Evolutionary Game Theory

Explaining the Evolution of Cooperation

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29. Mai 2007

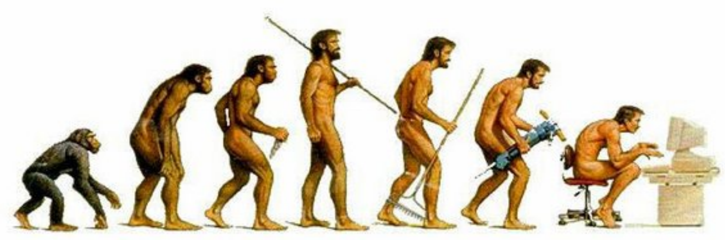
Outline

Darwins Theory and the Evolution of Cooperation

- Individuals live in continous competition
- Principle of sexual selection holds
- $\rightsquigarrow$ Individuals should maximize number of offspring
- $\rightsquigarrow$ Selfish behaviour is favoured

Question

Is life really that hard and simple?



http://lifewithalacrity.blogs.com/

Ants Colonies - The Superorganisms

- Live in colonies with more than 1 million individuals
- Population consists of infertile females (worker), fertile males (drones) and fully-fertile females (queens)
- Fraction of reproducing individuals is very low
- Worker sacrifices her life for the queen
- Same applies for wasps and bees

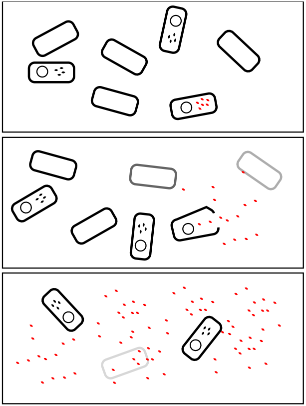
http://en.wikipedia.org

Question

How could a gene evolve that makes their carriers sterile?

Plasmids - Altruistic Molecules

- Not more than a piece of DNA
- Drives his host into production of deadly toxin
- Single plasmid can not infect an other bacteria $\longrightarrow$ suicide
- Toxin released and kills not infected bacteria
- Plasmid carrying bacteria proteced by antitoxin



Question

Why should a suicide gene evolve?

Naked Mole Rats - ACME of Social Living

- Live in groups of 20 to 80 individuals
- Only one female (queen) and three males reproduce
- Other individuals function as specialized worker (e.g. tunnlers, soldiers)
- When a queen dies the other females compete for becoming the new queen

http://www.oinkernet.com

Question

How should a behaviour develop that reduces the number of offspring?

Three Well Choosen Examples?

- Genes cooperate with each other in single cells
- Cells cooperate with each other in multicellular organisms
- Bacteria produce fruit body during prolonged starvation that serve as nutrition for some of them
- Baboons make friends and assist them in quarrels
- Territorial fights beetween animals of the same species rare end deadly
- ...

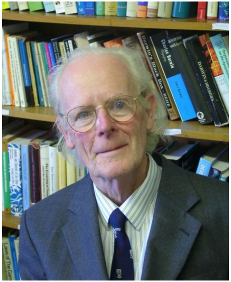
Conclusion

Under certain conditions cooperation must be advantageous.

Outline

Historical Development

- Deduced from classical game theory
- 1^{st} Game theoretical approach by R.A.Fisher $\rightsquigarrow$ Why is sex ratio 1:1?
- 1^{st} Explicit use of game theory in evol. biology by R.C.Lewontin
- J.M.Smith developed concept of Evolutionary Stable Strategies



John Maynard Smith

Games as Mathematical Objects(1)

- A game consists of
  - Set of players
  - Set of strategies
  - payoff for each combination of strategies
- Can be written in matrix notation

Example (Prisoner's Dilemma)

- Suspects A and B are arrested and questioned separatley
- Each of them is offered a deal:

	B stays silent	B betrays
A stays silent	fine(A)=2 fine(B)=2	fine(A)=10 fine(B)=0
A betrays	fine(A)=0 fine(B)=10	fine(A)=8 fine(B)=8

Games as Mathematical Objects(2)

Example (Hawk-Dove Game)

- Two individuals compete for a resource V
- Each individual follows one of two strategies
  - Hawk: Initiate aggressive behaviour, not stopping until injured or until one's opponent backs down
  - Dove: Retreat immediately if one's opponent initiates aggressive behaviour
- The cost of a conflict is C

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

The Concept of Evolutionary Stable Strategies(1)

Definition (Evolutionary Stable Strategy)

A strategy is called an ESS, if it has the property that if every member of the population follow it, no mutant can successfully invade.

