Evolutionary Games with Time Constraints

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Evolutionary game theory

1. There are many individuals of the same species that interact pair-wise
2. There is a finite number of different strategies in the population
3. Payoffs are obtained through games animals play
4. Each individual is selfish, i.e., maximizes its own benefit which leads to the Nash equilibrium
5. All interactions take the same time independently from the strategy individuals play (Typically, one interaction per unit of time)
6. Pairs are formed instantaneously and randomly

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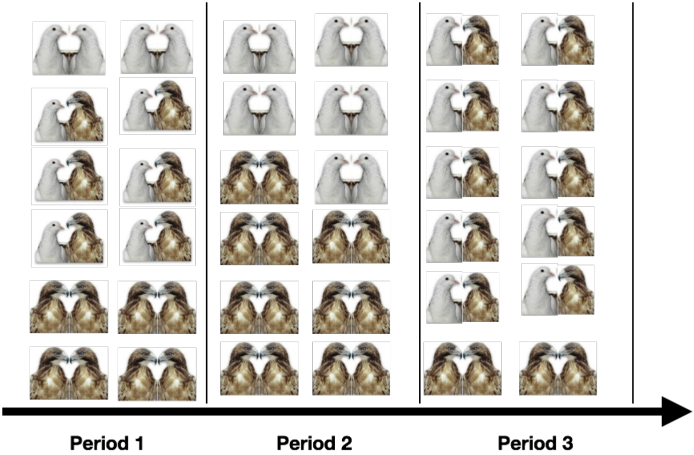
Hawk-Dove game (Maynard Smith and Price, 1973)



Payoffs for two-strategy games when all interactions take the same time

Payoff matrix (entries are payoffs per interaction):

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Interaction time matrix when all interactions take single unit of time:

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Fitnesses are frequency dependent but density independent

Assumption: Pairs are formed instantaneously and randomly, i.e., *the equilibrium distribution of pairs* is given by Hardy-Weinberg distribution

$$n_{11} = \left(\frac{N_1}{N}\right)^2 \frac{N}{2} = \frac{{N_1}^2}{2N}, \quad n_{12} = \frac{N_1 N_2}{N}, \quad n_{22} = \frac{{N_2}^2}{2N}.$$

$\frac{2n_{11}}{2n_{11}+n_{12}}$ - the probability an e_1 strategist is paired with another e_1 strategist

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Fitness of the first phenotype, defined as the expected payoff per interaction is

$$W_1 = \frac{2n_{11}}{2n_{11}+n_{12}}\pi_{11} + \frac{n_{12}}{2n_{11}+n_{12}}\pi_{12} = \frac{N_1}{N}\pi_{11} + \frac{N_2}{N}\pi_{12} = p_1\pi_{11} + p_2\pi_{12}$$

and similar expression W_2 holds for the fitness of the e_2 strategists.

Observation

The expected payoffs (fitnesses) are frequency dependent but density independent.

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Evolutionary games: Mathematical description of evolution by natural selection (Maynard Smith and Price, 1973)

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John Maynard Smith (1920-2004)

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To predict the eventual behavior of individuals in a single species without considering complex dynamical systems of evolution that may ultimately depend on many factors such as genetics, mating systems etc.

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Classification of possible evolutionary outcomes

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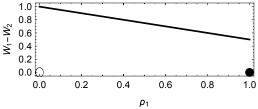
$$W_1 = p_1\pi_{11} + p_2\pi_{12}, \quad W_2 = p_1\pi_{21} + p_2\pi_{22}$$

Classification of evolutionarily stable states

1. Strategy e_1 is a Nash equilibrium and evolutionarily stable ($\pi_{11} > \pi_{21}$, $\pi_{12} > \pi_{22}$).



2. There exists exactly one interior NE which is also evolutionarily stable ($\pi_{11} < \pi_{21}$, $\pi_{12} > \pi_{22}$)

3. Strategies e_1 and e_2 are evolutionarily stable ($\pi_{11} > \pi_{21}$, $\pi_{22} > \pi_{12}$. There is an interior NE which is not evolutionarily stable.

