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Swiss Federal Institute of Technology Zurich

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Evolutionary game theory

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Outline

- Evolutionary games
- Evolutionary stability
- The replicator equation
- The Prisoner’s Dilemma

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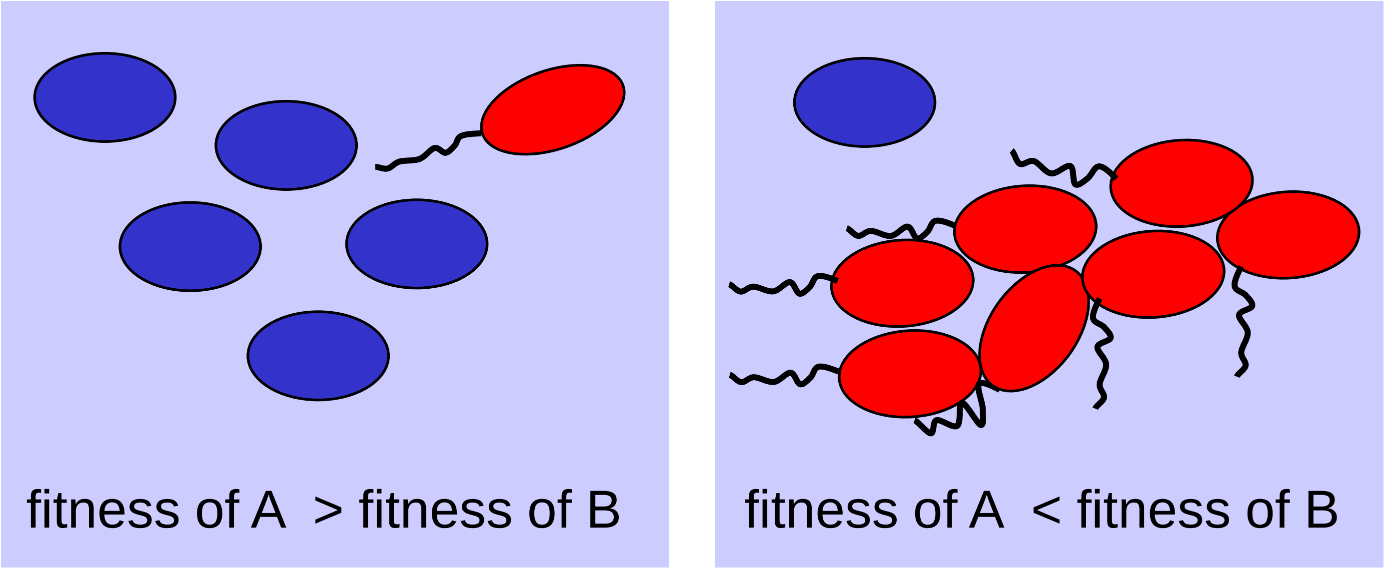
Constant selection

- So far, we have assumed that fitness is a constant parameter (*constant selection*).
- Example: Type A can move faster than type B.

fitness of A = 1.1 fitness of B = 1

Frequency-dependent selection

- But the selective advantage might actually decrease with increasing density of type A (e.g., because faster movements are impossible due to blocked space).



Frequency-dependent selection between two types

- Consider two types A and B, with frequencies x_A and x_B, respectively.
- The vector $x(t) = (x_A(t), x_B(t))^T$ describes the population.
- Denote by $f_A(x(t))$ the fitness of A and by $f_B(x(t))$ the fitness of B. The average fitness is $\phi(x) = x_A f_A(x) + x_B f_B(x)$.
- The deterministic selection dynamics are given by

$$
\begin{aligned}
\dot{x}_A &= x_A\,[f_A(x) - \phi(x)] \\
\dot{x}_B &= x_B\,[f_B(x) - \phi(x)]
\end{aligned}
$$

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Equilibria

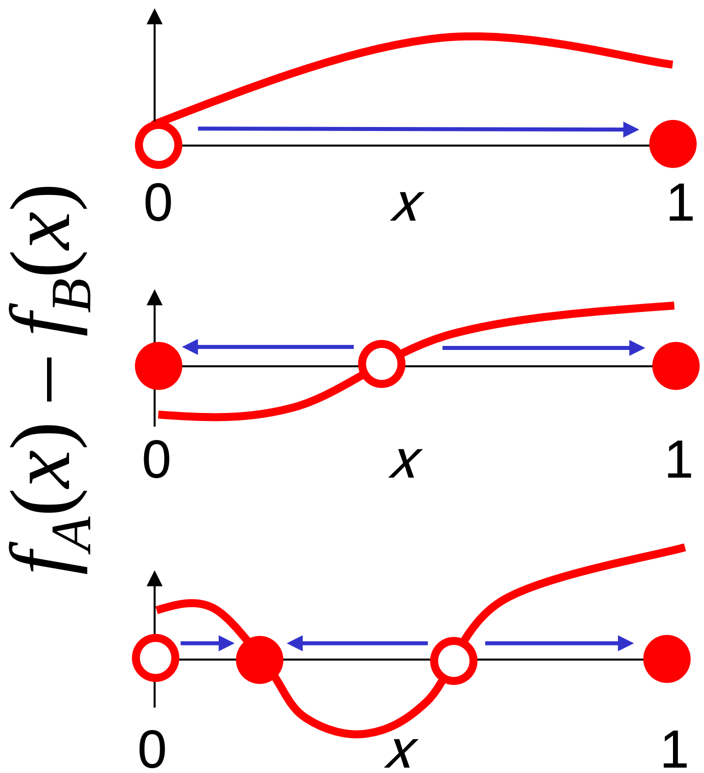
- With $x := x_A$ and $1 - x = x_B$, the system is equivalent to

$$\dot{x} = x(1-x)\left[f_A(x) - f_B(x)\right]$$

- Equilibria: $x = 0$, $x = 1$, and $\{x \in (0, 1) \mid f_A(x) = f_B(x)\}$
- $x^* = 0$ is stable if $f_A(0) < f_B(0)$
- $x^* = 1$ is stable if $f_A(1) > f_B(1)$
- An interior equilibrium x^* is stable if

$$\frac{\partial f_A}{\partial x}(x^*) < \frac{\partial f_B}{\partial x}(x^*)$$

Stability of equilibria



x ... abundance of A

$1-x$ ... abundance of B

fitness difference between A and B

selection dynamics

● ... stable equilibrium

○ ... unstable equilibrium

The general idea of evolutionary game theory

- Evolutionary game theory is the study of *frequency-dependent selection*.