in mathematical terms:

$$F(\sigma) = F_0 + (1-p)\Delta F(\sigma,\sigma) + p\Delta F(\sigma,\mu)$$
$$F(\mu) = F_0 + (1-p)\Delta F(\mu,\sigma) + p\Delta F(\mu,\mu)$$

since σ is an ESS $F(\sigma) > F(\mu)$
furthermore μ is an emerging mutant, thus $p << 1$

$$\Delta F(\sigma,\sigma) > \Delta F(\mu,\sigma)$$
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The Concept of Evolutionary Stable Strategies(2)

Example (ESS in the Hawk-Dove Game)

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Dove	0	$\frac{V}{2}$

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- Dove

$$F(Dove,Dove)=\frac{V}{2} \quad F(Hawk,Dove)=V$$
$$\frac{V}{2} \not\geq V$$

- Hawk

$$F(Hawk,Hawk)=\frac{1}{2}(V-C) \quad F(Dove,Hawk)=0$$
$$\frac{1}{2}(V-C)>0 \text{ iff } V>C$$

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The Evolutionary Dynamics Approach(1)

- Model the evolution of a population of strategies that repeatedly plays a game e.g. the prisoner's dilemma

Variation of Fitness:

$$W_C = F_0 + p_c \Delta F(C,C) + p_d \Delta F(C,D)$$
$$W_D = F_0 + p_c \Delta F(D,C) + p_d \Delta F(D,D)$$
$$\bar{W} = p_c W_C + p_d W_D$$

Variation of Strategies:

$$p'_c = p_c \frac{W_C}{\bar{W}} \quad p'_d = p_d \frac{W_D}{\bar{W}}$$

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Variation of Strategies:

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The Evolutionary Dynamics Approach(2)

Example (Dynamics of the Repeated Prisoner's Dilemma)

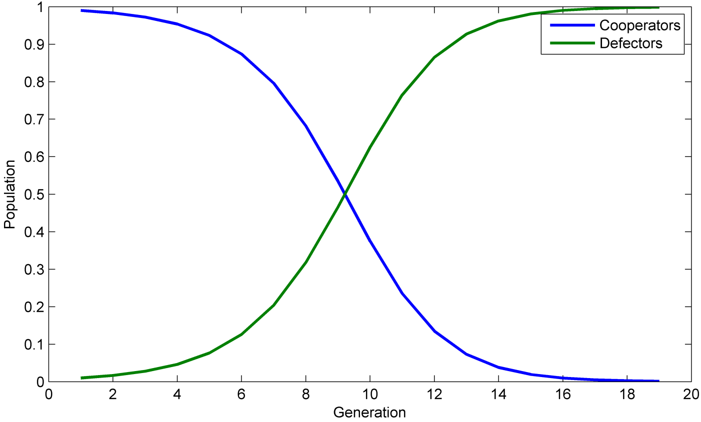
	Cooperate	Defect
Cooperate	(R,R)	(S,T)
Defect	(T,S)	(P,P)

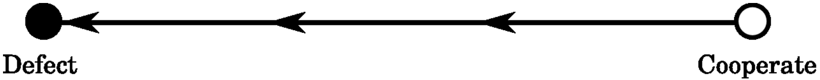
where $T > R > P > S$

$$W_C = F_0 + p_c R + p_d S$$
$$W_D = F_0 + p_c T + p_d P$$

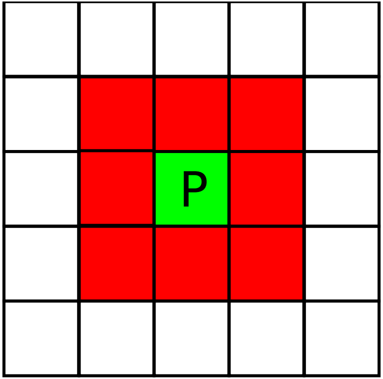
since $T > R$ and $P > S$, it follows that $W_D > W_C$ and hence $W_D > \bar{W} > W_C$

The Evolutionary Dynamics Approach(3)





Dynamics in a Local Interaction Model



Outline

What is cooperation?

- Cooperation: Interaction between a donor and a receiver
- Cooperator: Pays a cost c to give another one a benefit b
- Defector: Never pays a cost but takes benefits from cooperators

$$\text{benefit} > \text{costs} \tag{1}$$

- Cooperation in higher lifeforms
- Cooperation in lower lifeforms

Cooperation and Survival of the Fittest

Definition

Fitness is the capability to reproduce in a specific amount of time. The faster someone reproduces the fitter he is.

