An introduction to evolutionary game theory

Decisions, Games, and Evolution
Bangalore 2025

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An informal introduction: A few examples

The rock–paper–scissors game and the evolution of alternative male strategies

B. Sinervo & C. M. Lively

Department of Biology and Center for the Integrative Study of Animal Behavior, Indiana University, Bloomington, Indiana 47405, USA

Example 1: Mating behavior among male lizards (Sinervo & Lively 1996)

- Among side-blotched lizards (*Uta Stansburiana*), there are three male morphs. One can distinguish them by their throat color: yellow, blue, orange.

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  - Males with yellow throats resemble female lizards; they are sneakers and do not defend any territory

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Question: How can we make sense of this coexistence of different morphs?

An informal introduction: A few examples

Example 2: Cooperation and punishment among humans (Fehr & Gächter 2000)

Cooperation and Punishment in Public Goods Experiments

By Ernst Fehr and Simon Gächter*

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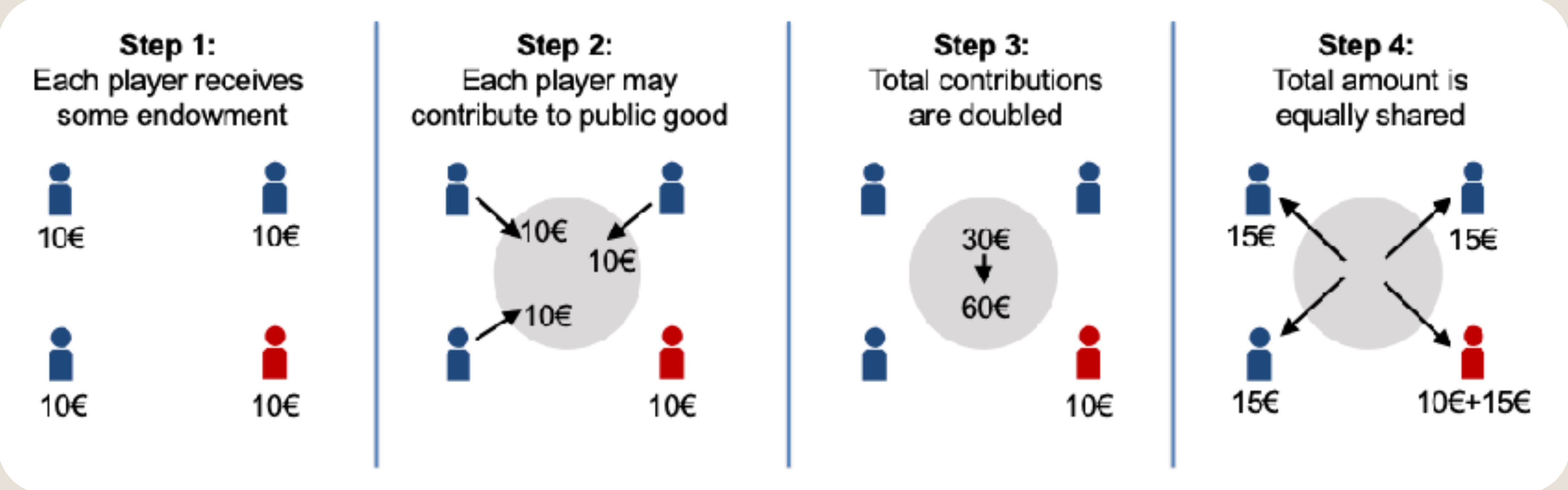

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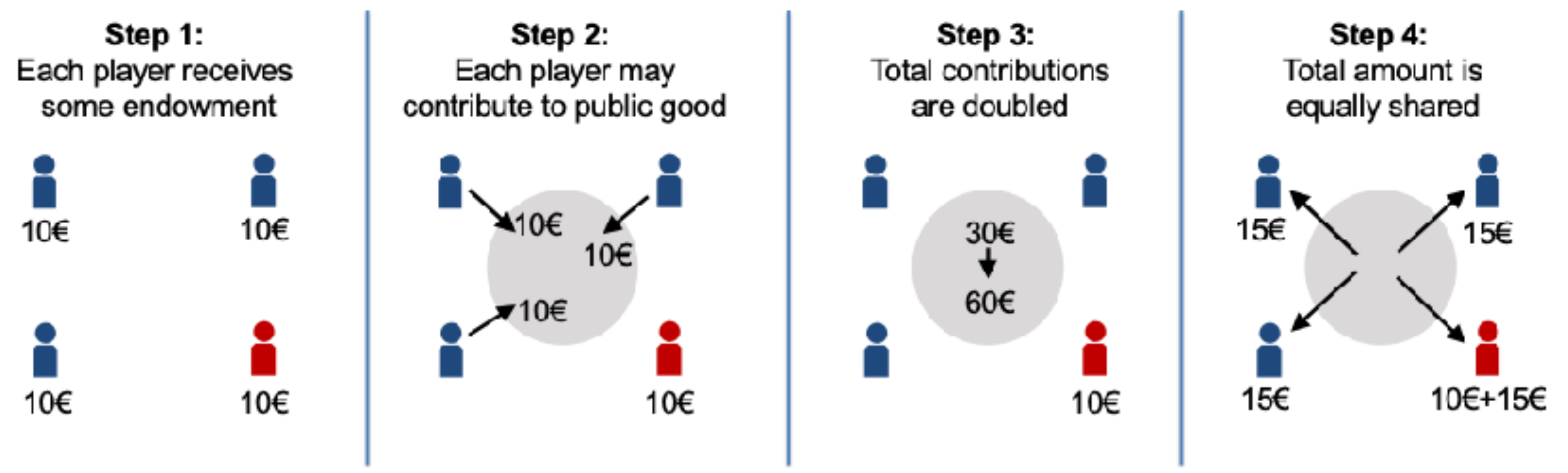

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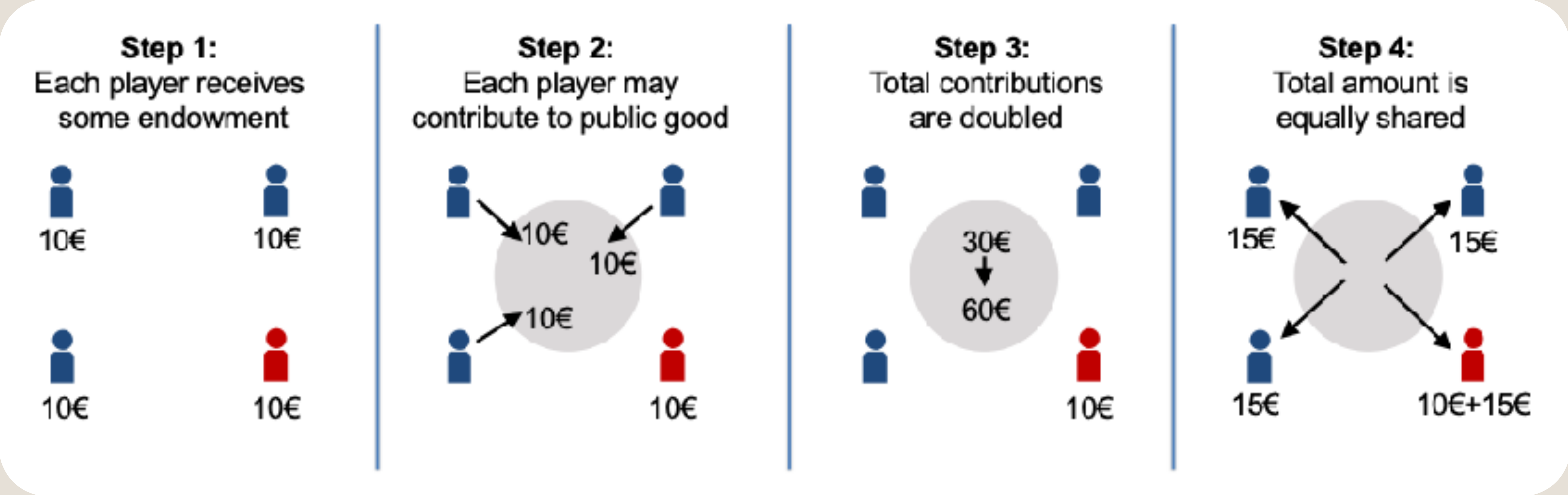

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- Experimental results:
  - Without punishment, cooperation goes down
  - With punishment, cooperation goes up even if participants never meet again (at least in most Western countries)

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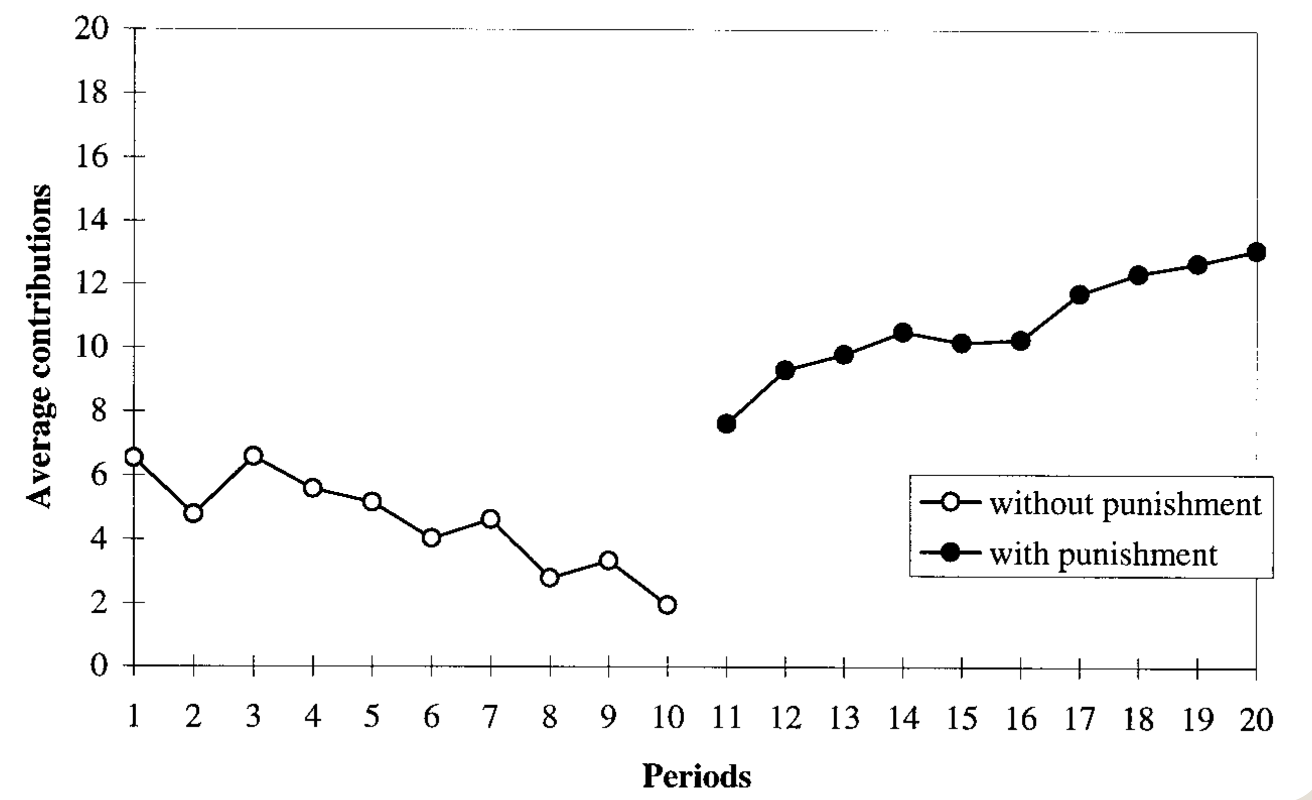

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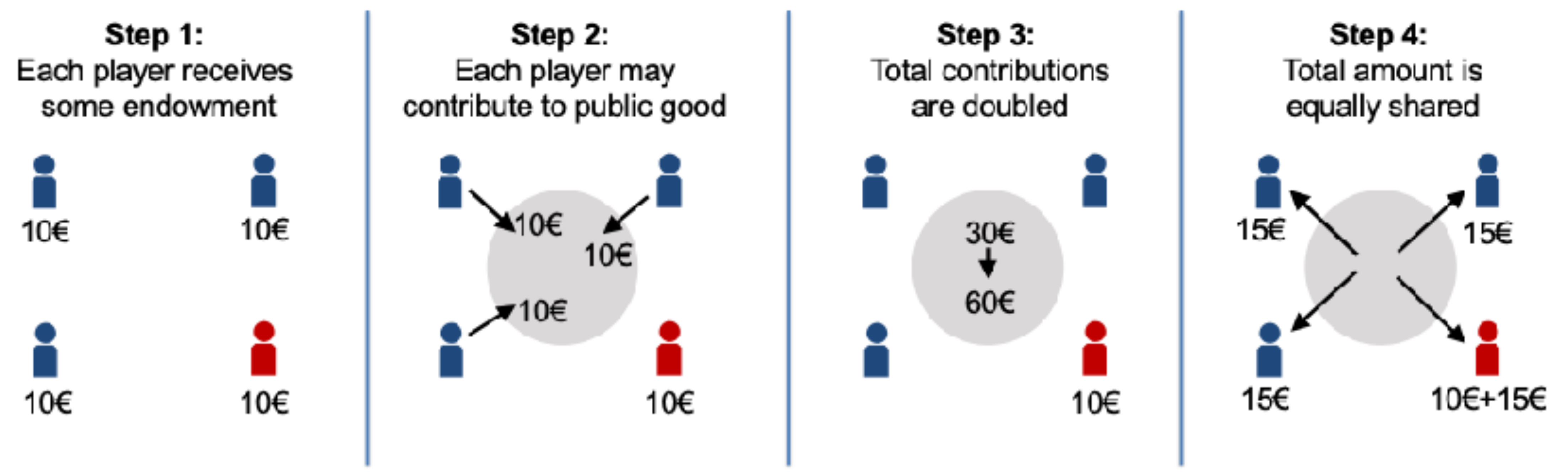