- We consider a population of players.
- Each player has a fixed strategy.
- Players interact (play the game) randomly.
- Success in the game is translated into reproductive success: Good strategies reproduce faster.

Evolutionary games with two players

- A two-player game is defined by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

A gets payoff

B gets payoff

when playing against *B*

when playing against *A*

Fitness = expected payoff

- We define fitness as the expected payoff,

$$\begin{aligned} f_A(x_A, x_B) &= a x_A + b x_B \\ f_B(x_A, x_B) &= c x_A + d x_B \end{aligned}$$

- Setting $x := x_A$ we have $1 - x = x_B$ and we obtain the selection dynamics

$$\dot{x} = x(1-x)\left[(a-b-c+d)x + b - d\right]$$

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \quad \text{i.e.} \quad \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

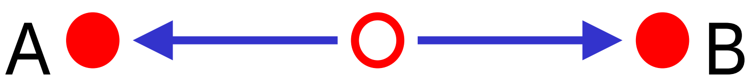
(i) A dominates B, if a>c and b>d:

A is always the best strategy.
A is always fitter than B.

(ii) B dominates A, if a<c and b<d:

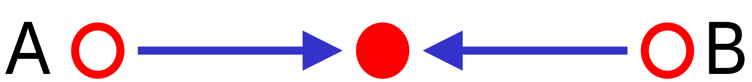
B is always the best strategy.
B is always fitter than B.

(iii) A and B are bistable, if a>c and b<d:



Playing the same strategy than your opponent is the best strategy.
$x^* = (d – b)/(a – b – c + d)$

(iv) A and B coexist, if a<c and b>d:



Playing the opposite strategy than your opponent is the best strategy.
$x^* = (d – b)/(a – b – c + d)$

(v) A and B are neutral, if a=c and b=d:

No matter what you do, the two payoffs are always the same.

Nash equilibrium

- **Definition**: If two players play the same strategy and neither player can increase its payoff by changing strategy, then the strategy is at *Nash equilibrium*. Mathematically,
  - A is a strict Nash equilibrium, if a > c.
  - A is a Nash equilibrium, if a $\geq$ c.

  - B is a strict Nash equilibrium, if d > b.
  - B is a Nash equilibrium, if d $\geq$ b.

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

- A Nash equilibrium is the best reply to itself.

Examples

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \end{array}$$

A is not Nash.
B is Nash.
B dominates A.

Note: Both playing B has lower total payoff than both playing A.

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 3 & 1 \\ 5 & 0 \end{pmatrix} \end{array}$$

A is not Nash.
B is not Nash.

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 5 & 0 \\ 3 & 1 \end{pmatrix} \end{array}$$

A is Nash.
B is Nash.

Evolutionary stable strategy (ESS)

- Suppose an infinitesimally small quantity ϵ of B invades an all-A population. Then selection will oppose invasion, if

$$\begin{aligned} f_A(1-\epsilon) &> f_B(\epsilon) \\ a(1-\epsilon)+b\epsilon &> c(1-\epsilon)+d\epsilon \end{aligned}$$

  i.e., if in the limit as $\epsilon \to 0$

$$(a > c) \text{ or } (a = c \text{ and } b > d)$$

- **Definition**: A is ESS if either (i) $a > c$, or
  (ii) $a = c$ and $b > d$

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More than two strategies

$$
\begin{array}{c|cccc}
 & S_1 & S_2 & \cdots & S_n \\
\hline
S_1 & a_{11} & a_{12} & \cdots & a_{1n} \\
S_2 & a_{21} & \ddots & & \\
\vdots & \vdots & & & \vdots \\
S_n & a_{n1} & & \cdots & a_{nn}
\end{array}
$$

- The payoff for strategy S_i versus S_j is $E(S_i, S_j) = a_{ij}$.

Generalized definitions

- S_k is a *strict Nash* equilibrium, if $a_{kk} > a_{ik}$ for all $i \neq k$.
- S_k is a *Nash* equilibrium, if $a_{kk} \geq a_{ik}$ for all $i \neq k$.
- S_k is *ESS* if for all $i \neq k$, either
  - $a_{kk} > a_{ik}$, or
  - $a_{kk} = a_{ik}$ and $a_{ki} > a_{ii}$
- S_k is *weak ESS* if for all $i \neq k$, either
  - $a_{kk} > a_{ik}$, or
  - $a_{kk} = a_{ik}$ and $a_{ki} \geq a_{ii}$
- S_k is *unbeatable* if for all $i \neq k$, both
  - $a_{kk} > a_{ik}$, **and**
  - $a_{ki} > a_{ii}$

Hierarchy of concepts

unbeatable

↓

strict Nash

↓

ESS

↓

weak ESS

↓

Nash

stable against invasion

Frequency-dependent fitness among *n* players

- Fitness = expected payoff:

$$f_i(x) = f_{S_i}(x) = \sum_{j=1}^{n} x_j a_{ij}$$

- Average population fitness:

$$\phi(x) = \sum_{i=1}^{n} x_i f_i(x)$$

The replicator equation

$$\dot{x}_i = x_i \left[f_i(x) - \phi(x) \right] \qquad i = 1, \ldots, n$$

$$x_1 + \cdots + x_n = 1$$

- Fitness is frequency-dependent, usually in a linear fashion
- Generalizes constant selection dynamics
- The interior of the simplex S_n is invariant.
- Each face is invariant.
- Depending on the payoff matrix there can be fixed points in the interior and in every face of the simplex.