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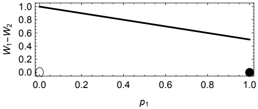

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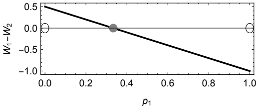

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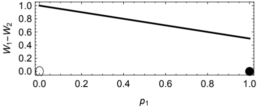

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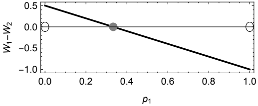

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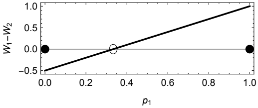

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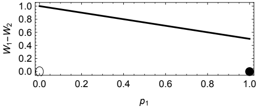

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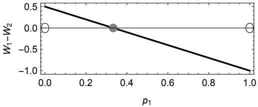

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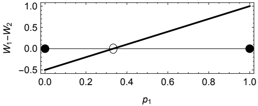

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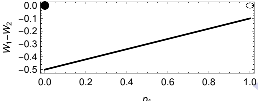

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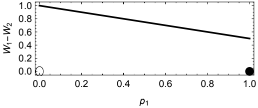

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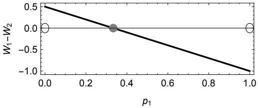

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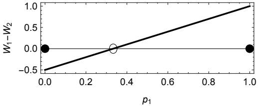

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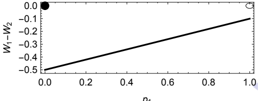
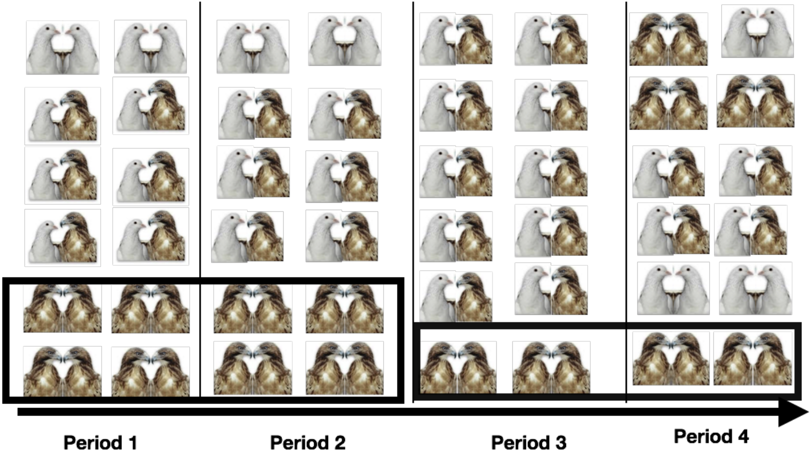


Distributional dynamics when interactions take different time (Křivan and Cressman, 2017)



Two-strategy games with interaction times

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- n_{22}– number of $e_2 e_2$ pairs
- $N_1 = 2n_{11} + n_{12}$–total number of individuals playing strategy e_1
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Two-strategy games with interaction times

Payoff matrix:

$$\begin{array}{c c} & \begin{array}{cc} e_1 & e_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \begin{pmatrix} \pi_{11} & \pi_{12} \\ \pi_{21} & \pi_{22} \end{pmatrix} \end{array}$$

Interaction time matrix:

$$\begin{array}{c c} & \begin{array}{cc} e_1 & e_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \begin{pmatrix} \tau_{11} & \tau_{12} \\ \tau_{21} & \tau_{22} \end{pmatrix} \end{array}$$

