.

We assume that escalating properties of **R** allow it to **handle Dove D** a little **better** than does Dove D handle Retaliator R (see 1.1 and 0.9 in the matrix).

All playing <u>**Retaliator R</u> is an ESS** since V(R,R)=1 is greater than either V(D,R)=0.9 or V(H,R)=-1. But can we find stable strategies by using mixed strategies?</u>

Yes, we can. **Mixing I=0.5H+0.5D** leads to V(H,I)=0.5, V(D,I)=0.5, V(R,I)=0.05 and V(I,I)=0.5. We find a **second stable point**!

Hawk-Dove-Retaliator Game

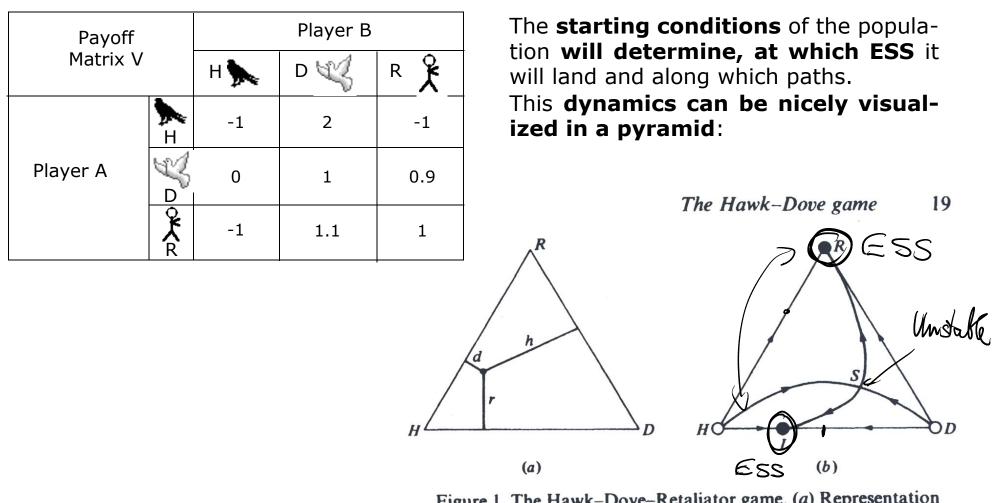


Figure 1. The Hawk-Dove-Retaliator game. (a) Representation of the state of a polymorphic population; h, d and r are the frequencies of pure H, D and R respectively. (b) Flows for the H-D-R game given in Table 2. There are attractors at I and Rand a saddle point at S.

From: J.M. Smith: Evolution and the theory of Games

Motivation: The Selfish Gene

Following works of George Williams and William Hamilton, Richard Dawkins used the term "selfish gene" to subsume findings in biology and molecular biology where one gene is found to fight against other genes.

Instead of seeing organisms compete, Dawkins inverts the viewpoint: the organism is only a vehicle of the genes to replicate themselves. "A chicken is just an egg's way of making more eggs."

"Replicators began not merely to exist, but to construct for themselves containers, vehicles for their continued existence. The replicators that survived were the ones that built survival machines for themselves to live in."

The first edition of the book had not included cooperation findings of game theory and was criticized based on its simple understanding of "selfish". It was wrongly misunderstood as an attack on culturally rich society from evolutionary biology.

I will hope, review of core ideas of game theory will show that this is only a lack of our scientific fantasy. Memory plays a crucial role to explore the efficient and more complicated social schemes by explaining frequency-dependent selection and stable evolution traps.

OXFORD

'the sort of popular science writing that makes the reader feel like a genius' *The New York Times*

selfis

RICHARD

DAWKINS

Motivation: The Selfish Gene

"Social" Ants.

Social insects such as ants have haplodiploid genes, e.g. male ants only have a **single copy of the gene**, as opposed to the female ant which is diploid.

This increases the significance of kin selection: **male ants are "supersisters"** to their collaborators, sharing 75% of their genes. This means they are **more related to their sisters** than to **any offspring** they might have: this would give 50% genetic identity.

From the viewpoint of the selfish gene, this makes them much more interested in helping their coworkers. Helping them is better for their genes than trying to replicate their own genes by sexual reproduction: **ants are selfless because of selfish genes**.

This phenomenon is called **Eusociality**, i.e. the reproductive specialization found in some species of animal, whereby a specialized caste carries out reproduction in a colony of non-reproductive animals.

The selfish embryo.

A foetus only shares 50% of the mother's genes. David Haig found that the **foetus and its placenta act more like a internal para-site** than like friends.

The foetus **destroys muscle cells that control the central artery**, removing the mothers control over it. The **foetus** also uses hormones to **induce high blood pressure** and to divert as much blood as possible to itself.

Likewise there is a **hormone-battle over blood sugar levels**.

The mother-foetus relationship is **not purely love and mutual aid**.

This can be understood from the 50% selfishness of the foetus.

Eigen & Schuster: Selfreplicative Molecules

$$\dot{\mathbf{n}}_{i} = (\mathbf{k}_{pi}\mathbf{q}_{i} - \mathbf{k}_{mi})\mathbf{n}_{i} + \sum_{i \neq j} \mathbf{k}_{m, ji}\mathbf{n}_{j}$$

$$\sum_{i} n_{i} = \text{const}$$

1871

Take molecules the number of molecules n_i of sequence i (also called species) and introduce the following population dynamics:

- k_{pi} Propagation rate,i.e. the ability to self-replicate
- k_{mi} Mortality rate and rate to leave the area
- q_i<1 Replication fidelity
- k_{m,ji} Probability to mutate from another species j.

In the last slide, we focussed on **how the population** determines the selection pressure and **the profit of an individual**. To recall, in the Eigen model (above): the fitness was determined by k_{pi} and k_{mi} , but not explicitly by the state of the population n_i . However in nature, games with frequency dependent selection are common.

Game Theory Comments

Stephen Jay Gould:

"One day, at the New York World's Fair in 1964, I entered the Hall of Free Enterprise to escape the rain. Inside, prominently displayed, was an ant colony bearing the sign: 'Twenty million years of evolutionary stagnation. Why? Because the ant colony is a socialist, totalitarian system."

A society with memory and ways to punish its members can very well enforce an evolutionary unstable strategy with higher profit for all its participants.

In this sense, **memory-enabled and state-supporting human beings** can be superior to a **state-less fully competing pool of individuals**.

Note that **money** is a very important **memory element** in modern societies.

We probably have to **adjust our meaning of "egoistic"** along the lines of game theory. In such a sense, **really egoistic societies** might **not at all look like egoistic societies** in the popular meaning of the word.

Concerning **molecular evolution**, we are only at the beginning of harvesting the **evolutionary scope of game theory**. It is not improbable that we find imprints if **game theory even down to the molecular level**. Proteins and DNA most probably play a very intricate and complex game. Life might be **indeed the game of selfish genes**.