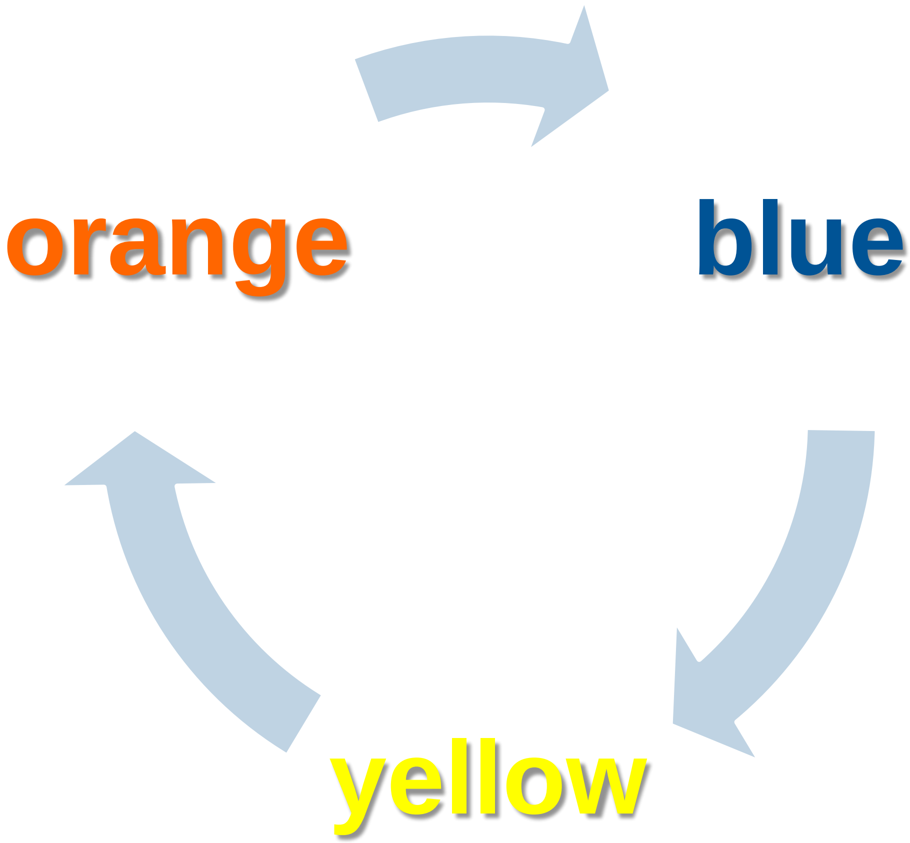
Three mating strategies among side-blotched lizards

- Orange-throated males
  - strongest
  - do not form strong pair bonds
  - fight blue-throated males for their females

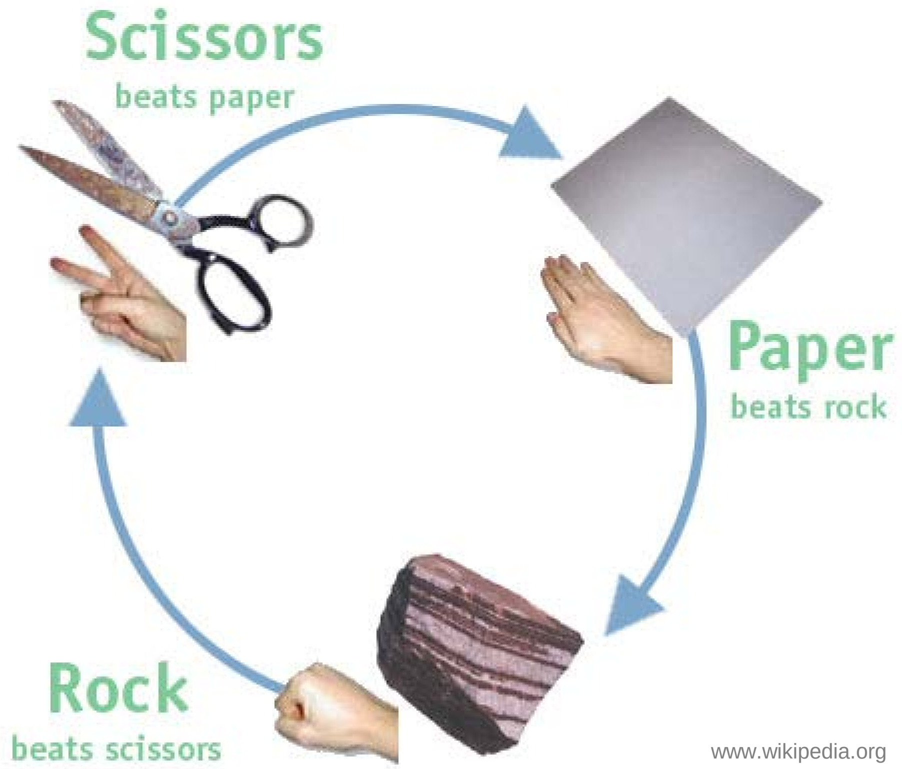
- Blue-throated males
  - middle-sized
  - form strong pair bonds
  - can defend against yellow-throated males

- Yellow-throated males
  - smallest
  - color mimics females
  - can approach orange-throated males in disguise and mate with their females while engaged in fighting

Cyclic dominance



Rock-paper-scissors (RPC)



www.wikipedia.org

Payoff matrix for the RPC game

- We can re-scale any column of the payoff matrix.
- For the symmetric RPC game, we have

$$\begin{array}{cc} & \begin{array}{ccc} R & S & P \end{array} \\ \begin{array}{c} R \\ S \\ P \end{array} & \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix} \end{array}$$