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Pair dynamics

- A pair n_{ij} splits up following a Poisson process with parameter τ_{ij}, i. e., in a unit of time, the number of pairs that disband is $\frac{n_{ij}}{\tau_{ij}}$
- Per unit of time there will be $2\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}$ individuals playing strategy e_1 disbanded from pairs and $2\frac{n_{22}}{\tau_{22}} + \frac{n_{12}}{\tau_{12}}$ individuals playing strategy e_2 disbanded from pairs
- Free individuals immediately and randomly form new pairs
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- To get the number of newly formed n_{11} pairs we multiply this proportion by the number of all newly formed pairs $\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}$ and obtain

$$\frac{(2\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}})^2}{4(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}})}$$

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and similarly for the number of newly formed n_{12} and n_{22} pairs

Pair dynamics

$$\frac{dn_{11}}{dt} = -\frac{n_{11}}{\tau_{11}} + \frac{\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)^2}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}$$

$$\frac{dn_{12}}{dt} = -\frac{n_{12}}{\tau_{12}} + \frac{2\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)\left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}}\right)}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}$$

$$\frac{dn_{22}}{dt} = -\frac{n_{22}}{\tau_{22}} + \frac{\left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}}\right)^2}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}$$

Pair dynamics

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Pair dynamics

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Pair equilibrium

$$\frac{n_{11}}{\tau_{11}} = \frac{\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)^2}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}$$

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$\frac{n_{11}}{\tau_{11}}, \frac{n_{12}}{\tau_{12}}, \frac{n_{22}}{\tau_{22}}$ are in Hardy-Weinberg proportions, i. e.,

$$\frac{n_{11}}{\tau_{11}}\frac{n_{22}}{\tau_{22}} = \frac{1}{4}\left(\frac{n_{12}}{\tau_{12}}\right)^2$$

Pair equilibrium

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Pair equilibrium distribution as a function of number N_1 of e_1 strategists

When $\tau_{12}^2 \neq \tau_{11}\,\tau_{22}$:

$$n_{11} = \frac{N_1\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) - \tau_{12}^2\frac{N}{2} + \tau_{12}\sqrt{N_1(N_1 - N)\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) + \left(\frac{N}{2}\right)^2\tau_{12}^2}}{2(\tau_{12}^2 - \tau_{11}\tau_{22})}$$

$$n_{12} = \frac{\tau_{12}^2\frac{N}{2} - \tau_{12}\sqrt{N_1(N_1 - N)\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) + \left(\frac{N}{2}\right)^2\tau_{12}^2}}{\tau_{12}^2 - \tau_{11}\,\tau_{22}}$$

$$n_{22} = \frac{N}{2} - n_{11} - n_{12}$$

When $\tau_{12}^2 = \tau_{11}\,\tau_{22}$:

$$n_{11} = \frac{N_1^2}{2N}$$
$$n_{12} = \frac{N_1 N_2}{N}$$
$$n_{22} = \frac{N_2^2}{2N}$$

Pair equilibrium distribution as a function of number N_1 of e_1 strategists

When $\tau_{12}^2 \neq \tau_{11}\,\tau_{22}$:

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$$n_{12} = \frac{\tau_{12}^2\frac{N}{2} - \tau_{12}\sqrt{N_1(N_1 - N)\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) + \left(\frac{N}{2}\right)^2\tau_{12}^2}}{\tau_{12}^2 - \tau_{11}\,\tau_{22}}$$

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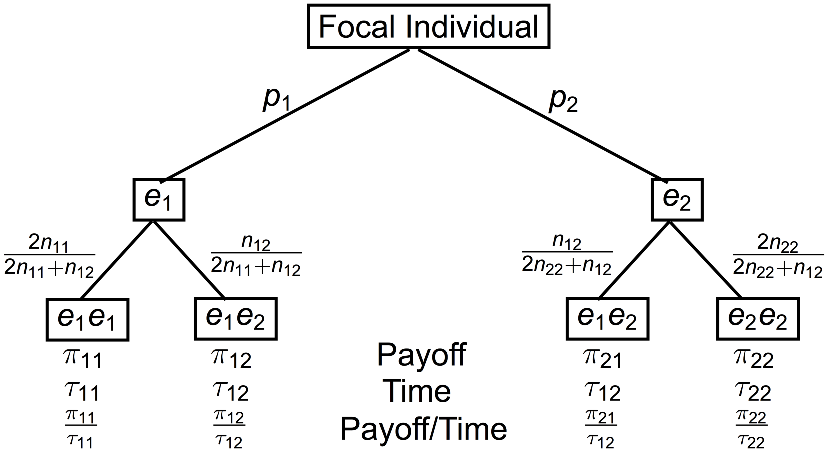
Payoffs