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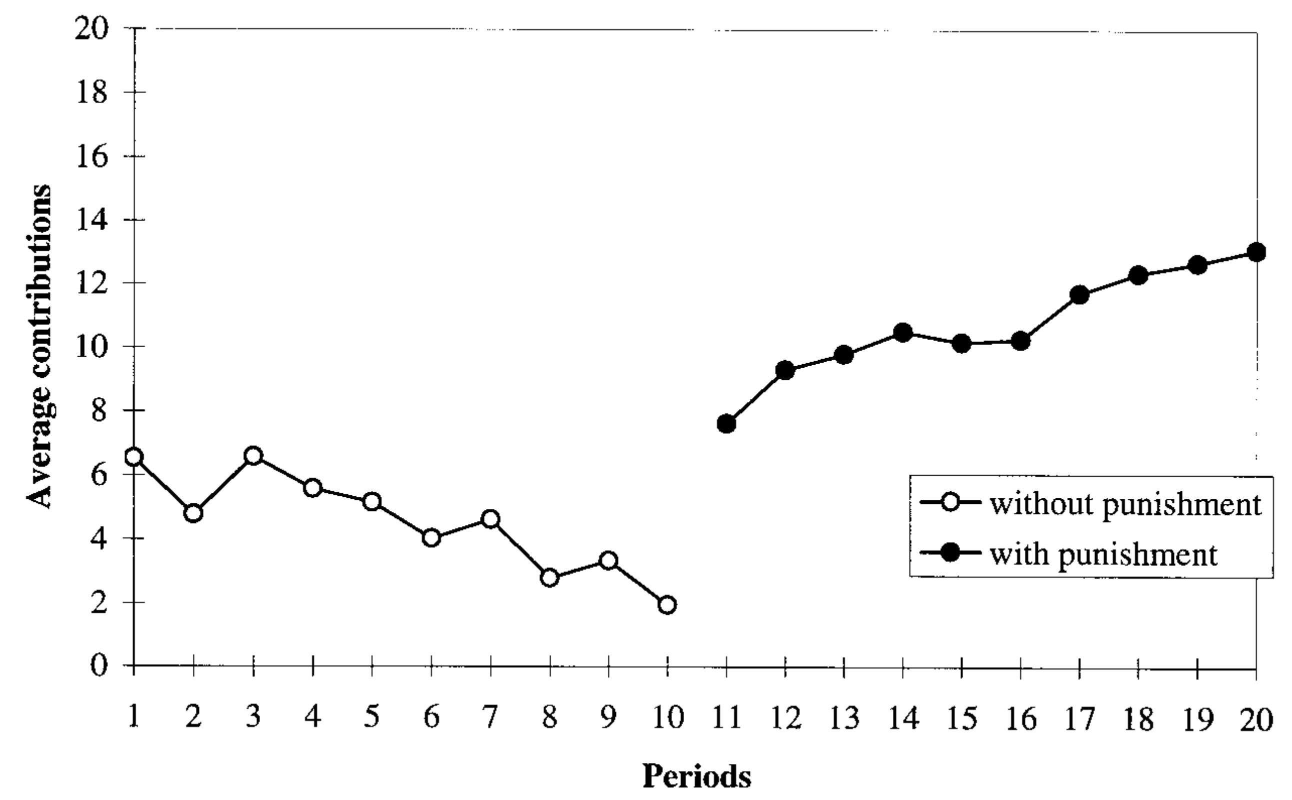

Question: How can we make sense of these behaviors?

An informal introduction: A few examples

Example 3: Signalling (Spence 1973, Zahavi 1973)

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- Two examples:
  - Getting an academic degree without using the respective skills in your job

JOB MARKET SIGNALING *

MICHAEL SPENCE

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Mate Selection—A Selection for a Handicap

AMOTZ ZAHAVI

An informal introduction: A few examples

Example 3: Signalling (Spence 1973, Zahavi 1973)

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- Two examples:
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Question: It has been suggested that these investments can be worthwhile when they act as (costly) signals. But how exactly do such signals work?

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Interesting observation

Not in all examples the respective behaviors and traits are consciously chosen.

An overview

Today's class (March 11, 2025)

- An introduction to evolutionary game theory
  (Replicator dynamics, games in finite populations)

Tomorrow's classes (March 12, 2025)

- Evolution of cooperation & direct reciprocity
- Social norms & indirect reciprocity

Thursday's class (March 13, 2025)

- Some current research: Reciprocity in complex environments

A short reminder: Some (classical) game theory

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Such games can be represented by a (bi)-matrix

	Action 1	…	Action *n*
Action 1	a_{11}, b_{11}	…	a_{1n}, b_{1n}
…	…	…	
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$A=(a_{ij})$ and $B=(b_{ij})$ are the payoff matrices of the two players.

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Definition: Dominated strategies

A pure strategy $\mathbf{e}_i$ for player 1 is called (strictly) dominated if there is a (possibly mixed) strategy $\mathbf{x}$ for player 1 that yields a better payoff, irrespective of the co-player's strategy $\mathbf{e}_j$, $\pi_1(\mathbf{e}_i, \mathbf{e}_j) < \pi_1(\mathbf{x}, \mathbf{e}_j)$ for all $\mathbf{e}_j$.

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Definition: Nash equilibrium

A strategy profile $(\mathbf{x}^*, \mathbf{y}^*)$ is called a Nash equilibrium if the following two conditions hold:

$$\pi_1(\mathbf{x}, \mathbf{y}^*) \leq \pi_1(\mathbf{x}^*, \mathbf{y}^*) \quad \text{for all } \mathbf{x} \in S_m. \qquad (1.13.1)$$

$$\pi_2(\mathbf{x}^*, \mathbf{y}) \leq \pi_2(\mathbf{x}^*, \mathbf{y}^*) \quad \text{for all } \mathbf{y} \in S_n. \qquad (1.13.2)$$

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Dominance solvability and the Nash equilibrium concept appear to make strong assumptions on cognitive abilities. In the following, we explore an approach to game theory that avoids these assumptions.

Evolutionary game theory: An example

Example 1.1: A model of animal conflict (Hawk-Dove)

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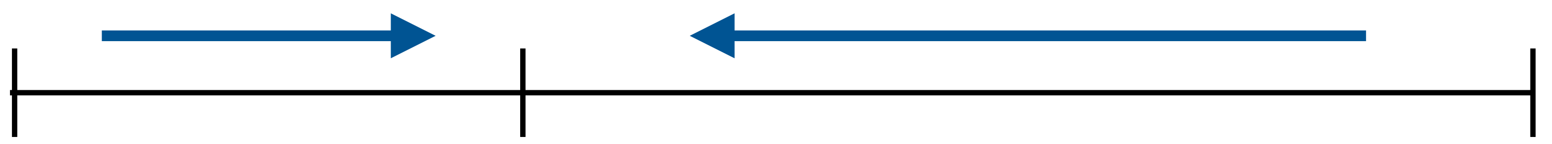

Only doves
$x = 0$

$x = b/c$

Only hawks
$x = 1$

- The larger the cost of serious injuries, the more doves we would expect.

Evolutionary game theory: An example

Example 1.2: Hawk-Dove as a classical game

- We could have also interpreted this interaction as a classical game with payoff matrix

	Hawk	Dove
Hawk	*(b-c)/2*, *(b-c)/2*	*b*, *0*
Dove	*0*, *b*	*b/2*, *b/2*

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- Note that this bi-matrix (A,B) is symmetric, meaning that $A=B^T$. For symmetric games it is common to only depict the first player's payoff.

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	Hawk	Dove
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- The game has exactly one symmetric Nash equilibrium $(\mathbf{x},\mathbf{y})$ with $\mathbf{x}=(x_H, x_D)$ and $\mathbf{y}=(y_H, y_D)$. In this equilibrium, $x_H = y_H = b/c$.

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Remark 1.3: Introducing matrix games for populations

- Consider an infinitely large population
- Individuals in that population can have one of n different traits ("strategies"). Let $\boldsymbol{x} = (x_1, \dots, x_n)^T$ describe the trait distribution in the population.

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- Individuals in that population can have one of n different traits ("strategies"). Let $\boldsymbol{x} = (x_1, \ldots, x_n)^T$ describe the trait distribution in the population.
- When an individual with trait i encounters an individual with trait j, let a_{ij} denote the fitness consequence for individual i. Let $A = (a_{ij})$ be the corresponding matrix.

Evolutionary game theory: An example

Example 1.2: Hawk-Dove as a classical game

- We could have also interpreted this interaction as a classical game with payoff matrix

	Hawk	Dove
Hawk	(b-c)/2, (b-c)/2	b, 0
Dove	0, b	b/2, b/2

- Note that this bi-matrix (A,B) is symmetric, meaning that $A=B^T$. For symmetric games it is common to only depict the first player's payoff.

	Hawk	Dove
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- The game has exactly one symmetric Nash equilibrium $(\boldsymbol{x},\boldsymbol{y})$ with $\boldsymbol{x}=(x_H, x_D)$ and $\boldsymbol{y}=(y_H, y_D)$. In this equilibrium, $x_H = y_H = b/c$.

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$$f_i = \sum_{j=1}^{n} a_{ij}x_j = (A\mathbf{x})_i$$

Evolutionary game theory: An example

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	Hawk	Dove
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Dove	*0, b*	*b/2, b/2*

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- Similarly, the population's average fitness is

$$\bar{f} = \sum_{i=1}^{n} x_i f_i = \mathbf{x}^T A \mathbf{x}$$

Evolutionary game theory: Replicator equation

Definition 1.4: Replicator equation / Replicator dynamics

The replicator equation is the system of ordinary differential equations

$$\dot{x}_i = x_i\big(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})\big) \,.$$

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Proposition 1.5: Properties of replicator dynamics

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$$= \frac{x_i}{x_j}\big(f_i(\mathbf{x}) - f_j(\mathbf{x})\big) < -\delta\left(\frac{x_i}{x_j}\right)$$

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$$= \frac{x_i}{x_j}\big(f_i(\mathbf{x}) - f_j(\mathbf{x})\big) < -\,\delta\left(\frac{x_i}{x_j}\right)$$

Therefore, the fraction x_i/x_j decreases exponentially.

Evolutionary game theory: Classification of 2x2 games

Remark 1.6: On representing the unit simplex

Consider the replicator equation $\dot{x}_i = x_i\big(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})\big)$.
For a game with n strategies in total, this is, in principle, an n-dimensional system. However, we are only interested in those orbits on the unit simplex:

$$S_n = \left\{\mathbf{z} \in \mathbb{R}^n : \; z_i \geq 0 \text{ for all } i \text{ and } \sum_{i=1}^{n} z_i = 1\right\}$$

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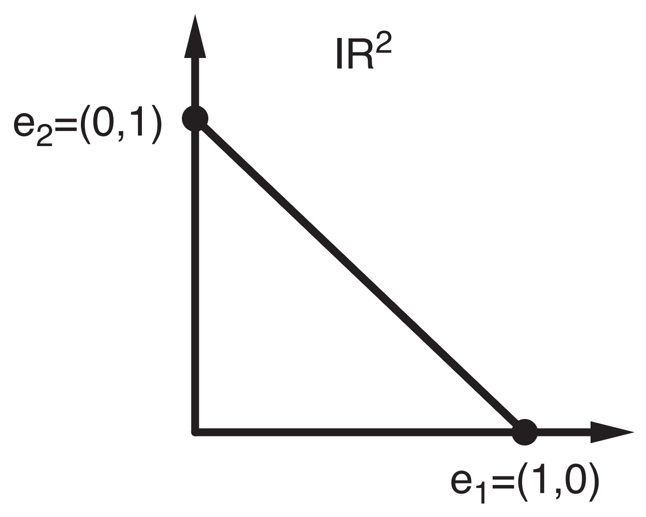

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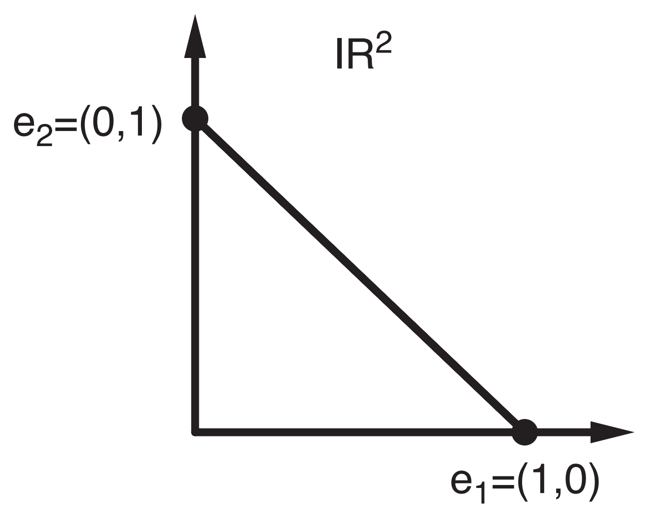

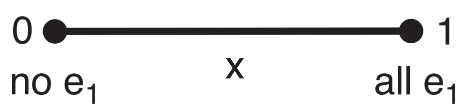

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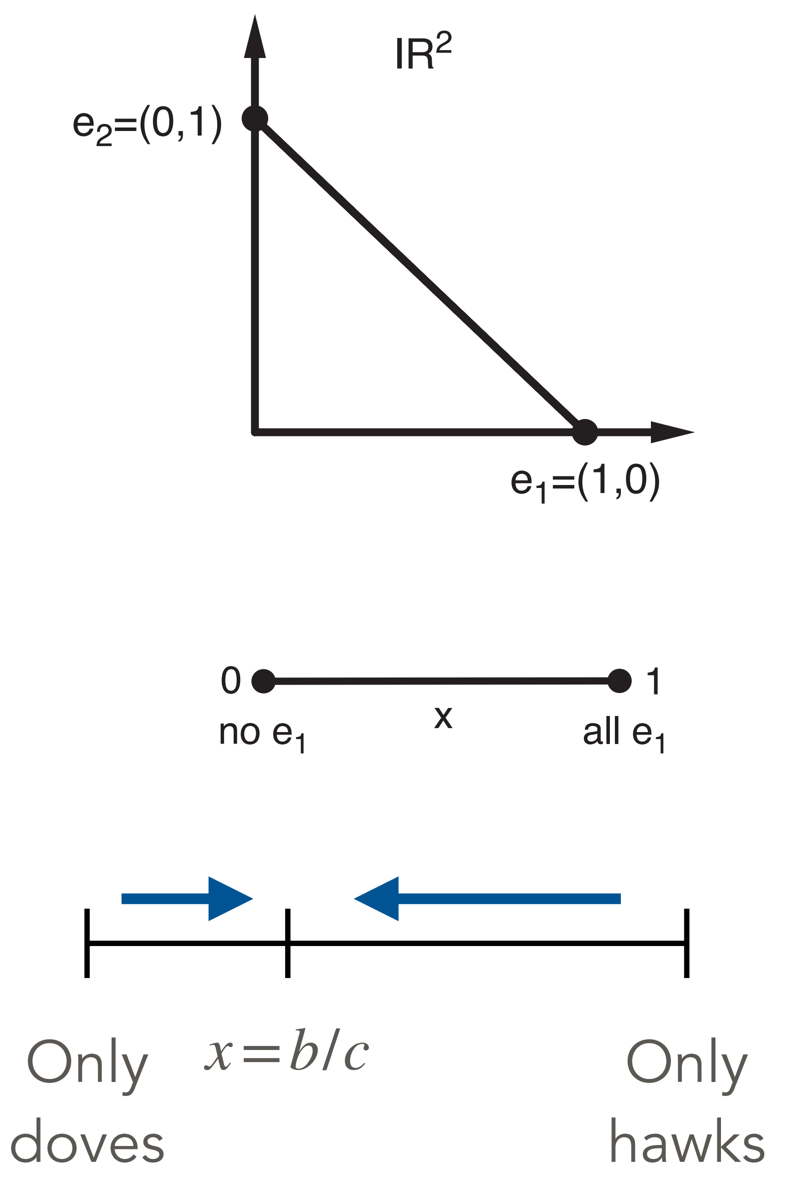