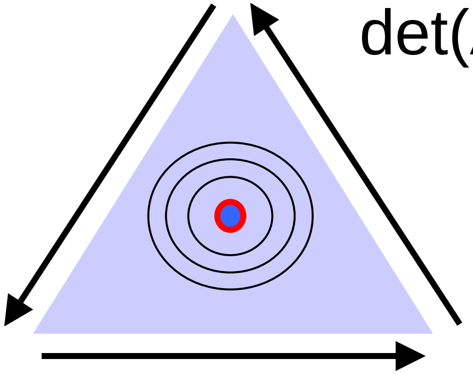
- RPC is a zero-sum game with average fitness ϕ = 0

Replicator dynamics of the RPC game

- The general RPC game is defined by the payoff matrix

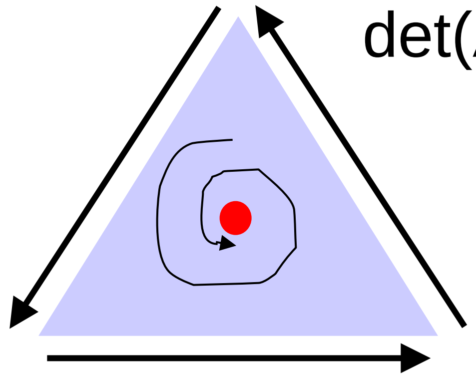
$$A = \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix}$$

- Case 1: det(A) > 0
  - Unique interior equilibrium which is globally stable
  - Trajectories converge to this point as damped oscillations
- Case 2: det(A) < 0
  - Unique interior equilibrium which is unstable
  - Trajectories converge to the boundary of the simplex in oscillations with increasing amplitude



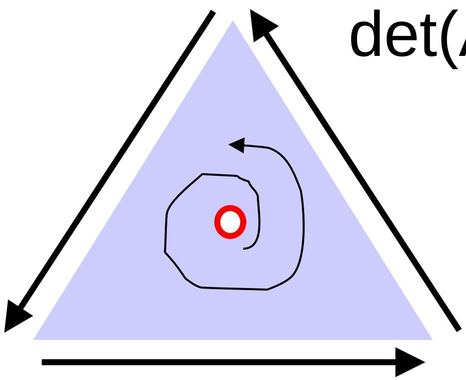
det(A) = 0

neutral oscillations



det(A) > 0

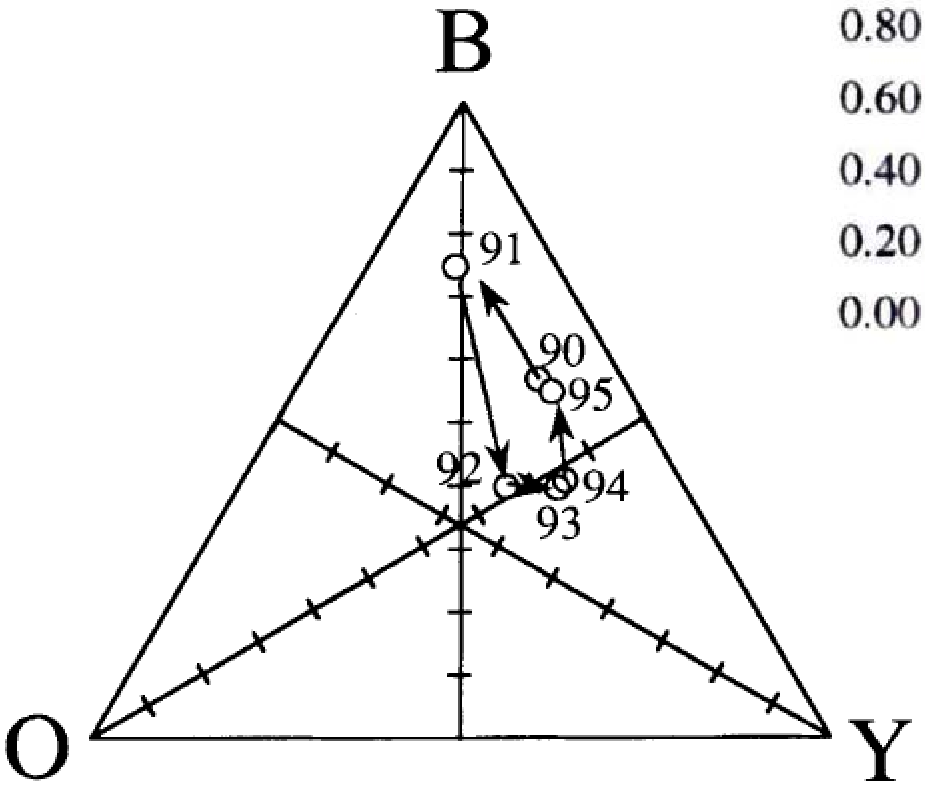
damped oscillations
to a stable equilibrium

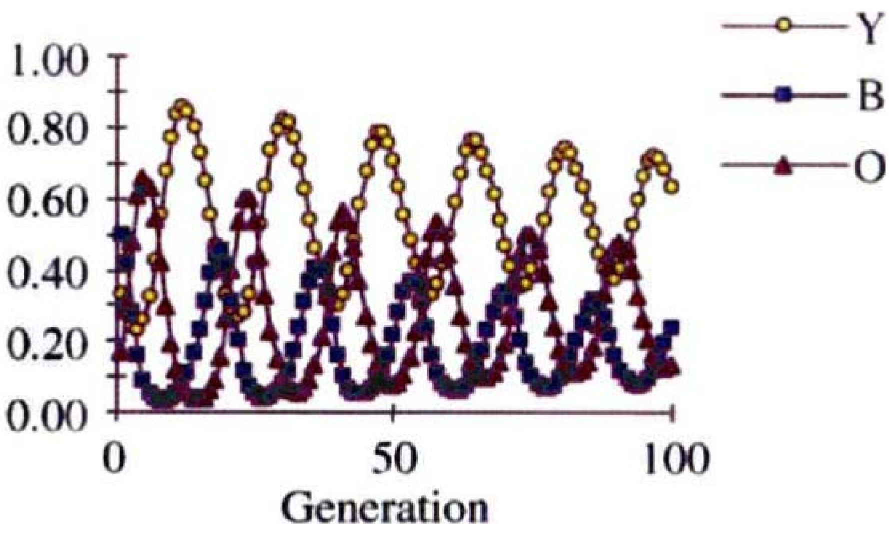


det(A) < 0

increasing oscillations
to a heteroclinic cycle

What happened to the lizards?