1. Evolution uses the Survival of the Fittest strategy
2. Cooperators vanish in mixed populations with defectors
3. Pure cooperator populations are the fittest

The last two points refer to many examples in nature but are not always true.

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Five rules for the evolution of cooperation

- Kin selection
- Direct reciprocity
- Indirect reciprocity
- Network reciprocity
- Group selection

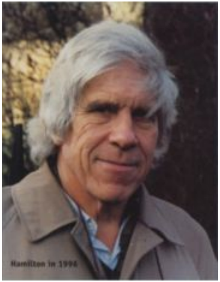
[Source: Nowak,M A. 2006. Five rules for the evolution of cooperation. Science,Vol.314.]

Kin selection

Definition

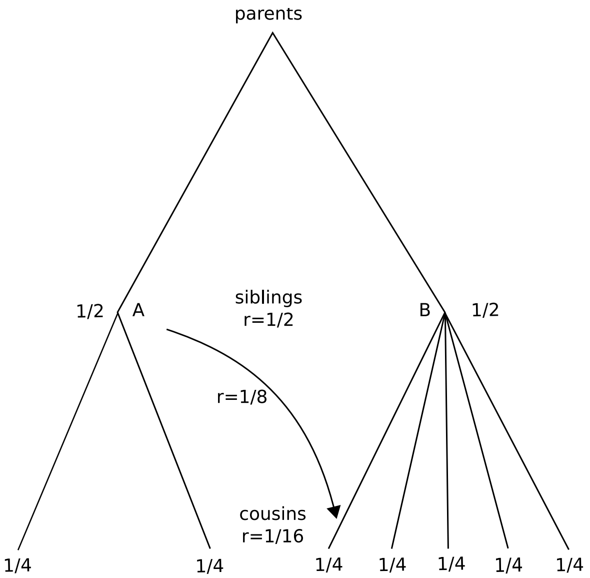
An altruistic act is based on an interaction between two individuals where one does something selfless for the welfare of the other.

- Based on altruistic actions
- First described mathematically by Hamilton in 1964



[Source: www.wikipedia.com]

Kin selection



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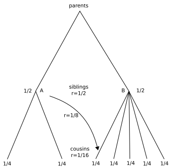
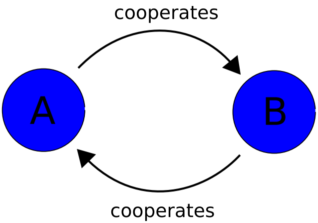


$$b/c > 1/r \quad (2)$$

$r :=$ genetical relatedness of recipient and donor
$c :=$ cost of the donor
$b :=$ benefit for the recipient

Direct reciprocity

- Two individuals have to meet at least twice
- If A cooperates now with B, B may cooperate later with A



- Repeated Prisoner's Dilemma

$$b/c > 1/w \quad (3)$$

w := probabilty of another encounter between A and B
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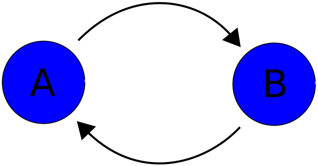

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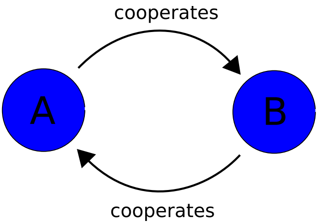

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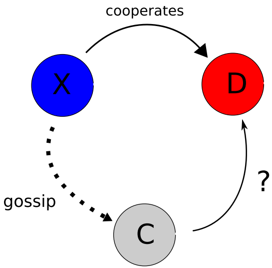
Indirect reciprocity

- Based on the individuals reputation



	C	D
C	$b-c$	$-c(1-q)$
D	$b(1-q)$	0

- Cognitive capabilities (speech, memory. . .) are necessary

$$b/c > 1/q \tag{4}$$

$q :=$ probabilty of knowing someones reputation

Indirect reciprocity

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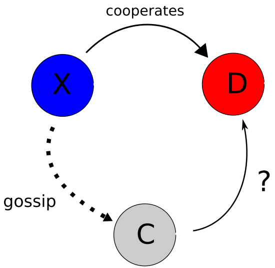

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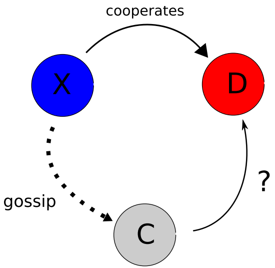