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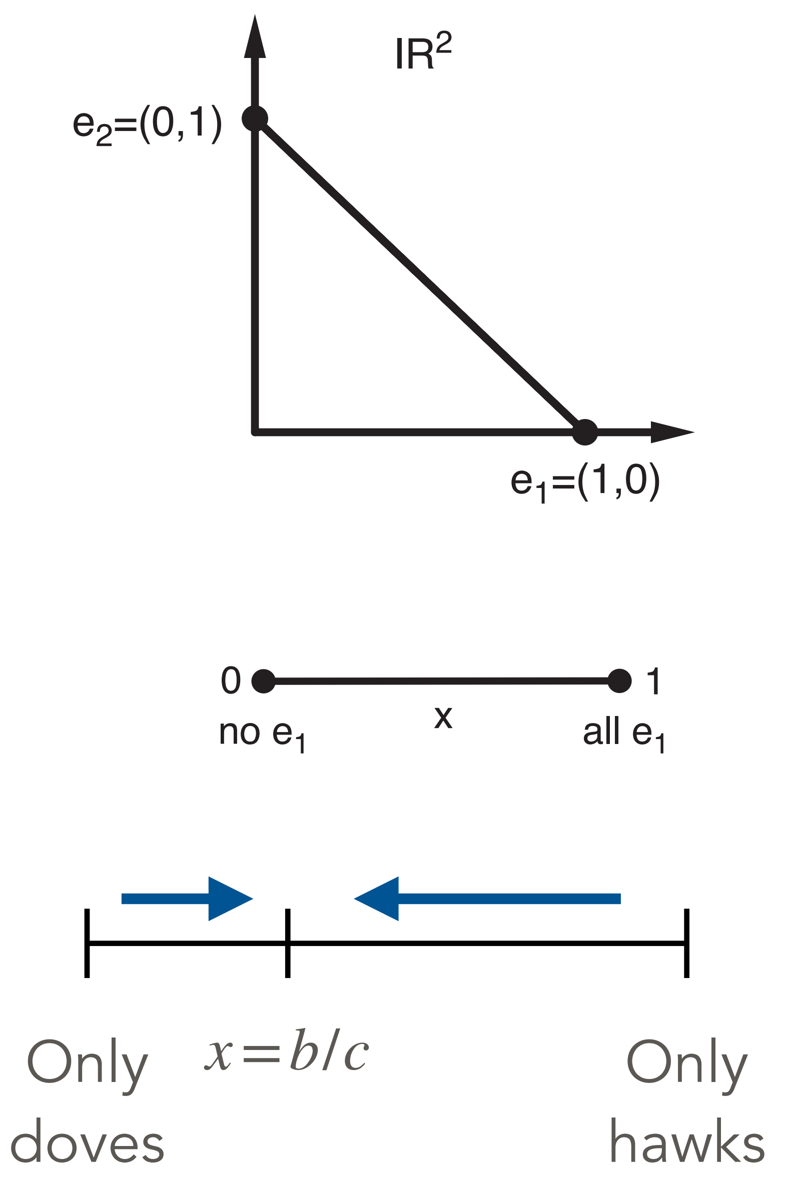
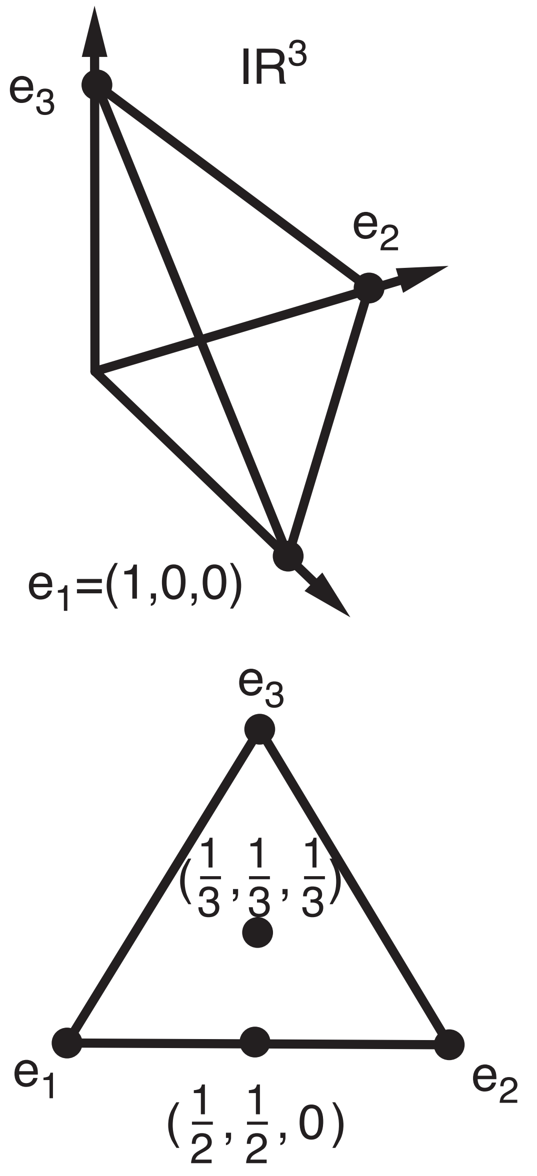


n = 3



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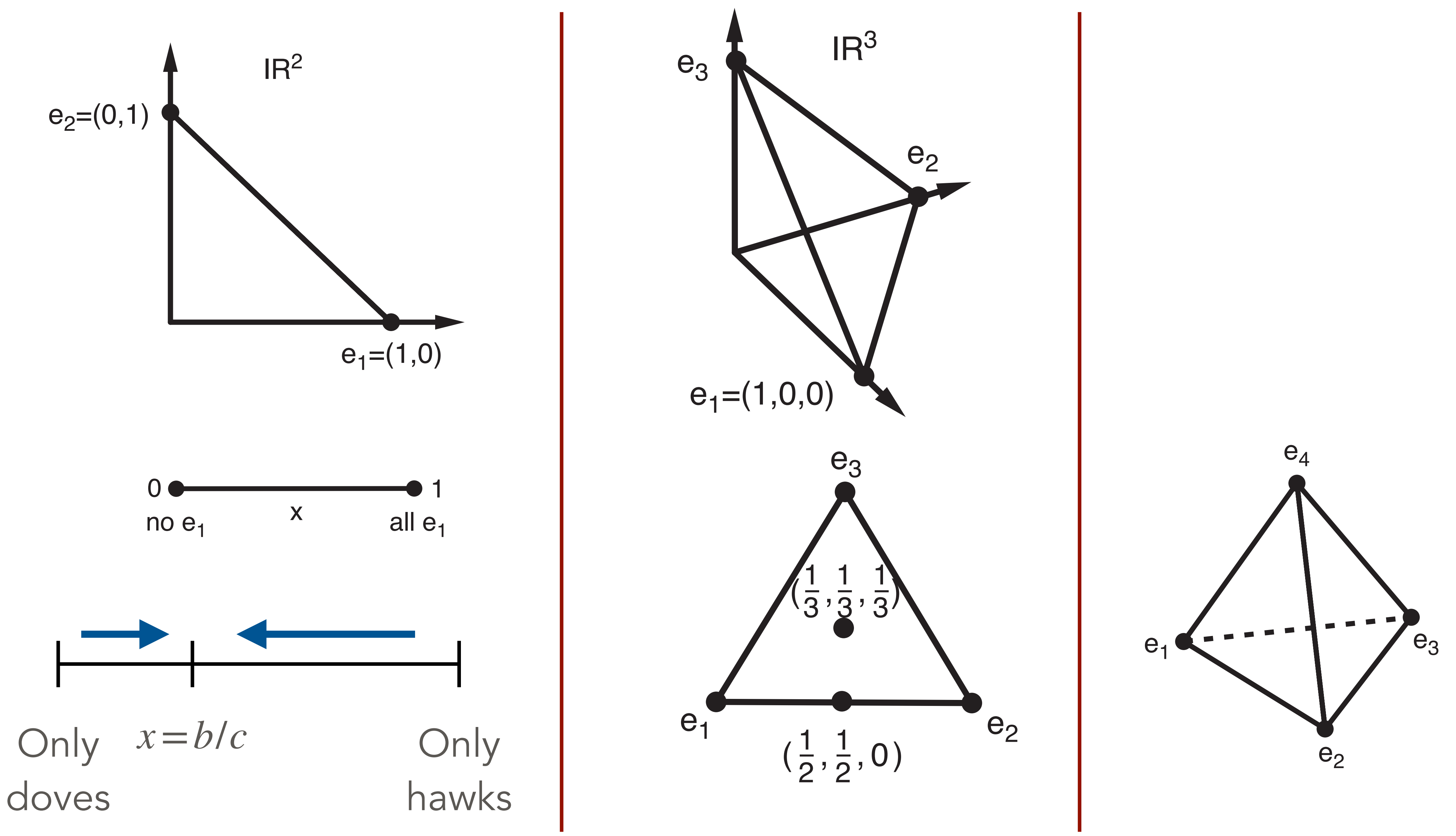
n = 2 | *n = 3* | *n = 4*



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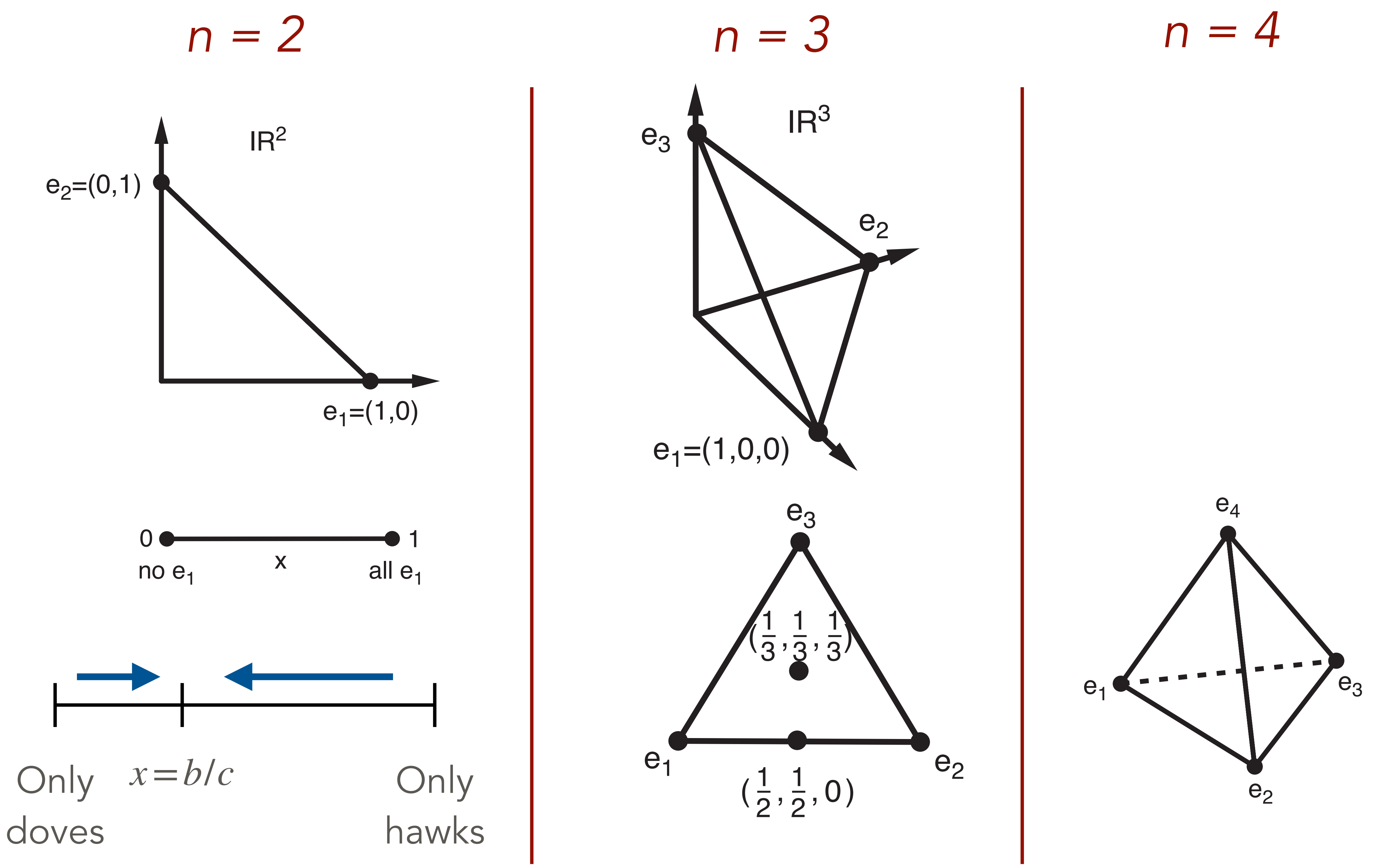

Remark 1.7: A classification of 2x2 games

To get some intuition, let us analyze the simplest non-trivial case: a symmetric game with two strategies:

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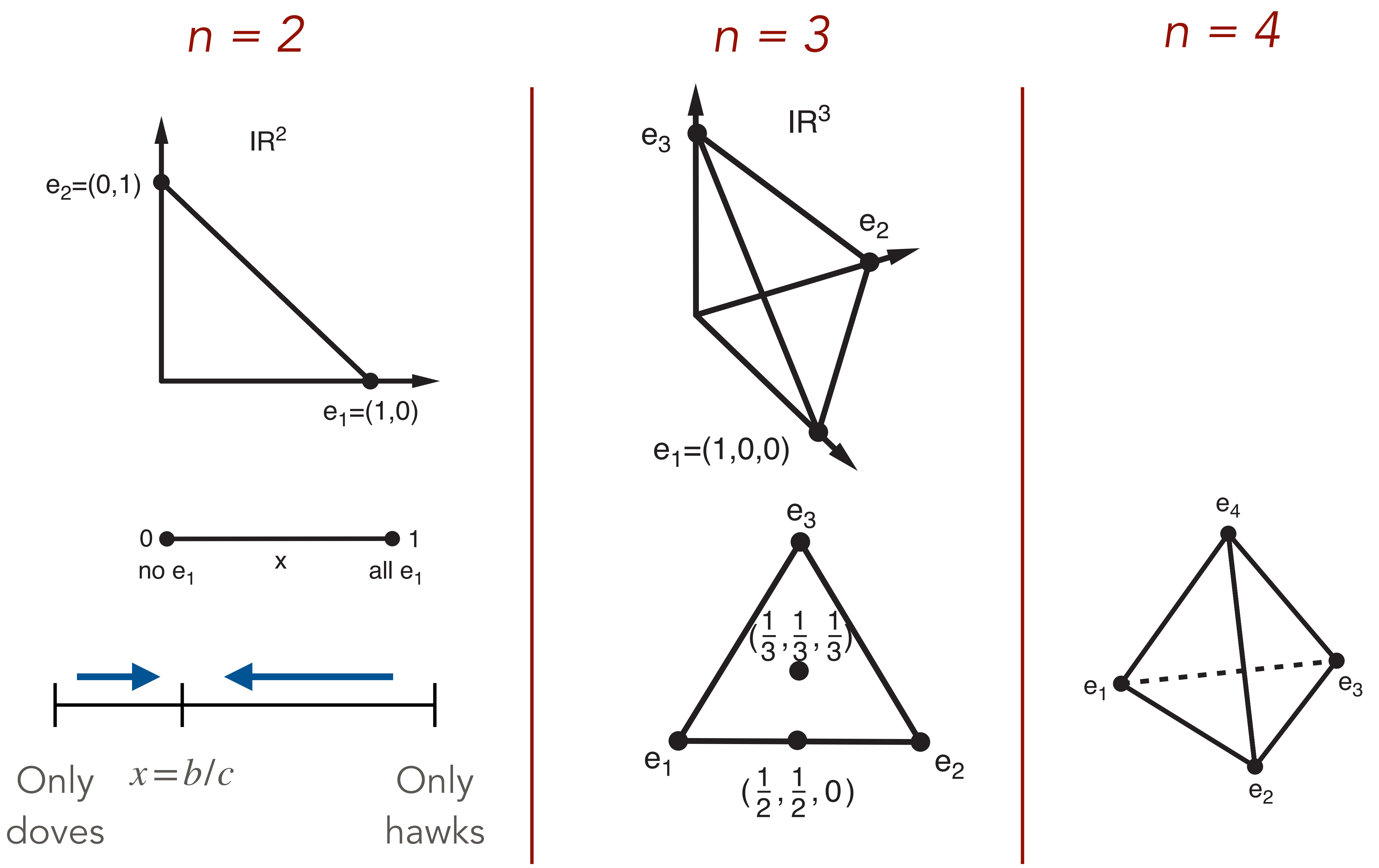

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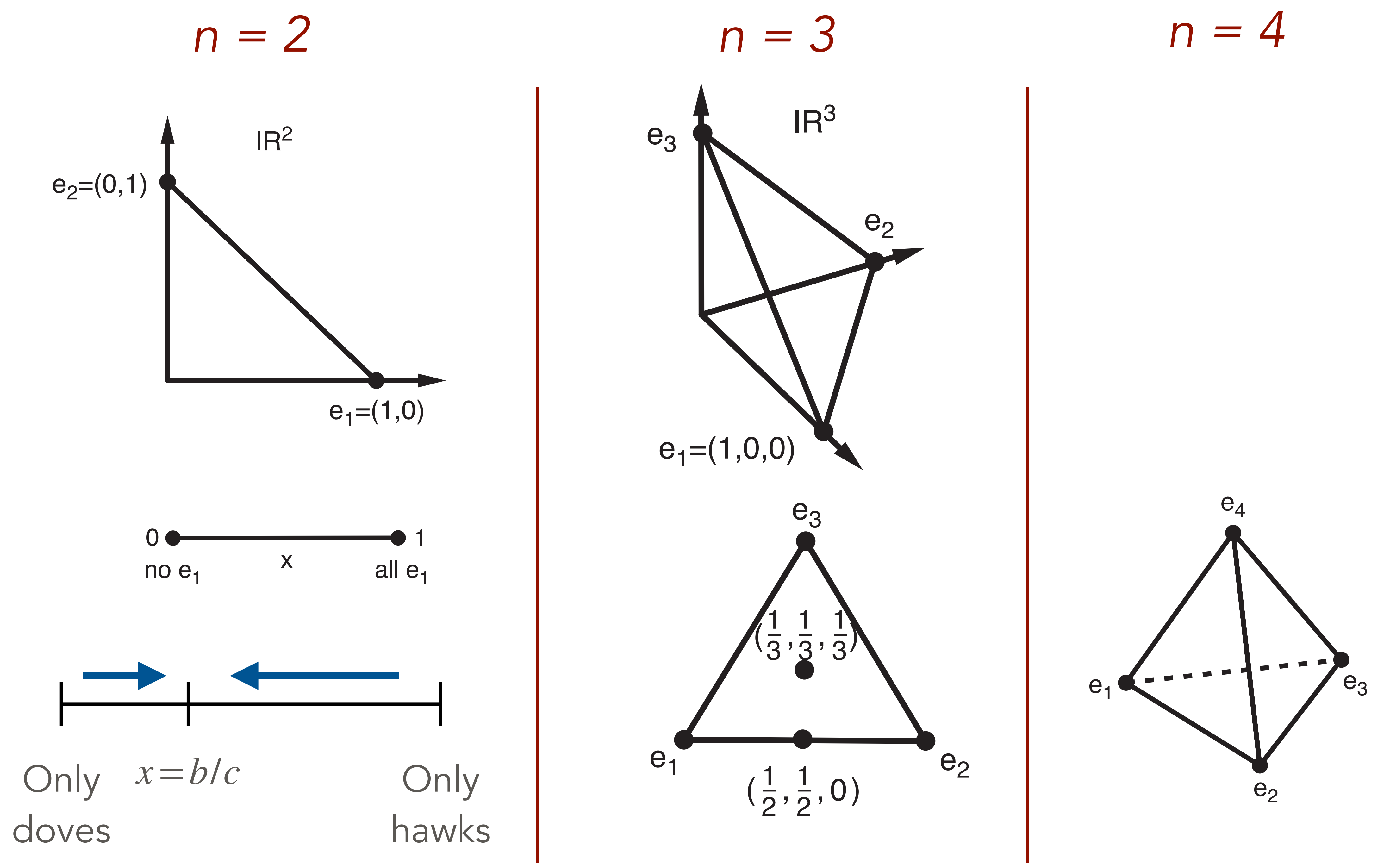

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Evolutionary game theory: Classification of 2x2 games

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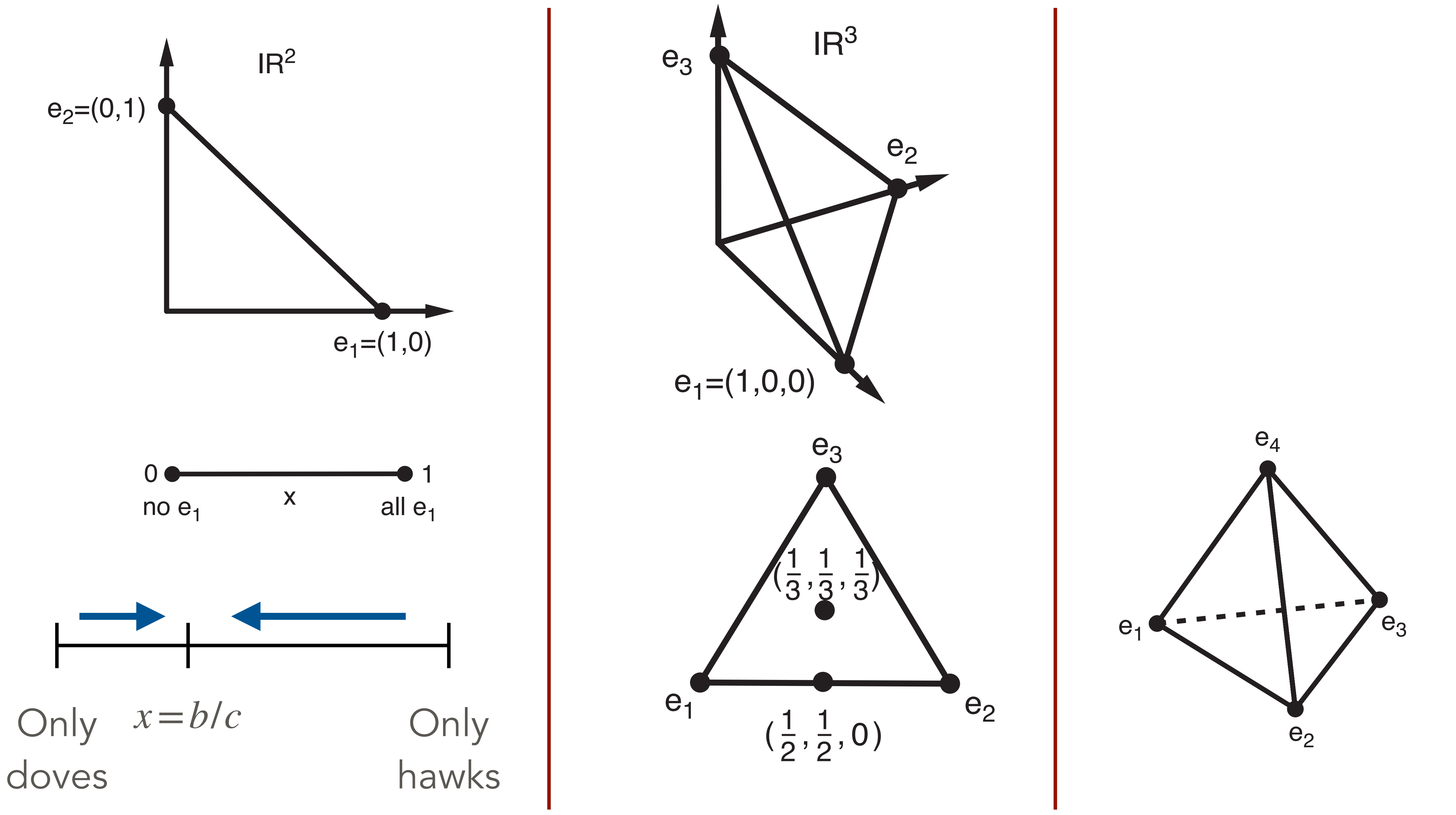
n = 2 *n = 3* *n = 4*



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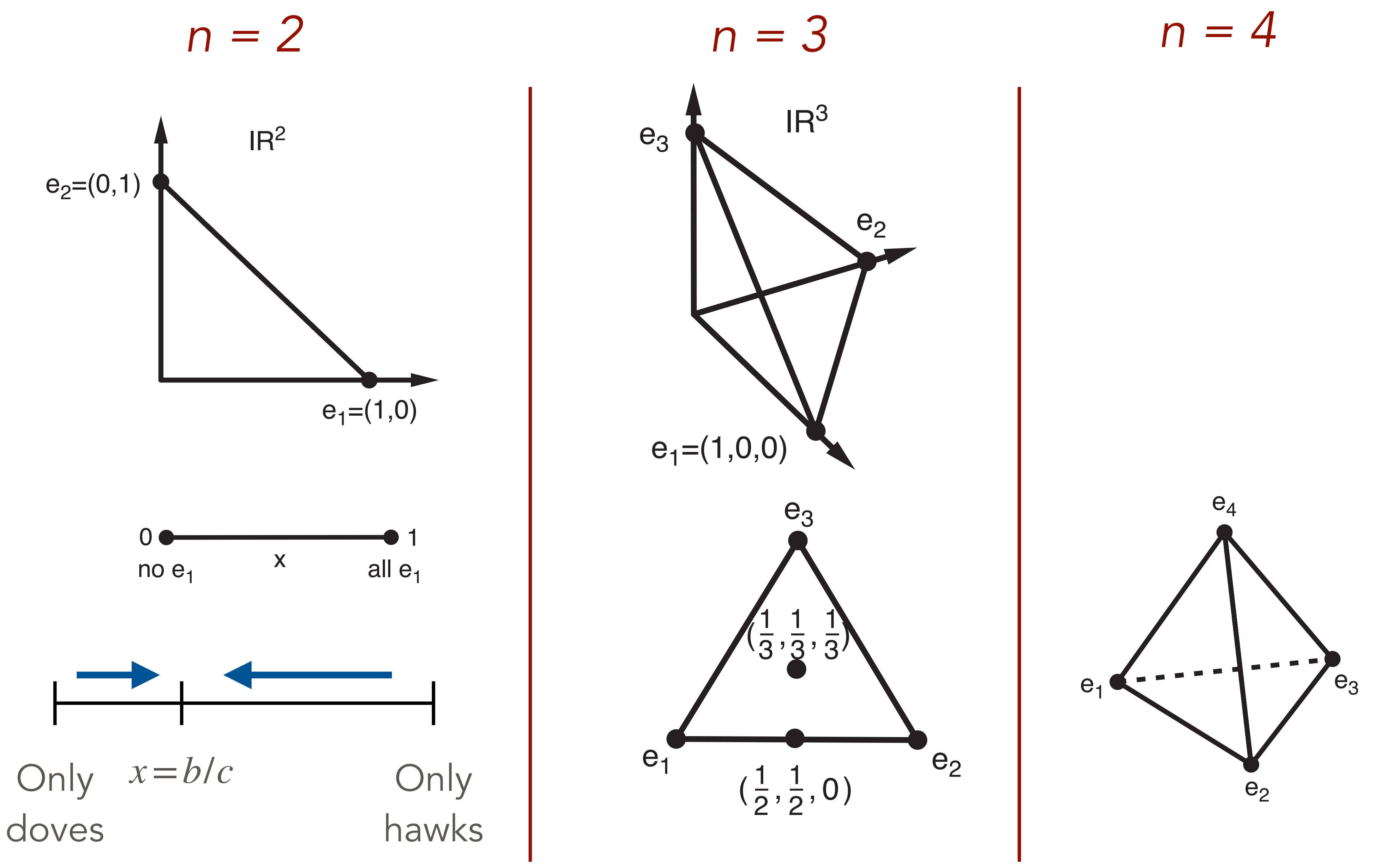