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More than three strategies

- For $n \geq 4$, the replicator equation allows for limit cycles and chaotic attractors.
- An interior equilibrium is given by the solution of the linear system $f_1 = \ldots = f_n$ and $x_1 + \ldots + x_n = 1$, which has one or zero non-degenerate solutions. There can be at most one isolated equilibrium in the interior.
- If there is no interior equilibrium, then all trajectories converge to the boundary of the simplex.

Conventional fights

- Many conflicts between animals do not escalate.
- In a *conventional fight*, threatening signals are exchanged that allow the contestants to assess each other's strength or determination, before one of them simply walks away.

Hawks and doves

- Let us analyze conventional fighting from the perspective of **individual selection** (rather than group selection).
- There are two basic strategies: Hawks (H) escalate fights, whereas doves (D) retreat.
- The benefit of winning a fight is b.
- The cost of injury is c.

$$
\begin{array}{cc}
 & \begin{array}{cc} \quad H \quad & \quad D \quad \end{array} \\
\begin{array}{c} H \\ D \end{array} & \begin{pmatrix} (b-c)/2 & b \\ 0 & b/2 \end{pmatrix}
\end{array}
$$

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Hawk and dove replicator dynamics

- Often, the cost of injury will be larger than the benefit of escalation ($b < c$).
- If $b < c$, then neither strategy is a Nash equilibrium.
- Hawks and doves can coexist. The equilibrium hawk frequency is

$$x_H^* = \frac{b}{c}$$

- If $b \ll c$, then there will be few hawks.

Mixed strategies

- Consider a strategy that plays “hawk” with probability p and “dove” with probability 1 – p.
- The space of strategies is the interval [0, 1], rather than the discrete space {H, D} as before.
- The payoff for strategy p_1 versus strategy p_2 is

$$
\begin{aligned}
E(p_1, p_2) \quad = \quad & p_1 p_2\, E(H, H) \\
& + p_1 (1 - p_2)\, E(H, D) \\
& + (1 - p_1) p_2\, E(D, H) \\
& + (1 - p_1)(1 - p_2)\, E(DD)
\end{aligned}
$$

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Mixed hawk and dove strategy

- We find

$$E(p_1, p_2) = \frac{b}{2}\left(1 + p_1 - p_2 - \frac{c}{b} p_1 p_2\right)$$

- The strategy p* = b/c is evolutionary stable:

$$\begin{aligned} E(p^*, p^*) &= (b/2)[1 - (b/c)] = E(p, p^*) \\ E(p^*, p) &= (b/2)[1 + (b/c) - 2p] \\ E(p, p) &= (b/2)[1 - (c/b)p^2] \end{aligned}$$

Thus p* is Nash, not strict Nash, and ESS, because E(p*, p) > E(p, p) for all p $\neq$ p*.

There is always a Nash equilibrium

- For a given n $\times$ n payoff matrix A, the payoff for strategy q $\in$ S_n versus strategy p $\in$ S_n is

$$E(q,p) = qAp = \sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} q_i p_j$$

- There exists at least one strategy q* such that

$$q^* A q^* \geq pAq \text{ for all } p$$

i.e., q* is a Nash equilibrium.

The prisoner's dilemma

- Two people are suspected of having committed a joint crime. The state attorney offers separately the same deal to both: confess, become a witness, and avoid prison.
- Payoff = – years in prison

$$\begin{array}{l c} & \begin{array}{cc} \text{remain silent} & \text{confess} \end{array} \\ \begin{array}{l} \text{remain silent} \\ \text{confess} \end{array} & \begin{pmatrix} -1 & -10 \\ 0 & -7 \end{pmatrix} \end{array}$$

- Rational analysis of the game leads to "confess" no matter what the partner does. They will not cooperate.

The Prisoner's Dilemma captures the essential problem of cooperation

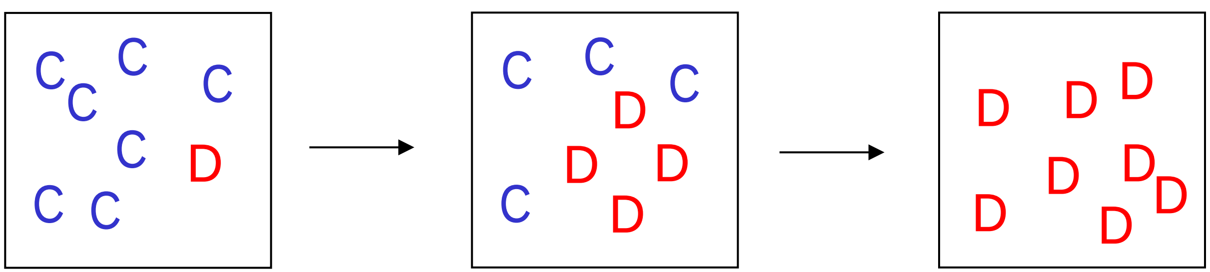
$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \end{array}$$

- Rational players defect in order to maximize their payoff.
- Yet, cooperation is abundant in nature. For example,
  - among organelles in a cell
  - among cells maintaining a tissue
  - among tissues forming an organ
  - among organs in a body
  - among bacteria and animals
  - ….

Can cooperation evolve?

- Let us consider the replicator equation.
- $f_C(x) = 3x \quad < \quad f_D(x) = 5x + 1 - x = 4x + 1$
- Thus natural selection favors defection.