Focal Individual
p_1
p_2
e_1
e_2
$\frac{2n_{11}}{2n_{11}+n_{12}}$
$\frac{n_{12}}{2n_{11}+n_{12}}$
$\frac{n_{12}}{2n_{22}+n_{12}}$
$\frac{2n_{22}}{2n_{22}+n_{12}}$
e_1e_1
e_1e_2
e_1e_2
e_2e_2
π_{11}
τ_{11}
$\frac{\pi_{11}}{\tau_{11}}$
π_{12}
τ_{12}
$\frac{\pi_{12}}{\tau_{12}}$
Payoff
Time
Payoff/Time
π_{21}
τ_{12}
$\frac{\pi_{21}}{\tau_{12}}$
π_{22}
τ_{22}
$\frac{\pi_{22}}{\tau_{22}}$

Expected payoff per unit of time

$\frac{2n_{11}}{2n_{11}+n_{12}}$ - the probability an e_1 strategist is paired with another e_1 strategist

$\frac{n_{12}}{2n_{11}+n_{12}}$ - the probability an e_1 strategist is paired with an e_2 strategist

The expected payoff per unit time to an e_1 strategist is frequency dependent, but not a linear function of proportion p_1 of e_1 strategists

$$W_1 = \frac{2n_{11}}{2n_{11}+n_{12}} \frac{\pi_{11}}{\tau_{11}} + \frac{n_{12}}{2n_{11}+n_{12}} \frac{\pi_{12}}{\tau_{12}}$$

and the expected payoff to an e_2 strategists is

$$W_2 = \frac{n_{12}}{n_{12}+2n_{22}} \frac{\pi_{21}}{\tau_{12}} + \frac{2n_{22}}{n_{12}+2n_{22}} \frac{\pi_{22}}{\tau_{22}}$$

Fitnesses W_1 and W_2 are non-linear functions of N_1 and N_2 (i.e., non-linear in frequencies p_1 and p_2)

Expected payoff per unit of time

$\frac{2n_{11}}{2n_{11}+n_{12}}$ - the probability an e_1 strategist is paired with another e_1 strategist

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Interior Nash equilibria

Equation

$$W_1 = W_2$$

has up to two positive solutions:

$$p_{1_\pm} = \frac{n_{1_\pm}}{N} = \frac{1}{2B}\Big(\pm(\pi_{11}\tau_{22} - \pi_{22}\tau_{11})\sqrt{A} + \pi_{22}^2\tau_{11}^2 +$$

$$\tau_{22}\left(2\pi_{12}^2\tau_{11} + 2\pi_{12}\pi_{21}\tau_{11} - 3\pi_{11}\pi_{12}\tau_{12} - \pi_{11}\pi_{21}\tau_{12} + \pi_{11}^2\tau_{22}\right)$$

$$-\pi_{22}\left(\tau_{12}\left(3\pi_{12}\tau_{11} + \pi_{21}\tau_{11} - 4\pi_{11}\tau_{12}\right) + 2\pi_{11}\tau_{11}\tau_{22}\right)\Big)$$