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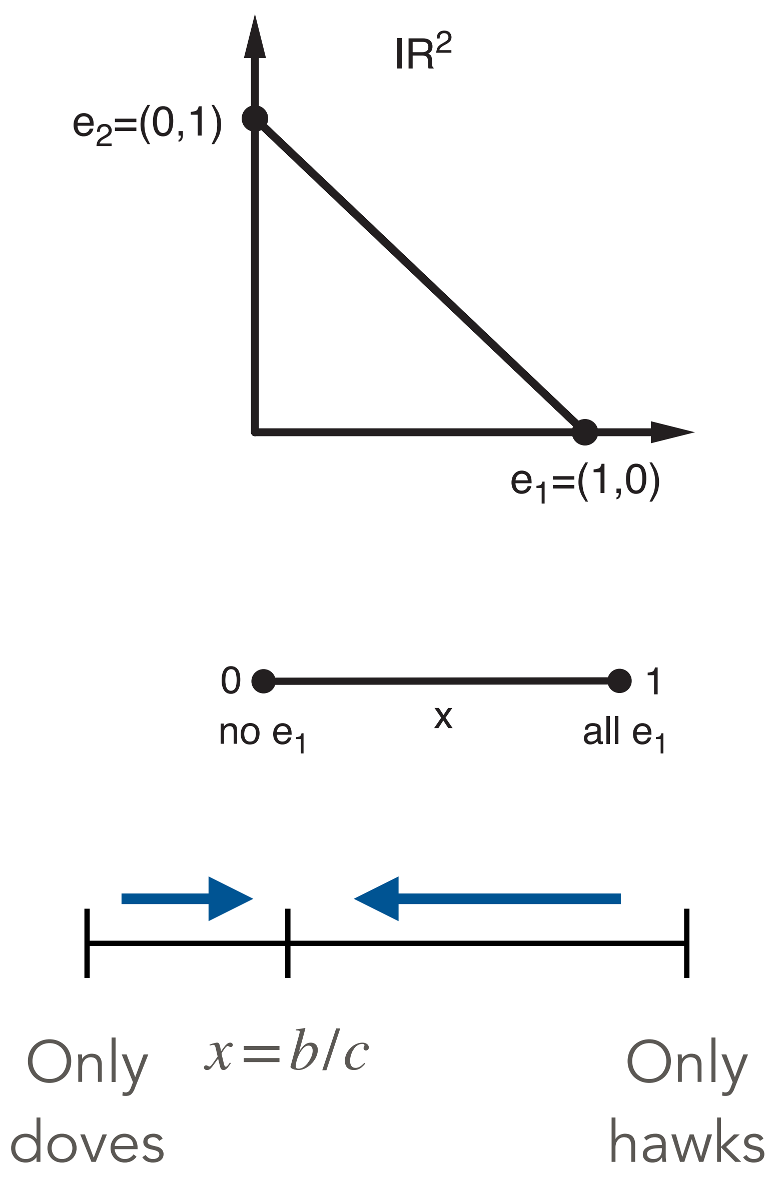

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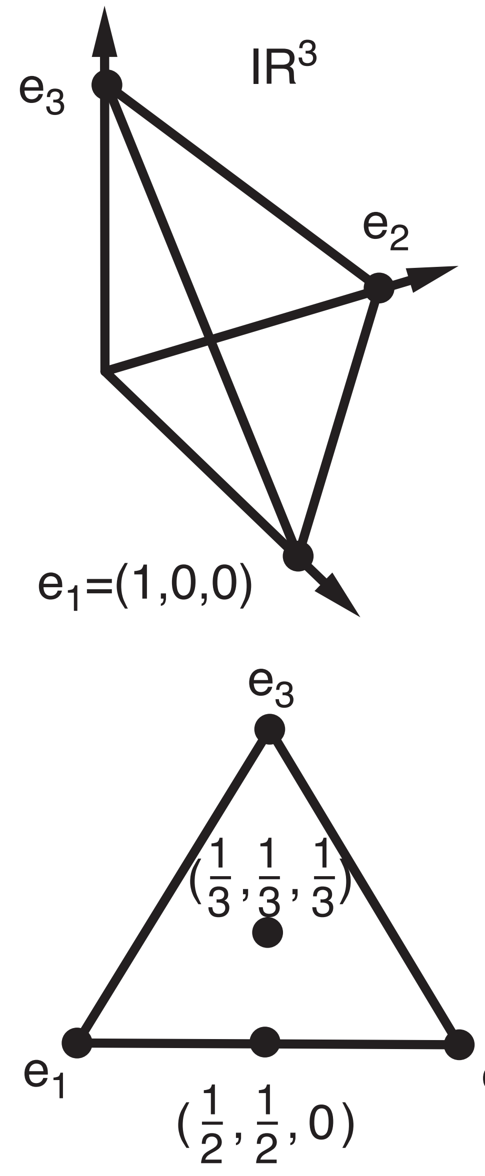

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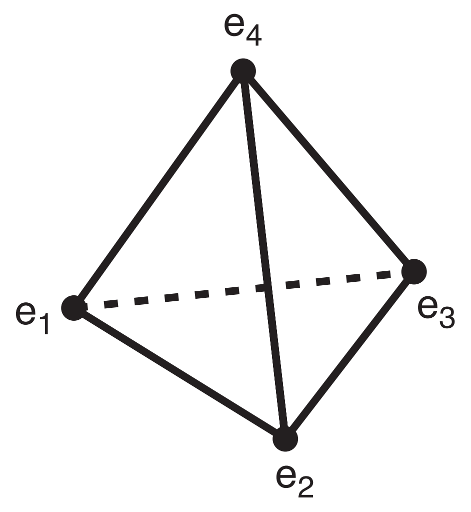

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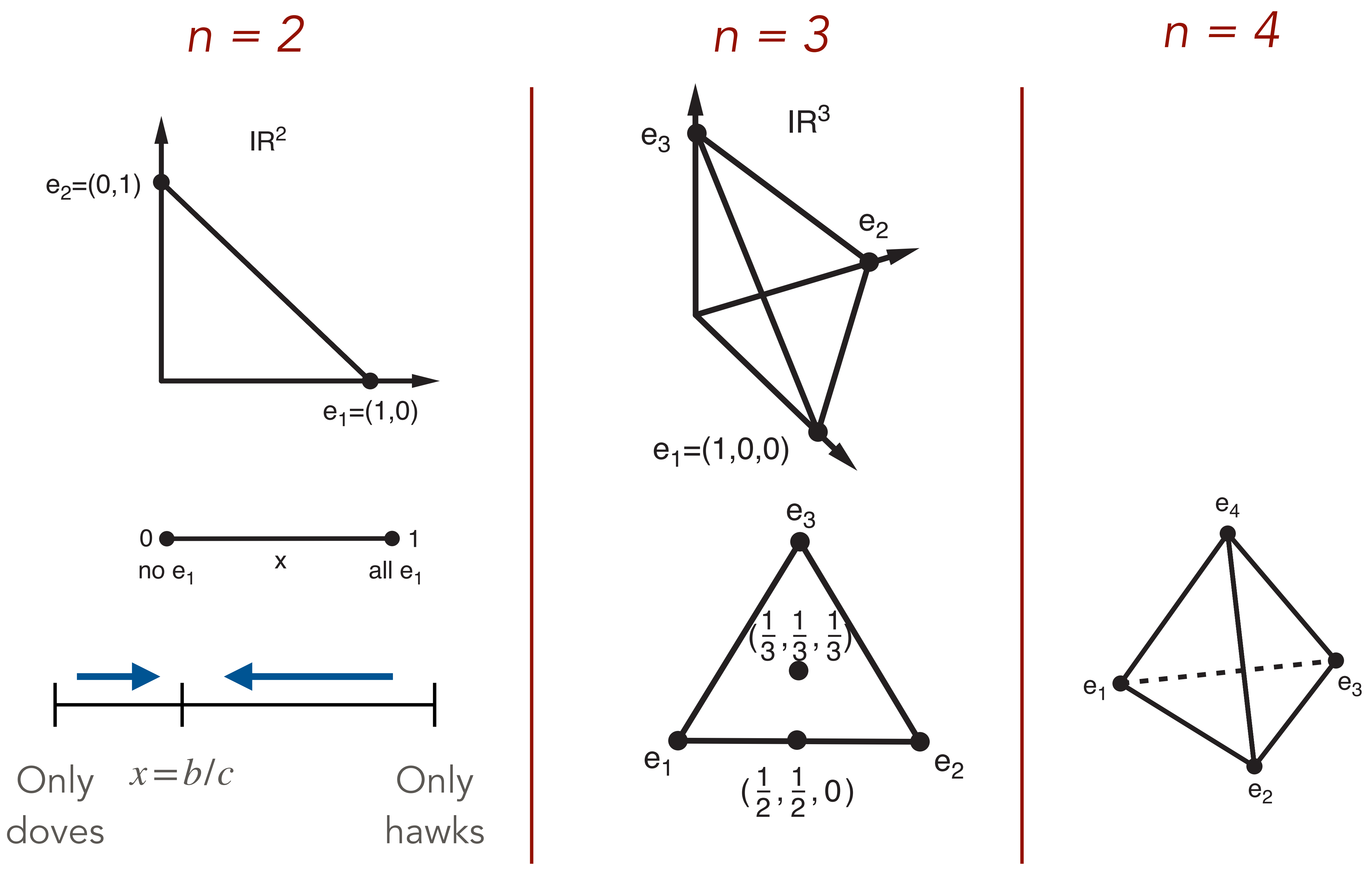

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(2) Interior: $x = \dfrac{d-b}{a-b-c+d}$, if $x \in (0,1)$

Evolutionary game theory: Classification of 2x2 games

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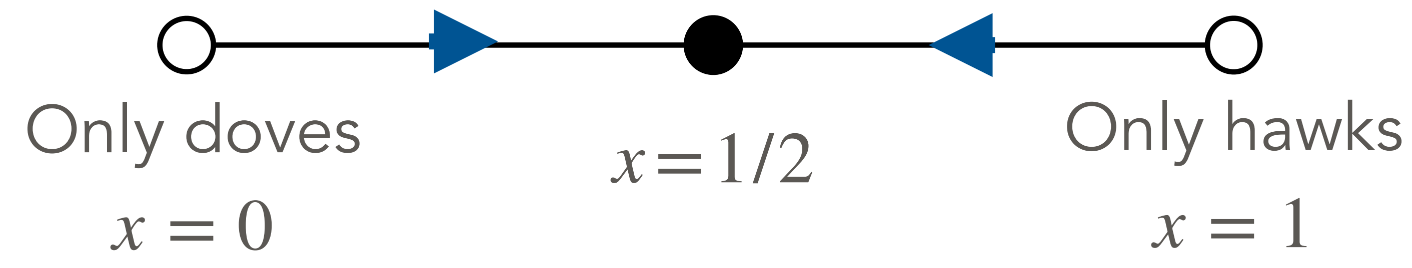

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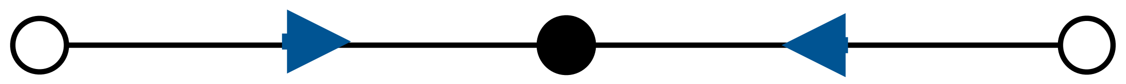

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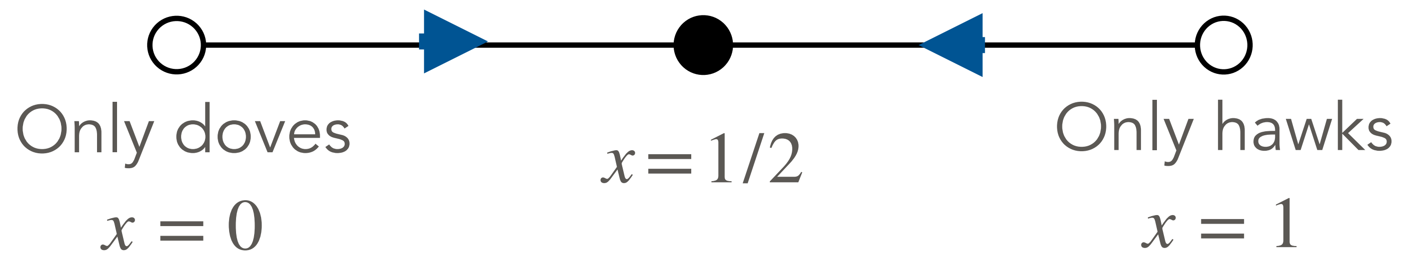

2. Stag-hunt game (coordination game)

	Stag	Hare
Stag	10	0
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Evolutionary game theory: Classification of 2x2 games

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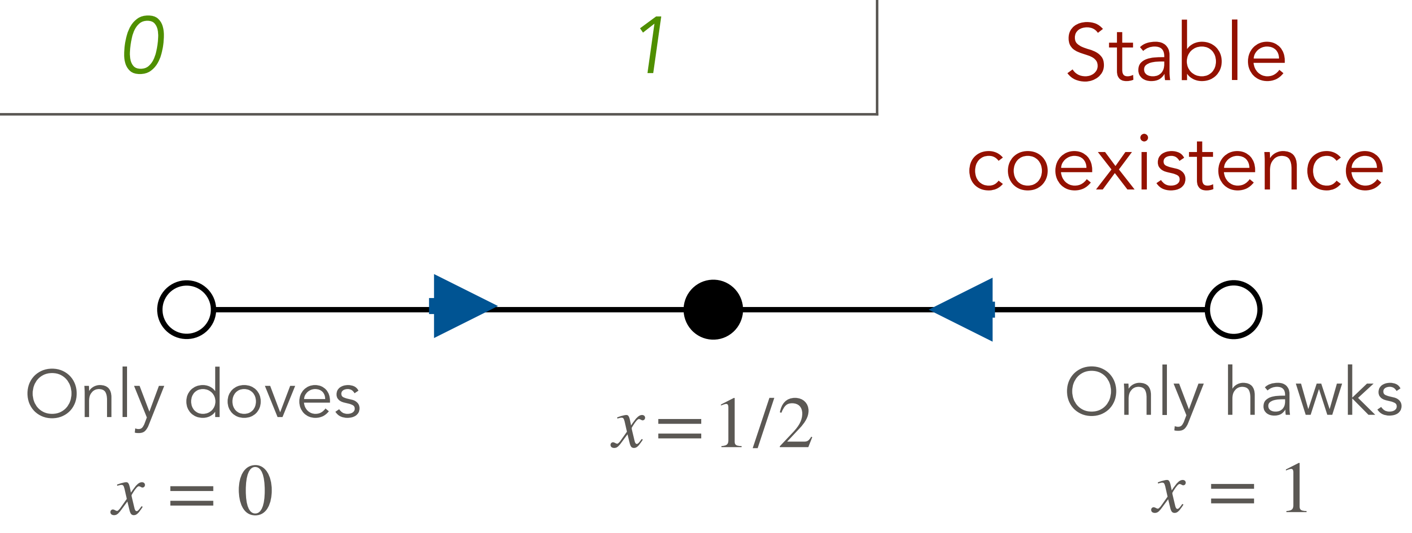