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \end{array}$$



$$C \longrightarrow D$$

D dominates C

The general Prisoner's Dilemma game

$$\begin{array}{ccc} & C & D \\ \begin{array}{c} C \\ D \end{array} & \multicolumn{2}{c}{\begin{pmatrix} R & S \\ T & P \end{pmatrix}} \end{array}$$

$$T > R > P > S \quad \text{and} \quad R > \frac{T+P}{2}$$

- DC: <u>T</u>emptation to defect
- CC: <u>R</u>eward for mutual cooperation
- DD: <u>P</u>unishment for mutual defection
- CD: <u>S</u>ucker's payoff

Direct reciprocity

- The Prisoner's Dilemma game is repeated m times.
- Consider two strategies:
  - GRIM: Cooperate initially, then as long as opponent does not defect
  - ALLD: Always defect

$$\begin{array}{cc} & \begin{array}{cc} \text{GRIM} & \text{ALLD} \end{array} \\ \begin{array}{c} \text{GRIM} \\ \text{ALLD} \end{array} & \begin{pmatrix} mR & S+(m-1)P \\ T+(m-1)P & mP \end{pmatrix} \end{array}$$

- If m > (T – P)/(R – P), then GRIM is strict Nash, ALLD cannot invade. However, ALLD is also strict Nash.
- Hence, direct reciprocity can only stabilize cooperation.

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Defecting in the last round

- If you know that you play m rounds, it is rational to defect in the last round. Use ( )* to denote this variant strategy.

$$\begin{array}{c} \\ \text{GRIM} \\ \text{GRIM}^* \end{array} \begin{array}{c} \begin{array}{cc} \quad\text{GRIM}\quad & \quad\text{GRIM}^* \end{array} \\ \begin{pmatrix} mR & (m-1)R+S \\ (m-1)R+T & (m-1)R+P \end{pmatrix} \end{array}$$

- GRIM* dominates GRIM, GRIM → GRIM*.
- But then:

GRIM → GRIM* → GRIM** → … → GRIM*$^{(m)}$ = ALLD

Variable number of rounds

- Suppose that after each round there is a probability w that another round will be played.
- The probability of playing k rounds is

$$w^{k-1}(1-w)$$

- Thus, the expected number of rounds is

$$\begin{aligned}\bar{m} &= (1-w) + 2w(1-w) + 3w^2(1-w) + \ldots \\ &= 1 - w + 2w - 2w^2 + 3w^2 - 3w^3 + \ldots \\ &= 1 + w + w^2 + w^3 + \cdots = \frac{1}{1-w}\end{aligned}$$

Prisoner's Dilemma with a variable number of rounds

- The payoff for GRIM versus ALLD is

$$\begin{array}{c} \\ \text{GRIM} \\ \text{ALLD} \end{array} \begin{array}{c} \begin{array}{cc} \quad\quad \text{GRIM} \quad\quad & \quad\quad \text{ALLD} \quad\quad \end{array} \\ \begin{pmatrix} \bar{m}R & S+(\bar{m}-1)P \\ T+(\bar{m}-1)P & \bar{m}P \end{pmatrix} \end{array}$$

- GRIM is evolutionary stable if $\bar{m} > (T-P)/(R-P)$.
- Defecting in the last round is no longer possible.

Tit-for-tat

- TFT strategy: start with cooperation, then do whatever your opponent has done in the previous round, i.e., answer C for C and D for D.
- TFT has won *Axelrod's tournaments*, an all-against-all competition between game strategies.
- Properties of TFT:
  - TFT is "nice": it is never first to defect.
  - TFT is not greedy: it will never have higher payoff than a single opponent.
  - TFT is cooperative.

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TFT versus ALLD

- I play TFT : C C C C C …
  You play TFT : C C C C C …
- I play TFT : C D D D D …
  You play ALLD : D D D D D …

$$\begin{array}{cc} & \begin{array}{cc} \text{TFT} & \text{ALLD} \end{array} \\ \begin{array}{c} \text{TFT} \\ \text{ALLD} \end{array} & \begin{pmatrix} \bar{m}R & S+(\bar{m}-1)P \\ T+(\bar{m}-1)P & \bar{m}P \end{pmatrix} \end{array}$$

- TFT can resist invasion by ALLD if $\bar{m} > (T-P)/(R-P)$.
- TFT can resume cooperation, if the opponent cooperates.

TFT in the presence of noise

- Suppose errors occur in playing TFT.

```
                  *
TFT  : C C C D C D C D D D ...
TFT  : C C C C D C D D D D ...
                         *
```

- In the long run, the payoff is as low as choosing randomly between C and D,

$$E(TFT, TFT) = (T + R + P + S)/4 \quad < \quad R$$

because $R > (T + P)/2$ and $R > P$.