where

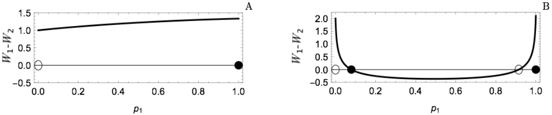
$$\begin{aligned} A &= (\pi_{22}\tau_{11} - \pi_{11}\tau_{22})^2 + (\pi_{12} - \pi_{21})^2\,\tau_{12}^2 \\ &\quad + 4(\pi_{11}\pi_{22}\tau_{12}^2 + \pi_{12}\pi_{21}\tau_{11}\tau_{22}) - 2(\pi_{12} + \pi_{21})\tau_{12}(\pi_{22}\tau_{11} + \pi_{11}\tau_{22}) \\ B &= A - (\pi_{12} - \pi_{21})^2(\tau_{12}^2 - \tau_{11}\tau_{22}). \end{aligned}$$

Observation

There are up to two interior equilibria, which contrasts with the classic result of evolutionary game theory with a single interior equilibrium.

Classification of evolutionarily stable states under time constraints

1. Strategy e_1 is stable and e_2 is unstable ($\frac{\pi_{11}}{\tau_{11}} > \frac{\pi_{21}}{\tau_{12}}, \frac{\pi_{12}}{\tau_{12}} > \frac{\pi_{22}}{\tau_{22}}$): One or two ESSs.



2. Strategies e_1 and e_2 are unstable ($\frac{\pi_{11}}{\tau_{11}} < \frac{\pi_{21}}{\tau_{12}}, \frac{\pi_{12}}{\tau_{12}} > \frac{\pi_{22}}{\tau_{22}}$): Single interior ESSs.

3. Strategies e_1 and e_2 are stable ($\frac{\pi_{11}}{\tau_{11}} > \frac{\pi_{21}}{\tau_{12}}, \frac{\pi_{12}}{\tau_{12}} < \frac{\pi_{22}}{\tau_{22}}$): Two boundary ESSs.

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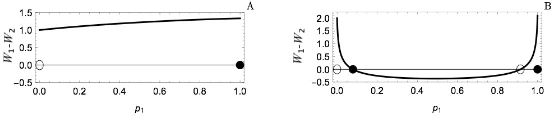

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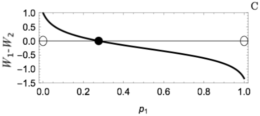

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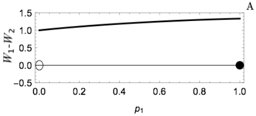

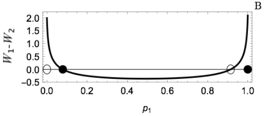

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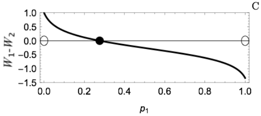

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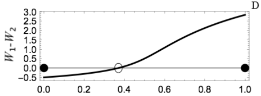

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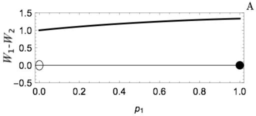

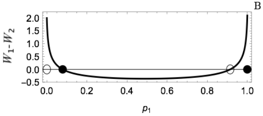

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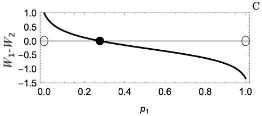

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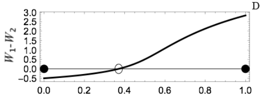

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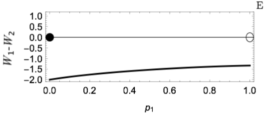
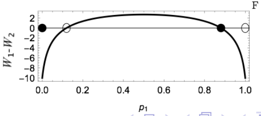
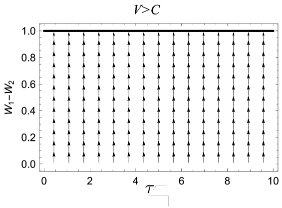




The Hawk-Dove game $\begin{array}{c c} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} V-C & 2V \\ 0 & V \end{pmatrix} \end{array}$ with $\begin{array}{c c} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} \tau & \tau \\ \tau & \tau \end{pmatrix} \end{array}$