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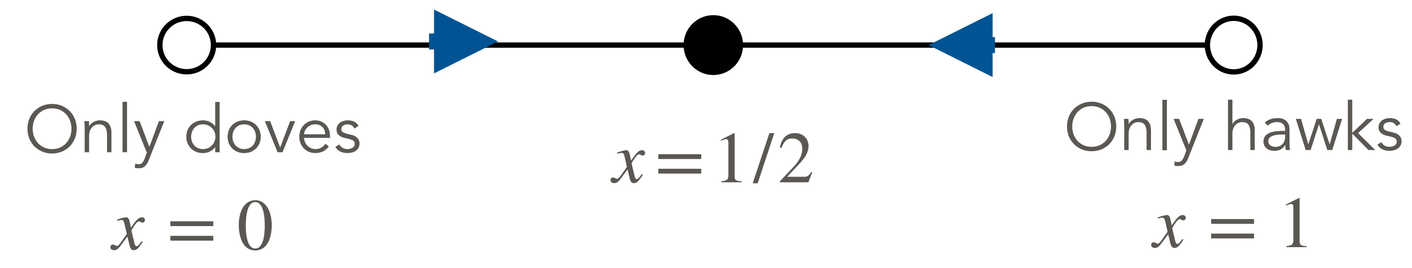

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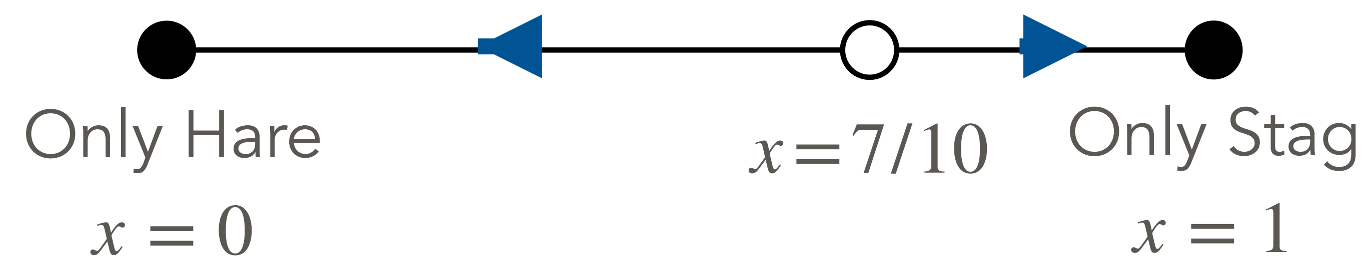

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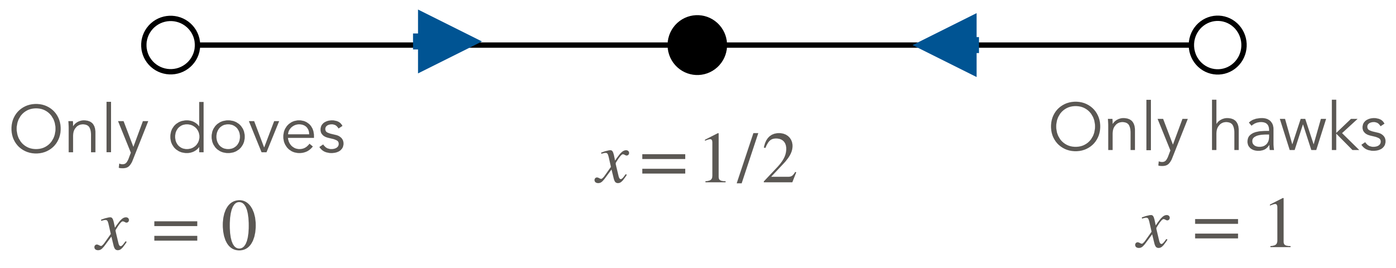

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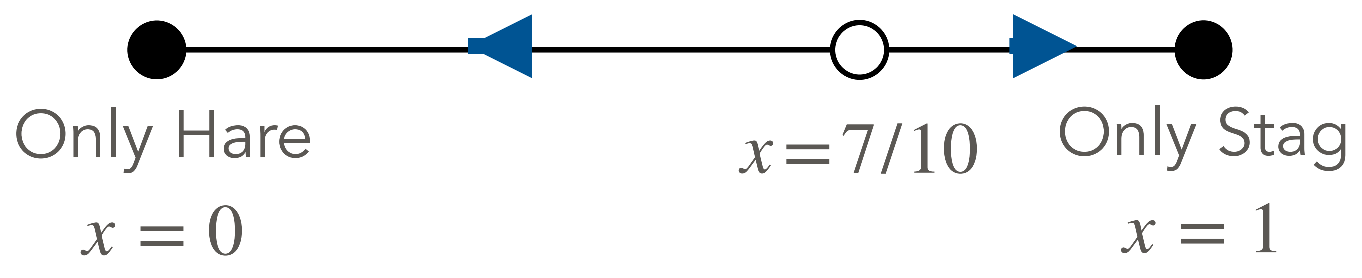

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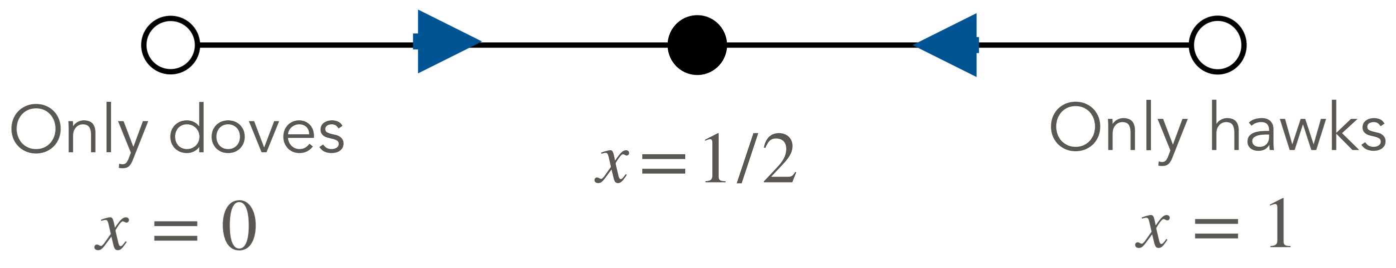

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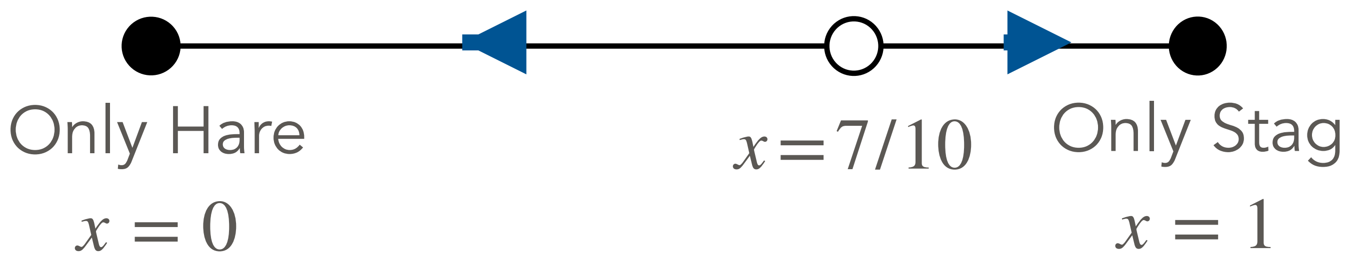

3. Prisoner's dilemma

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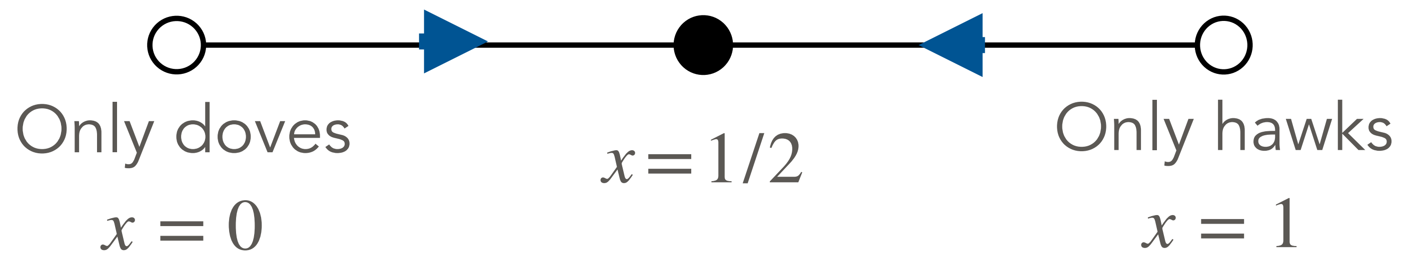

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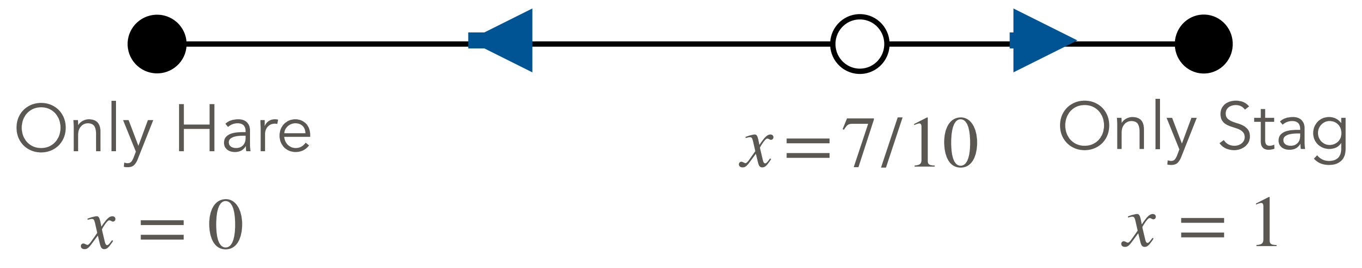

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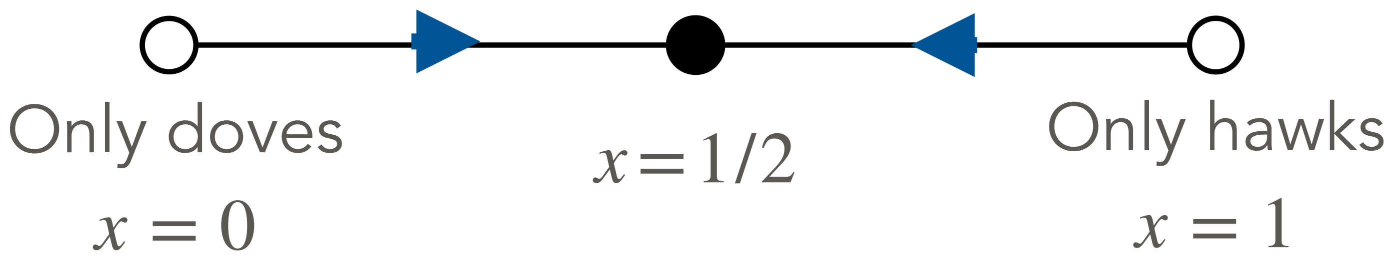

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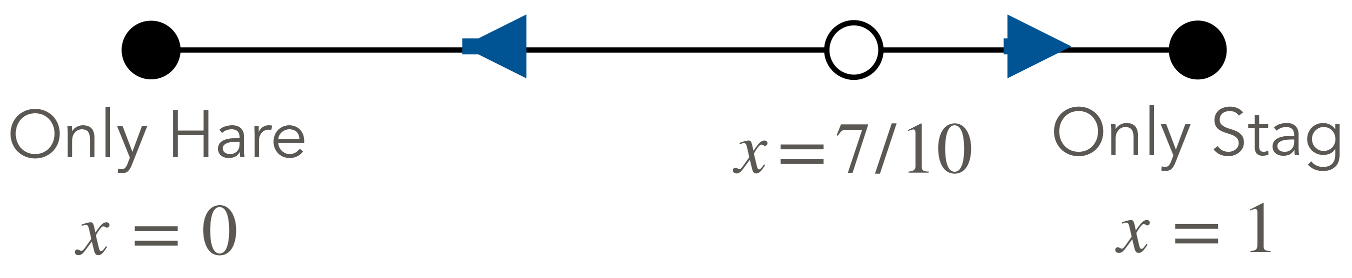

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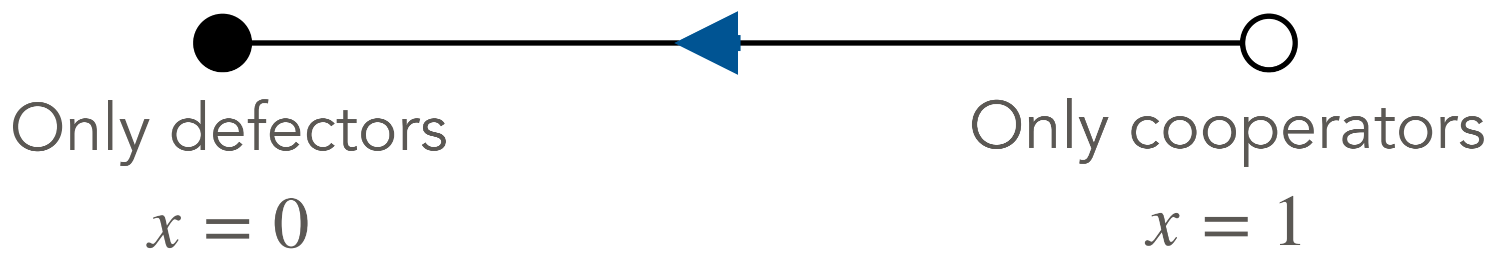