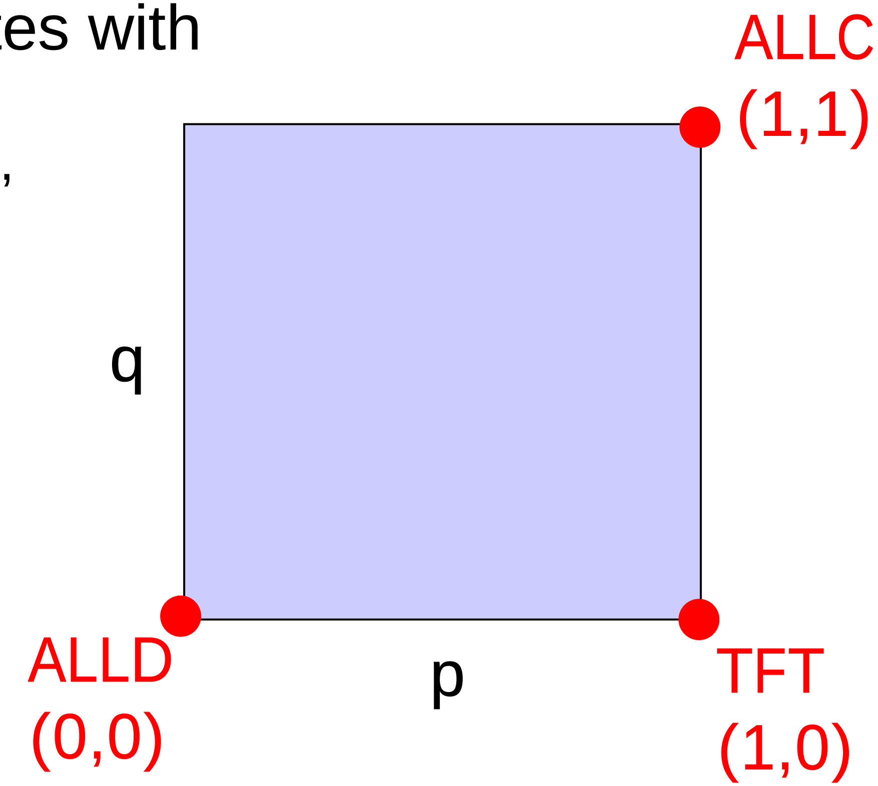
TFT versus ALLC

$$\begin{array}{c} \\ \text{TFT} \\ \text{ALLC} \end{array} \begin{array}{c} \begin{array}{cc} \text{TFT} & \text{ALLC} \end{array} \\ \begin{pmatrix} \bar{m}R & \bar{m}R \\ \bar{m}R & \bar{m}R \end{pmatrix} \end{array}$$

- TFT is not evolutionary stable.
- In a finite population, random drift can lead from TFT to ALLC.

Reactive strategies

- A reactive strategy is a probabilistic strategy that takes into account the opponent's action in the previous round.
- The strategy S(p, q) cooperates with
  - probability p if the opponent has cooperated in the previous move,
  - probability q if the opponent has defected in the previous move.
- Thus, p and q are conditional probabilities and each reactive strategy S(p, q) corresponds to a point (p, q) in the unit square.



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Reactive strategies for the repeated PD

- The repeated Prisoner's Dilemma between two reactive strategies $S_1(p_1, q_1)$ and $S_2(p_2, q_2)$ is a Markov chain with state space {CC, CD, DC, DD}, where, e.g., "CD" means "I play C and you play D".
- The transition probability matrix M is

$$
\begin{array}{c c}
 & \begin{array}{cccc} CC & CD & DC & DD \end{array} \\
\begin{array}{c} CC \\ CD \\ DC \\ DD \end{array} &
\begin{pmatrix}
p_1 p_2 & p_1(1-p_2) & (1-p_1)p_2 & (1-p_1)(1-p_2) \\
q_1 p_2 & q_1(1-p_2) & (1-q_1)p_2 & (1-q_1)(1-p_2) \\
p_1 q_2 & p_1(1-q_2) & (1-p_1)q_2 & (1-p_1)(1-q_2) \\
q_1 q_2 & q_1(1-q_2) & (1-q_1)q_2 & (1-q_1)(1-q_2)
\end{pmatrix}
\end{array}
$$

Stationary distribution of the Markov chain

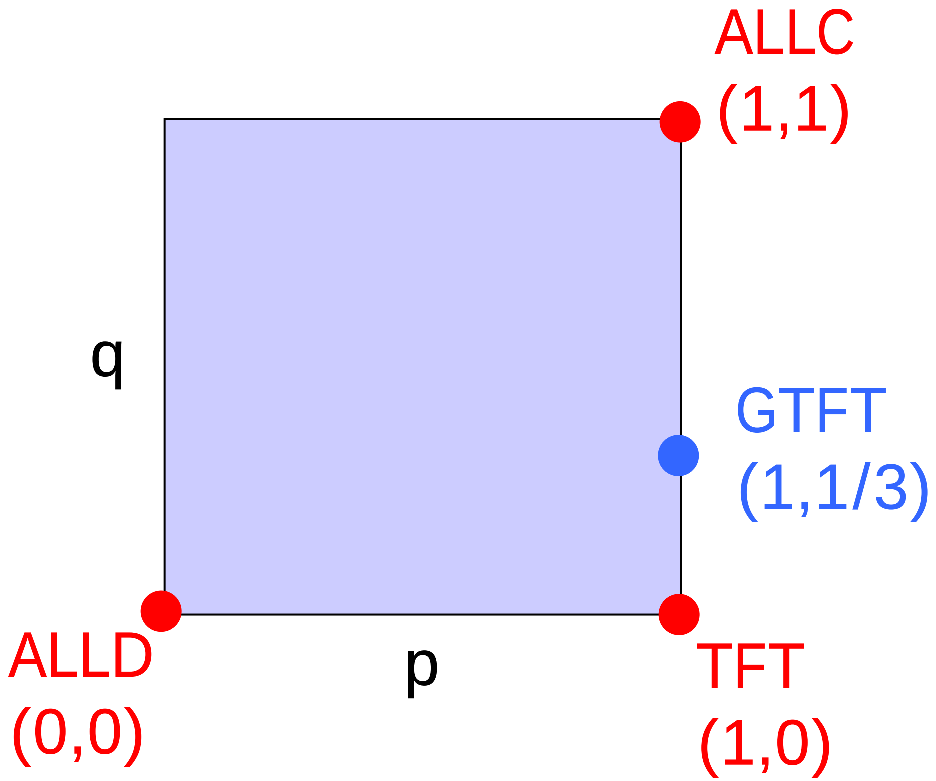
- Let $x(t) = (x_{CC}(t), x_{CD}(t), x_{DC}(t), x_{DD}(t))$ be the probability distribution of the game after t rounds.
- We have $x(t + 1) = x(t) \cdot M$.
- The payoff at the stationary distribution is

$$E(S_1, S_2) = R s_1 s_2 + S s_1 (1 - s_2) + \\ + T(1 - s_1) s_2 + P(1 - s_1)(1 - s_2)$$

where $s_1(p_1, p_2, q_1, q_2)$ and $s_2(p_1, p_2, q_1, q_2)$ are the probabilities that players 1 and 2, respectively, cooperate in the stationary distribution.

Generous Tit-for-tat (GTFT)

- For the Prisoner's Dilemma with R=3, T=5, S=0, P=1, GTFT is defined by p=1 and q=1/3, i.e., GTFT = S(1, 1/3).