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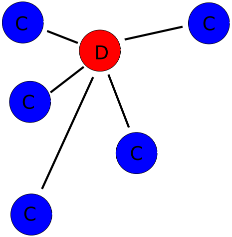
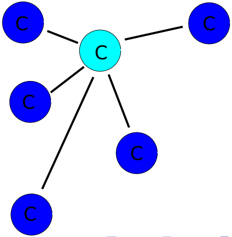
Network reciprocity

- Spatial structures seperate individuals so all cannot interact with each other equally
- Evolutionary Graph Theory is applied
- Fitness is selection and payoff dependent

F := fitness
ω := selection frequency
c := payoff

$$F = 1 - \omega + \omega c \quad (5)$$





Network reciprocity

- Spatial structures seperate individuals so all cannot interact with each other equally
- Evolutionary Graph Theory is applied
- Fitness is selection and payoff dependent

F := fitness
ω := selection frequency
c := payoff

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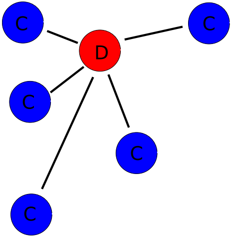

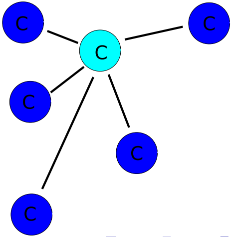

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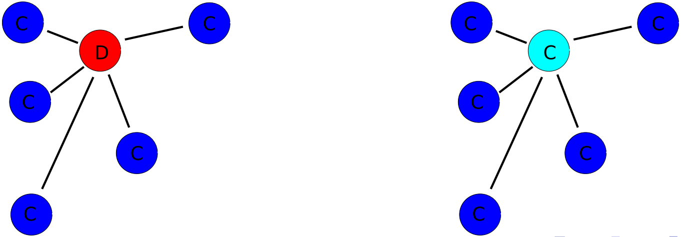

Network reciprocity

Remark: If some individual decides to cooperate with his k neighbors than he pays a cost c to give each of his k neighbors a benefit b.

- The bigger k the bigger ω
- The bigger k the bigger the payoff c

$$F = 1 - \omega + \omega c$$

- Defectors fitness decreases continuesly
- Cooperators fitness increases continuesly

$$b/c > k \tag{6}$$

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Group Selection

- Natural selection also works on groups
- Inner group behavior decides fitness of the group
- Pure Cooperator groups are fitter than pure defector groups
- In a mixed group defectors are the fittest

$$\Downarrow$$

- Selection within groups favors defectors
- Selection between groups favors cooperators

$$b/c > 1 + (n/m) \tag{7}$$

$n :=$ maximum size of a group

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Outline

Motivation

Evolutionary Game Theory

The Evolution of Cooperation

Cooperation and cheating viruses

Conclusion

Cooperation and cheating viruses

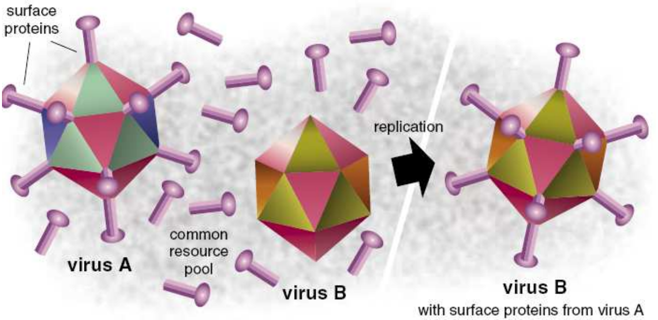
- Cheaters take advantage of others
- High fitness when they are rare
- Low fitness when "cooperators" resp. "suckers" are rare

$$\Downarrow$$

- Success and failure are frequency-dependent

Coinfection of the same cell by two viruses

1. Each of them uses the cells metabolism
2. Each virus can also use the others virus'-proteins
3. Complementation leads to evolutionary advantages
4. Phenotypic mixing



[Source: Turner,P E. 2005. Cheating Viruses and Game Theory. American Scientist,Vol.93.]

Viruses can also be parasites for other viruses

- Virus B “steals” the replication enzyme of virus A
- Population of virus B grows very fast compared to A
- Strong selection pressure leads to gene loss but higher replication rate in B
- If virus A becomes extinct virus B will die also

Outline

Conclusion

- Games model the situations where multiple players maximize their outcome
- Two different approaches two analyze mathematical games
- Five mechanisms for the Evolution of cooperation
- Evolution is caused on
    1. Mutation
    2. Natural selection
    3. Cooperation

Thank you for your attention.