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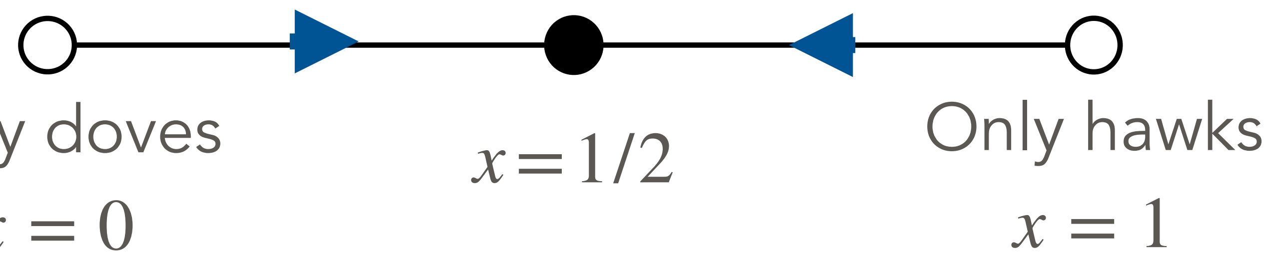

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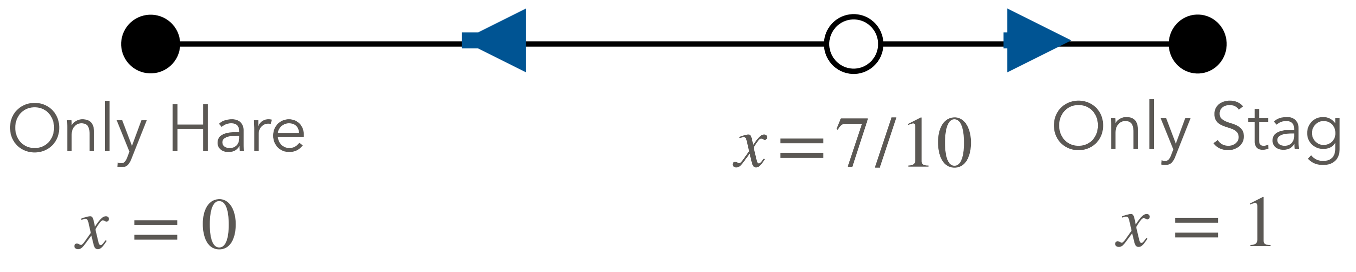

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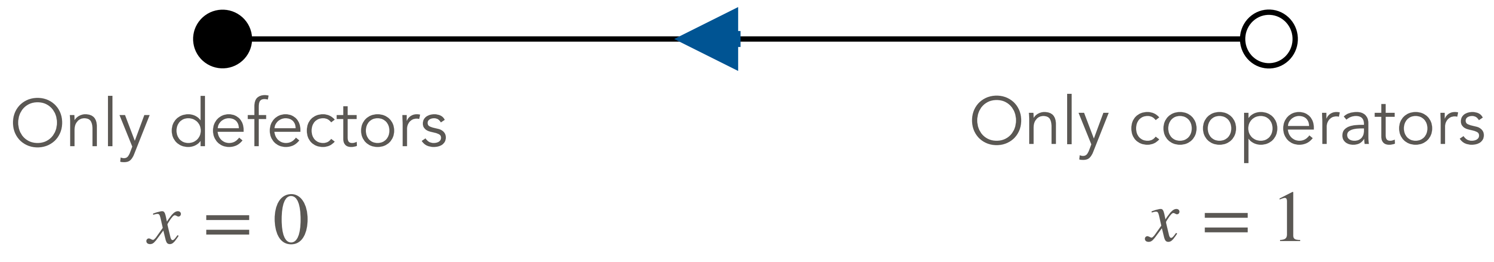

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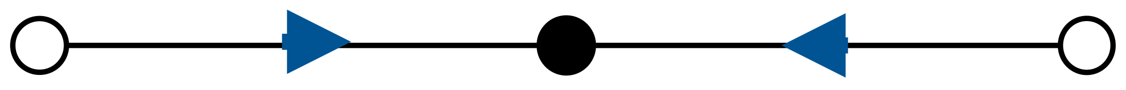

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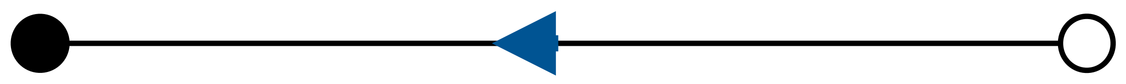

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	Action 1	Action 2
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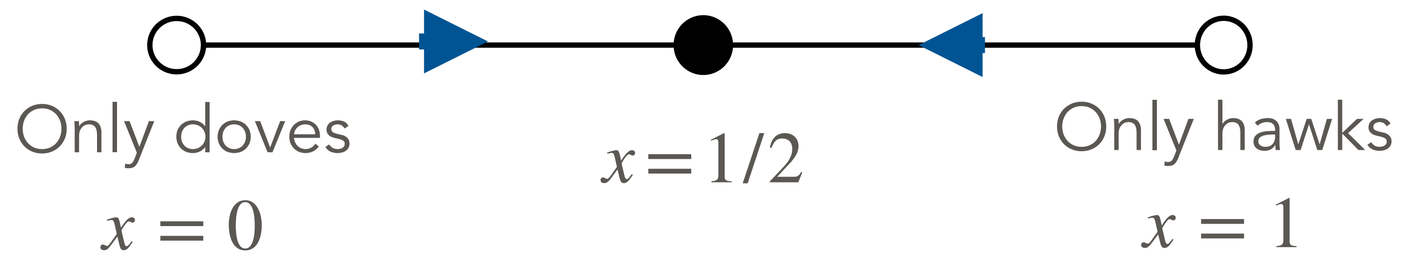

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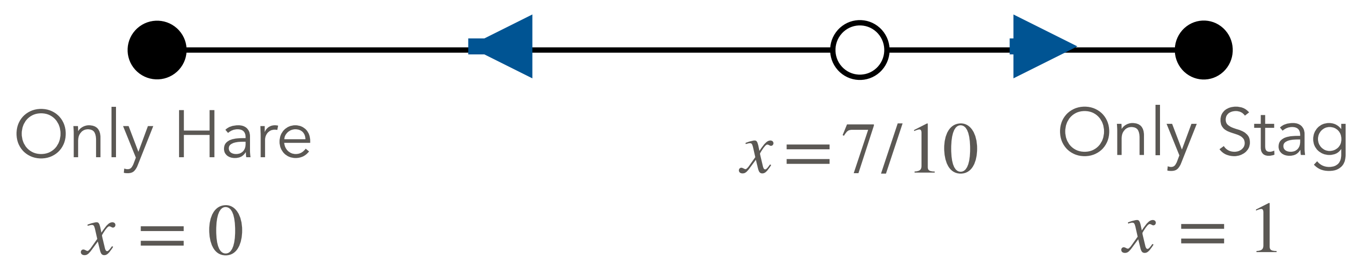

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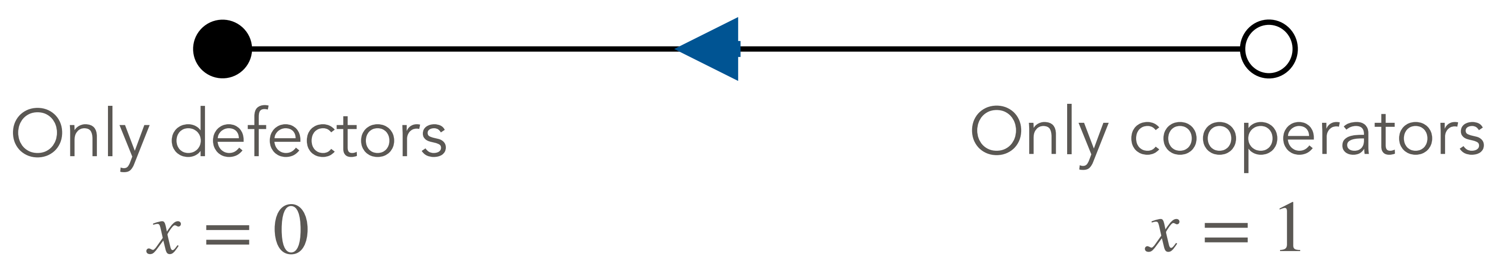

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	Action 1	Action 2
Action 1	*3*	*1*
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$\dot{x} = x(1-x) \cdot 0$

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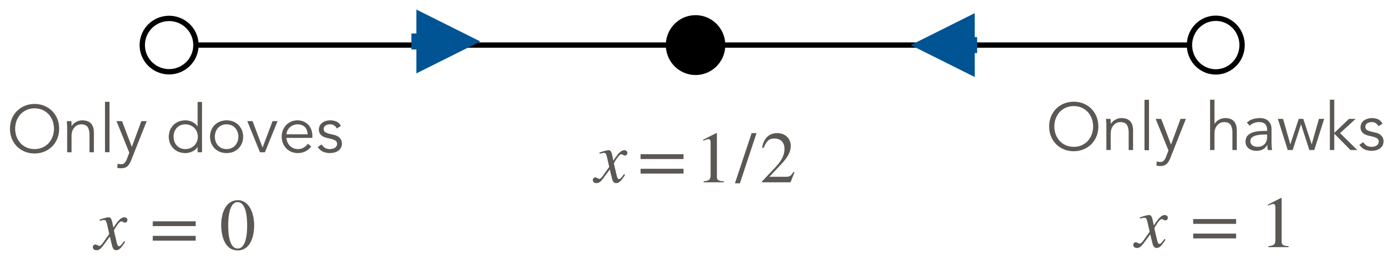

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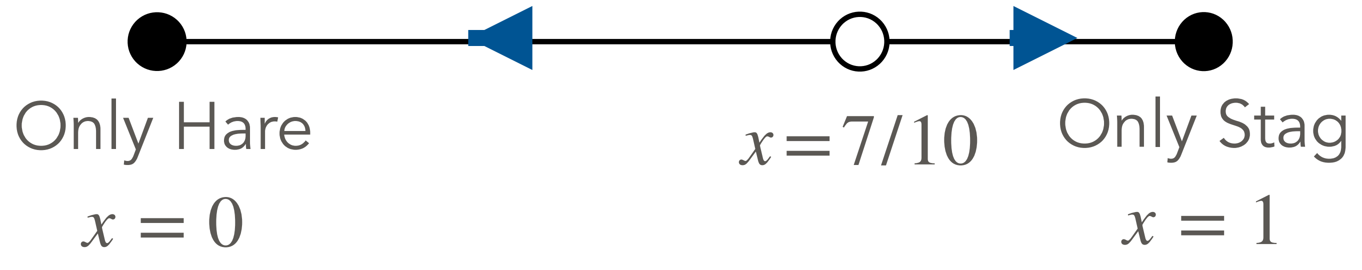

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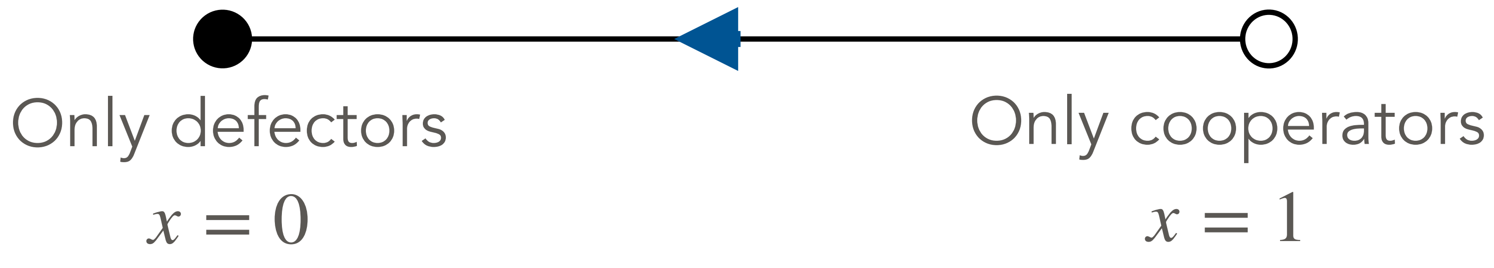

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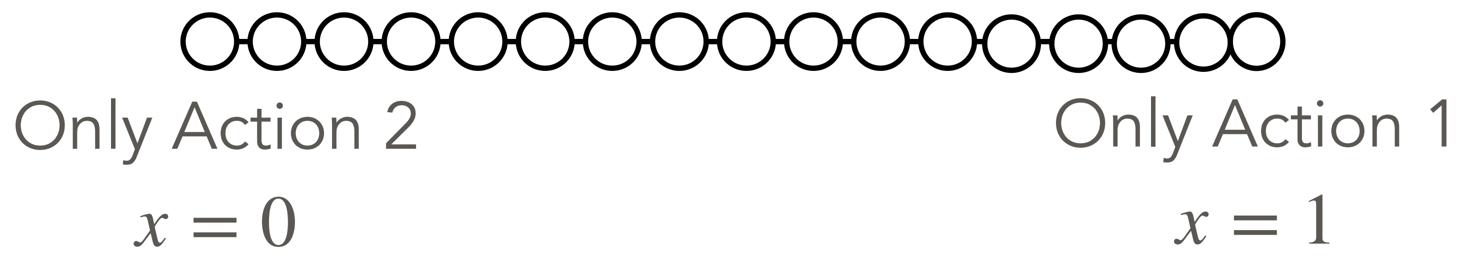

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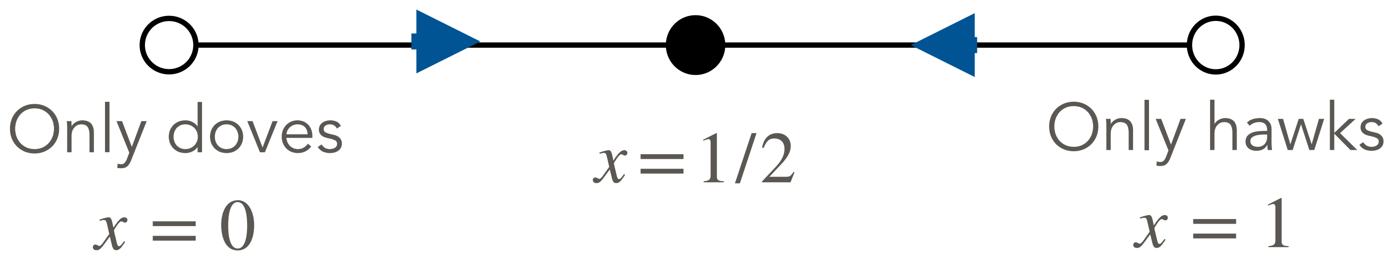
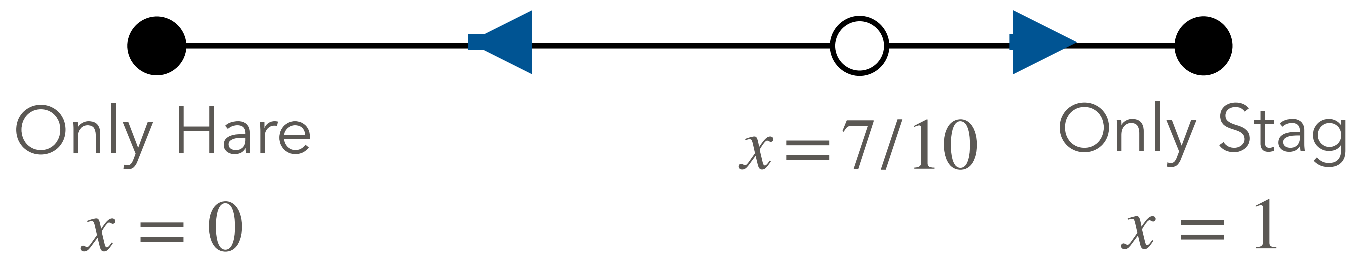