1. If $V > C$ strategy D is dominated by H. Thus, Hawk is a strict NE (i.e., an ESS) of the game.



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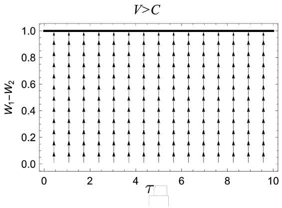

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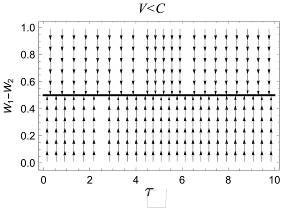

The Hawk-Dove game with time constraints

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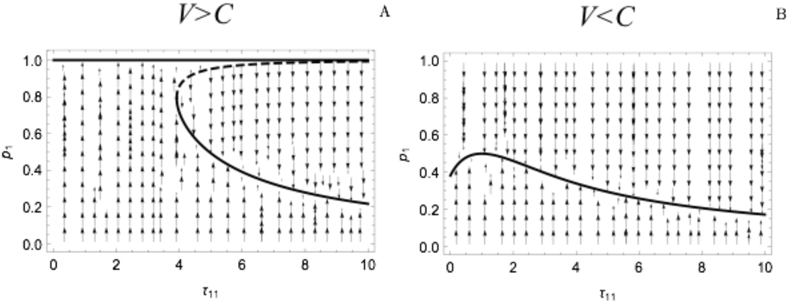

Prisoner's dilemma (single shot game)

C—cooperate

D—defect

$b =$ benefit of cooperation

$c =$ cost of cooperation

$$\begin{array}{c} \\ C \\ D \end{array}\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}$$

1. Defection is the only Nash equilibrium
2. Cooperation provides higher payoff when $b > c$

Question

How can cooperation evolve?

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$\rho =$ probability the game is played next time

$\frac{1}{1-\rho}$ =expected number of rounds

τ_{ij} =the expected number of rounds between e_i and e_j strategists

π_{ij} =payoff to strategy e_i when played against strategy e_j in a single-shot game

Payoff per interaction between two players (i.e., when single shot games are repeated several (τ_{ij}) times):

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Repeated Prisoner's dilemma (Opting-out game; Zhang et al., 2016), $b = 2$, $c = 1$, $\tau_{12} = \tau_{22} = 1$ (Křivan and Cressman, 2017)

Prisoner's dilemma payoff matrix
(single shot game)

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 1 & -1 \\ 2 & 0 \end{pmatrix} \end{array}$$

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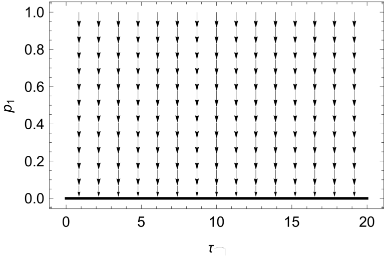

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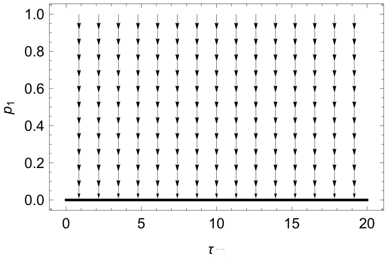