Generous Tit-for-tat is more forgiving

- GTFT is more forgiving than TFT: it will cooperate one out of three times if the opponent has defected.
- E(GTFT, GTFT) is close to R, because GTFT can correct mistakes:

```
                  *
GTFT : C C C D C D C C C C ...
GTFT : C C C C D C C C C C ...
```

- E(GTFT, ALLD) < E(TFT, ALLD), but in simulations of evolving strategies we often observe

$$\text{ALLD} \rightarrow \text{TFT} \rightarrow \text{GTFT}$$

GTFT for the general Prisoner's Dilemma

- GTFT = S(p, q) with

$$p = 1 \quad \text{and} \quad q = \min\left\{1 - \frac{T-R}{R-S}, \frac{R-P}{T-P}\right\}$$

- This is the highest level of forgiveness, q, that is still resistant against invasion by ALLD.
- Among all reactive strategies that can resist ALLD, GTFT leads to the highest payoff for the population adopting it.

Memory-one strategies

- We now consider strategies that decide between C or D based on both the opponent's and one's own last move.
- The conditional probabilities to cooperate given that the last round was CC, CD, DC, DD are p_1, p_2, p_3, p_4.
- The Markov chain for a game between $S(p_1, p_2, p_3, p_4)$ and $S'(p'_1, p'_2, p'_3, p'_4)$ is defined by

$$
\begin{array}{cc}
 & \begin{array}{cccc} CC & CD & DC & DD \end{array} \\
\begin{array}{c} CC \\ CD \\ DC \\ DD \end{array} &
\begin{pmatrix}
p_1 p'_1 & p_1(1-p'_1) & (1-p_1)p'_1 & (1-p_1)(1-p'_1) \\
p_2 p'_3 & p_2(1-p'_3) & (1-p_2)p'_3 & (1-p_2)(1-p'_3) \\
p_3 p'_2 & p_3(1-p'_2) & (1-p_3)p'_2 & (1-p_3)(1-p'_2) \\
p_4 p'_4 & p_4(1-p'_4) & (1-p_4)p'_4 & (1-p_4)(1-p'_4)
\end{pmatrix}
\end{array}
$$

Old friends

- Each memory-one strategy is a point in $[0, 1]^4$.

  For example:

- ALLD = S(0, 0, 0, 0)
- ALLC = S(1, 1, 1, 1)
- TFT = S(1, 0, 1, 0)
- GTFT = (1, 1/3, 1, 1/3)
- Reactive strategies = $\{S(p_1, p_2, p_3, p_4) \mid p_1 = p_3, \; p_2 = p_4\}$

Win-stay, lose-shift (WSLS)

- WSLS = S(1, 0, 0, 1), i.e., cooperate after CC or DD, defect after CD or DC.
- WSLS stays with high payoffs T or R, and shifts with low payoffs P or S.
- WSLS is stable against invasion by ALLD if R > (T + P)/2, but:

```
WSLS : C D C D C D C …
ALLD : D D D D D D D …
```

WSLS can correct mistakes

(2) mistake

(4) friendship resumed

```
WSLS : C C C D D C C C …
WSLS : C C C C D C C C …
```

(1) friendly cooperation

(3) brief argument

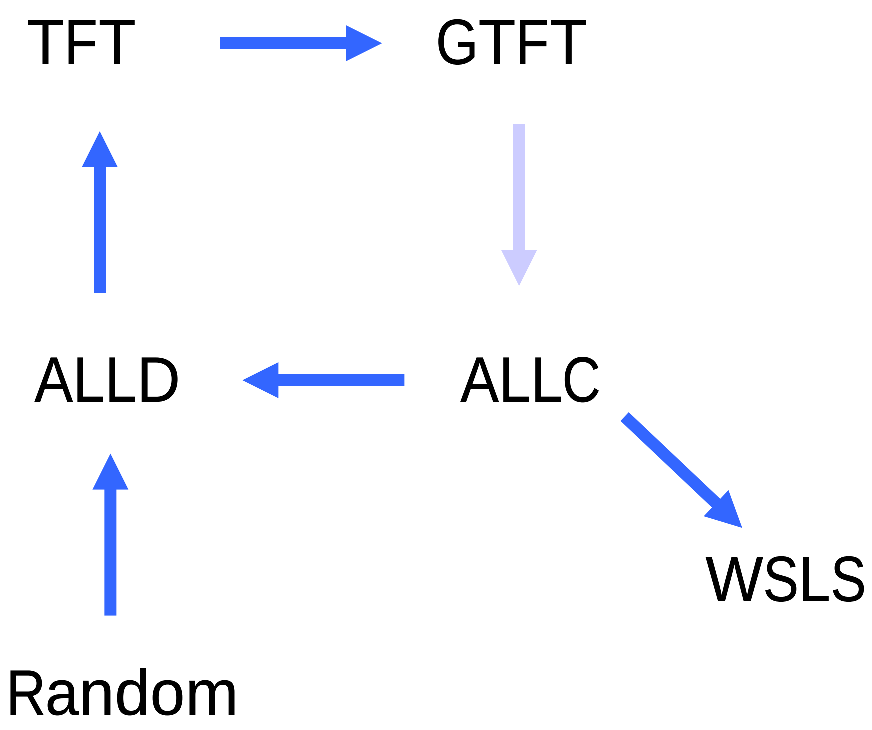
- WSLS is a deterministic corrector, whereas GTFT is a stochastic corrector.

WSLS dominates ALLC

```
                  *
WSLS : C C C D D D D D …
ALLC : C C C C C C C C …
```

- “Unconditional cooperators are exploited.”
- Note that GTFT does not dominate ALLC.

War and peace



Further reading

- Nowak MA. *Evolutionary Dynamics*, Chapters 4, 5.
- Maynard Smith J. *Evolution and the Theory of Games*.
- Sinervo B, Lively CM (1996). The Rock-Paper-Scissors Game and the evolution of alternative male strategies. Nature 380:240-243.