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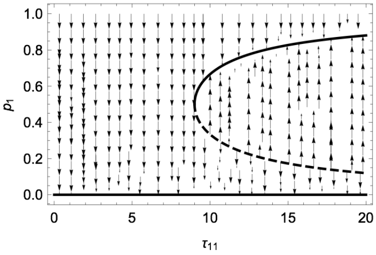
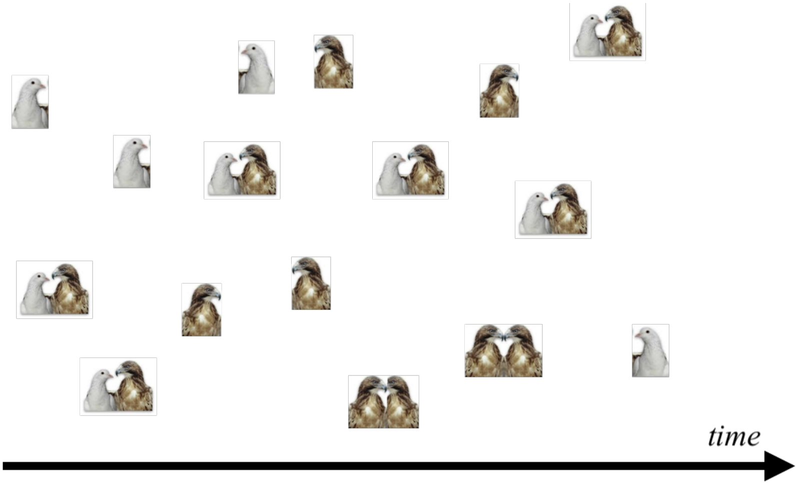


Distributional dynamics when pairing is non-instantaneous (Křivan et al., In review)



Distributional dynamics of singles and pairs

n_1 =# of singles using strategy e_1
n_2 =# of singles using strategy e_2

Distributional dynamics at fixed population numbers:

$$e_1 \text{ singles:} \quad \frac{dn_1}{dt} = -\lambda n_1^2 - \lambda n_1 n_2 + 2\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}$$

$$e_2 \text{ singles:} \quad \frac{dn_2}{dt} = -\lambda n_2^2 - \lambda n_1 n_2 + 2\frac{n_{22}}{\tau_{22}} + \frac{n_{12}}{\tau_{12}}$$

$$e_1 e_1 \text{ pairs:} \quad \frac{dn_{11}}{dt} = -\frac{n_{11}}{\tau_{11}} + \frac{\lambda}{2} n_1^2$$

$$e_1 e_2 \text{ pairs:} \quad \frac{dn_{12}}{dt} = -\frac{n_{12}}{\tau_{12}} + \lambda n_1 n_2$$

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HW distribution at the population equilibrium:

$$n_{11} = \frac{1}{2}\lambda\tau_{11} n_1^2, \quad n_{12} = \lambda\tau_{12} n_1 n_2, \quad n_{22} = \frac{1}{2}\lambda\tau_{22} n_2^2$$

Distributional dynamics of singles and pairs

n_1 =# of singles using strategy e_1
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Fitnesses

π_i- payoff per unit of time of a single e_i strategist

π_{ij}- payoff per interaction of an e_i strategists paired with an e_j strategist

τ_{ij}- average interaction time of an e_i strategist when paired with an e_j strategist

$\frac{\pi_{ij}}{\tau_{ij}}$- payoff per unit of time of an e_i strategist when paired with an e_j strategist

Fitnesses are defined as expected payoffs per unit of time:

$$W_1 = \frac{2n_{11}}{2n_{11}+n_{12}+n_1}\frac{\pi_{11}}{\tau_{11}} + \frac{n_{12}}{2n_{11}+n_{12}+n_1}\frac{\pi_{12}}{\tau_{12}} + \frac{n_1}{2n_{11}+n_{12}+n_1}\pi_1$$

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Fitness calculated at the equilibrium population distribution

Using HW at the distribution equilibrium

$$n_{11} = \frac{1}{2}\lambda\tau_{11}n_1^2$$
$$n_{12} = \lambda\tau_{12}n_1 n_2$$
$$n_{22} = \frac{1}{2}\lambda\tau_{22}n_2^2$$

allows us to express fitnesses in singles

$$W_1 = \frac{\pi_{11}\lambda n_1 + \pi_{12}\lambda n_2 + \pi_1}{\lambda n_1\tau_{11} + \lambda n_2\tau_{12} + 1}$$

$$W_2 = \frac{\pi_{21}\lambda n_1 + \pi_{22}\lambda n_2 + \pi_2}{\lambda n_1\tau_{12} + \lambda n_2\tau_{22} + 1}$$

At the interior Nash equilibrium (n_1, n_2) must satisfy:

$$\begin{cases} W_1 = W_2 \\ N = N_1 + N_2 = n_1(n_1\lambda\tau_{11} + n_2\lambda\tau_{12} + 1) + n_2(n_2\lambda\tau_{22} + n_1\lambda\tau_{12} + 1) \end{cases}$$

Fitness calculated at the equilibrium population distribution

Using HW at the distribution equilibrium

$$n_{11} = \frac{1}{2}\lambda\tau_{11}n_1^2$$
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Nash equilibrium when all interaction times are the same ($\tau_{11} = \tau_{12} = \tau_{21} = \tau$)

$$n_1 = \frac{(\pi_{22} - \pi_{12})(\sqrt{4\lambda N\tau + 1} - 1) + 2\tau(\pi_2 - \pi_1)}{2\lambda\tau(\pi_{22} - \pi_{21} - \pi_{12} + \pi_{11})}$$

$$n_2 = \frac{(\pi_{11} - \pi_{21})(\sqrt{4\lambda N\tau + 1} - 1) + 2\tau(\pi_1 - \pi_2)}{2\lambda\tau(\pi_{22} - \pi_{21} - \pi_{12} + \pi_{11})}$$

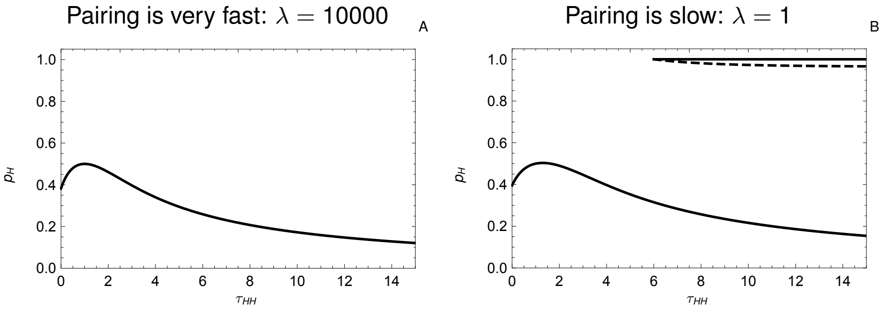
and

$$p_1 = \frac{N_1}{N} = \frac{\pi_{22} - \pi_{12}}{\pi_{22} - \pi_{21} - \pi_{12} + \pi_{11}} + \frac{(\pi_2 - \pi_1)\left(\sqrt{4\lambda N\tau + 1} + 1\right)}{2\lambda N(\pi_{22} - \pi_{21} - \pi_{12} + \pi_{11})}.$$

Observation

The equilibrium depends on population size N, which contrasts with the classic result of evolutionary game theory whereby the strategy proportion at Nash equilibrium are independent of the population size.

Nash equilibria for Hawk-Dove game when interaction times are not the same ($N = 100$, $V = 1$, $C = 2$, $\tau_{HD} = \tau_{DD} = 1$, $\pi_H = \pi_D = -1$).



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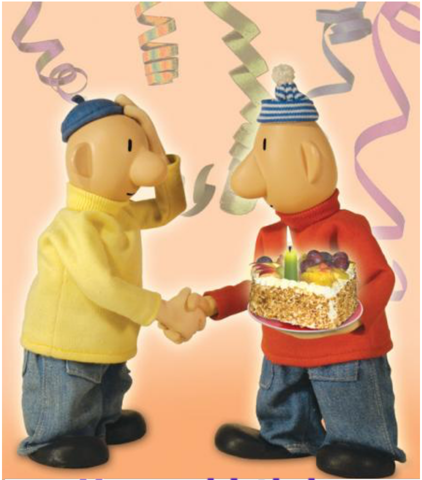

Happy birthday
Giovanni & Franco

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