2. Stag-hunt game (coordination game)

	Stag	Hare
Stag	*10*	*0*
Hare	*7*	*7*

Bistability

$\dot{x} = x(1-x)(10x-7)$

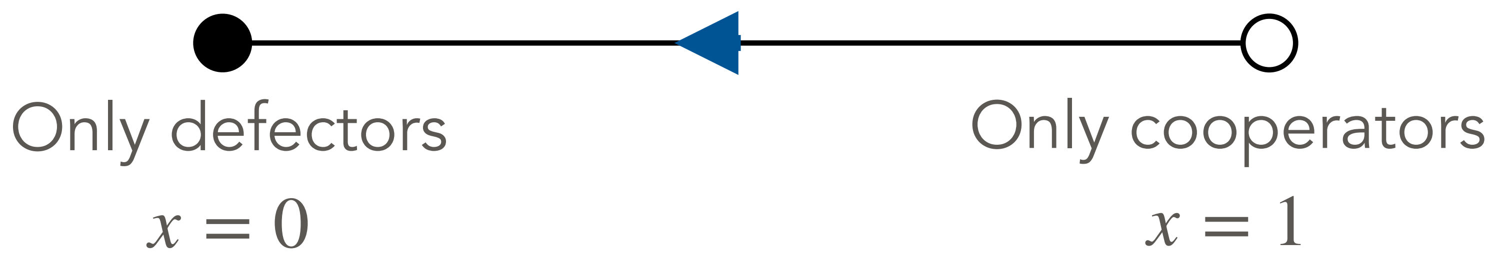


3. Prisoner's dilemma

	Cooperate	Defect
Cooperate	*2*	*-1*
Defect	*3*	*0*

Dominance

$\dot{x} = x(1-x)(-1)$

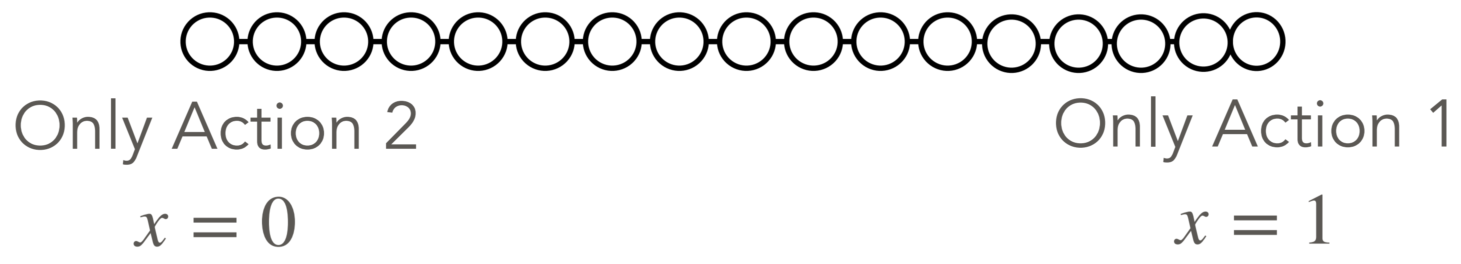


4. A trivial game

	Action 1	Action 2
Action 1	*3*	*1*
Action 2	*3*	*1*

Neutrality

$\dot{x} = x(1-x) \cdot 0$



Evolutionary game theory: Classification of 2x2 games

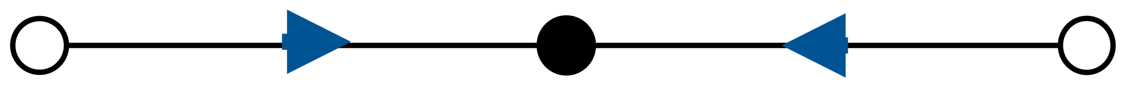
Examples 1.8: Some 2x2 games

1. The hawk-dove game (with b=2, c=4)

	Hawk	Dove
Hawk	*-1*	*2*
Dove	*0*	*1*

Stable coexistence

$\dot{x} = x(1-x)(1-2x)$



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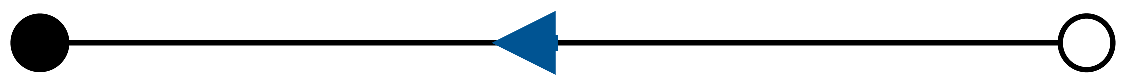

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	Action 1	Action 2
Action 1	*3*	*1*
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Neutrality

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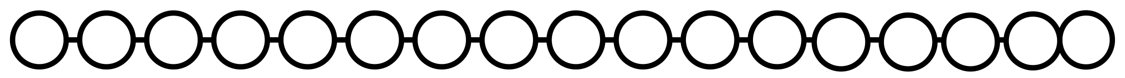

Qualitatively, these are all possible cases.

Evolutionary game theory: An example of a 3x3 game

Example 1.9. A 3x3 game: The volunteer's timing dilemma

Consider the following variant of a so-called volunteer's dilemma. There are two players; at least one of them should volunteer to do a task that benefits both of them.

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Replicator dynamics, $\mathbf{x} = (x_C, x_W, x_D)$

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Replicator dynamics, $\mathbf{x} = (x_C, x_W, x_D)$

1. **Dynamics at the edges:**
   - No defectors ($x_D = 0$): Coexistence among cooperators and wait & see, $\mathbf{x}^*_{CW} = (1/4, 3/4, 0)$
   - No wait&see ($x_W = 0$): Coexistence among cooperators and defectors, $\mathbf{x}^*_{CD} = (2/5, 0, 3/5)$
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   - No cooperators ($x_C = 0$): Coexistence among wait&see and defectors, $\mathbf{x}^*_{WD} = (0, 1/4, 3/4)$

2. **Fixed point in the interior:**

   If $\dot{x}_i = x_i\big(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})\big)$ has a fixed point with $x_i > 0 \ \forall i$, it must hold that $f_i(\mathbf{x}) = \bar{f}(\mathbf{x}) \ \forall i$.
   Equivalently, it must hold that $f_1(\mathbf{x}) = f_2(\mathbf{x}) = f_3(\mathbf{x})$.
   This is a simple linear system (and either has 0, 1, or infinitely many solutions).

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   Equivalently, it must hold that $f_1(\mathbf{x}) = f_2(\mathbf{x}) = f_3(\mathbf{x})$.
   This is a simple linear system (and either has 0, 1, or infinitely many solutions).
   In our case, solution: $\mathbf{x}^*_{\text{int}} = (1/4, 3/16, 9/16)$.

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

3. **Local stability analysis for the fixed points**

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

3. Local stability analysis for the fixed points

- For the equilibria on the edges, in each case it is true that the missing strategy can invade when rare.

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

3. Local stability analysis for the fixed points

- For the equilibria on the edges, in each case it is true that the missing strategy can invade when rare.
- The interior equilibrium is stable.

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

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- For the equilibria on the edges, in each case it is true that the missing strategy can invade when rare.
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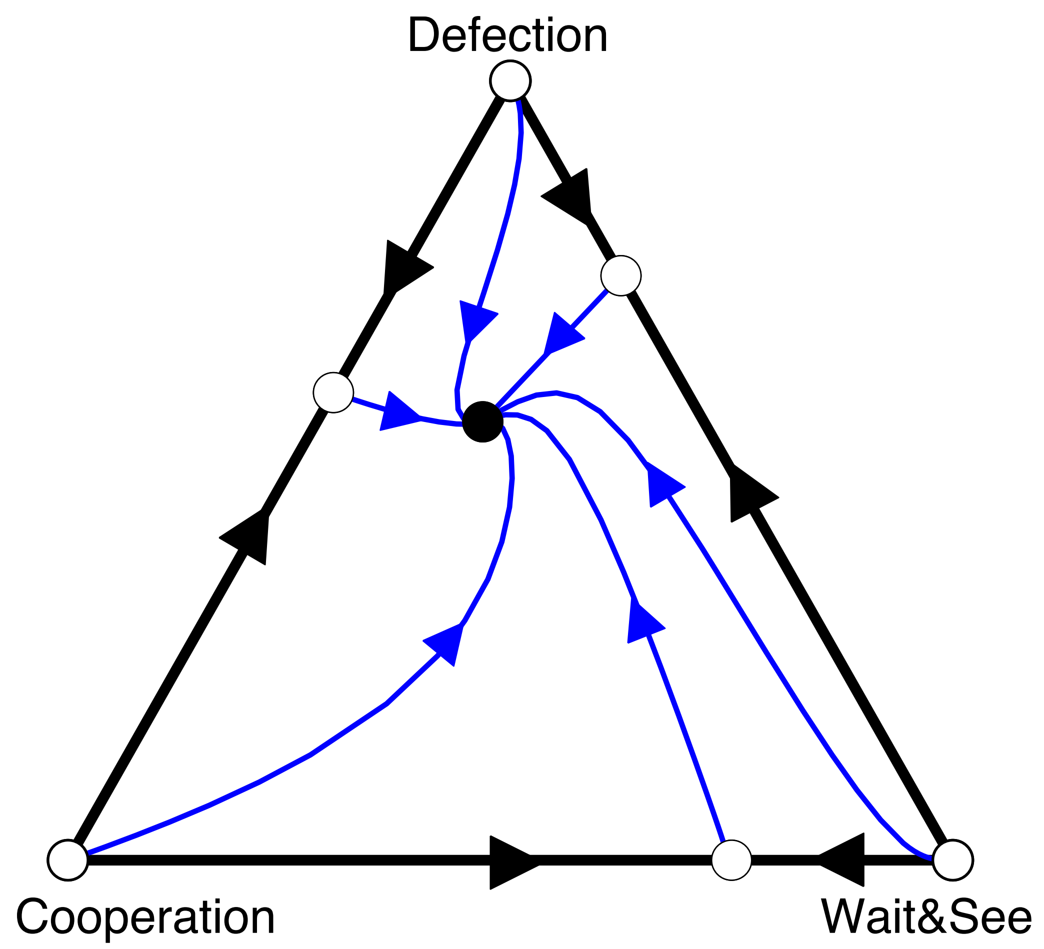
4. Plotting some orbits numerically



Evolutionary game theory: An example of a 3x3 game

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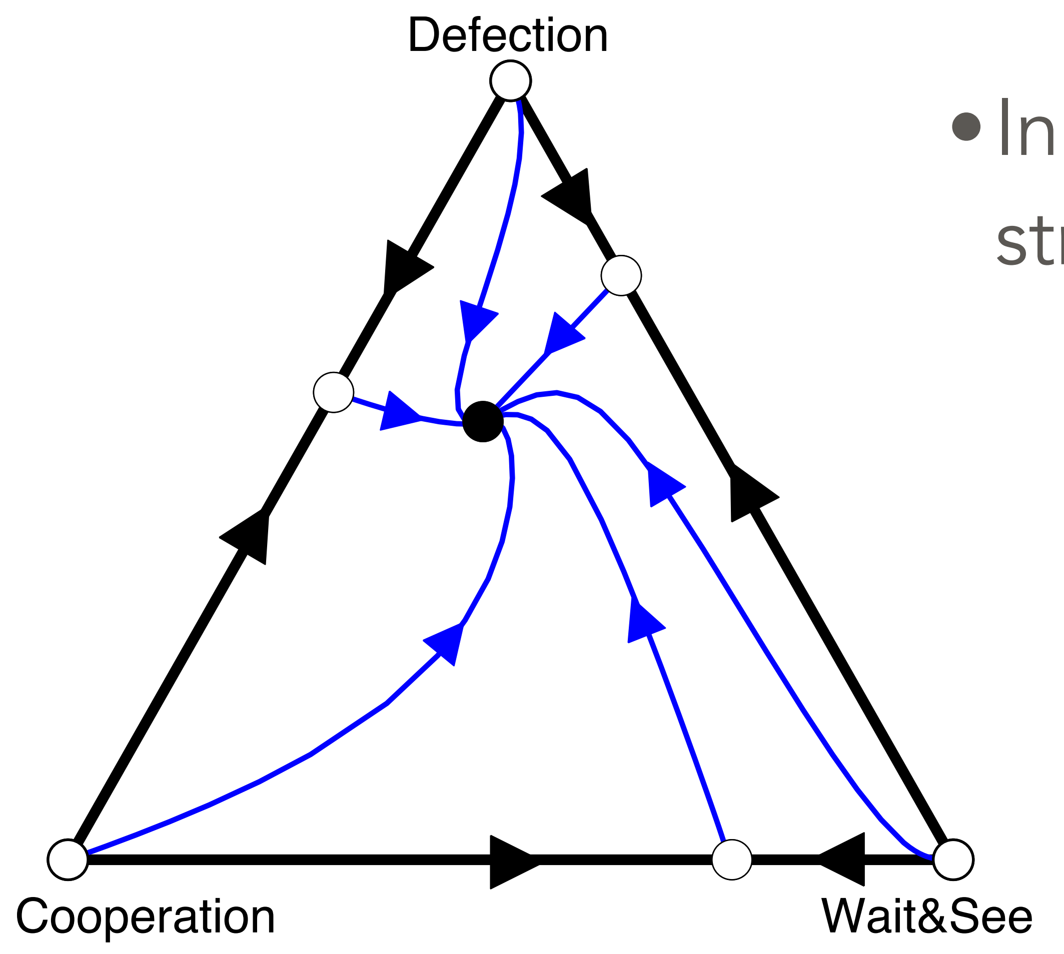

- In the end, all three strategies coexist.

Evolutionary game theory: An example of a 3x3 game

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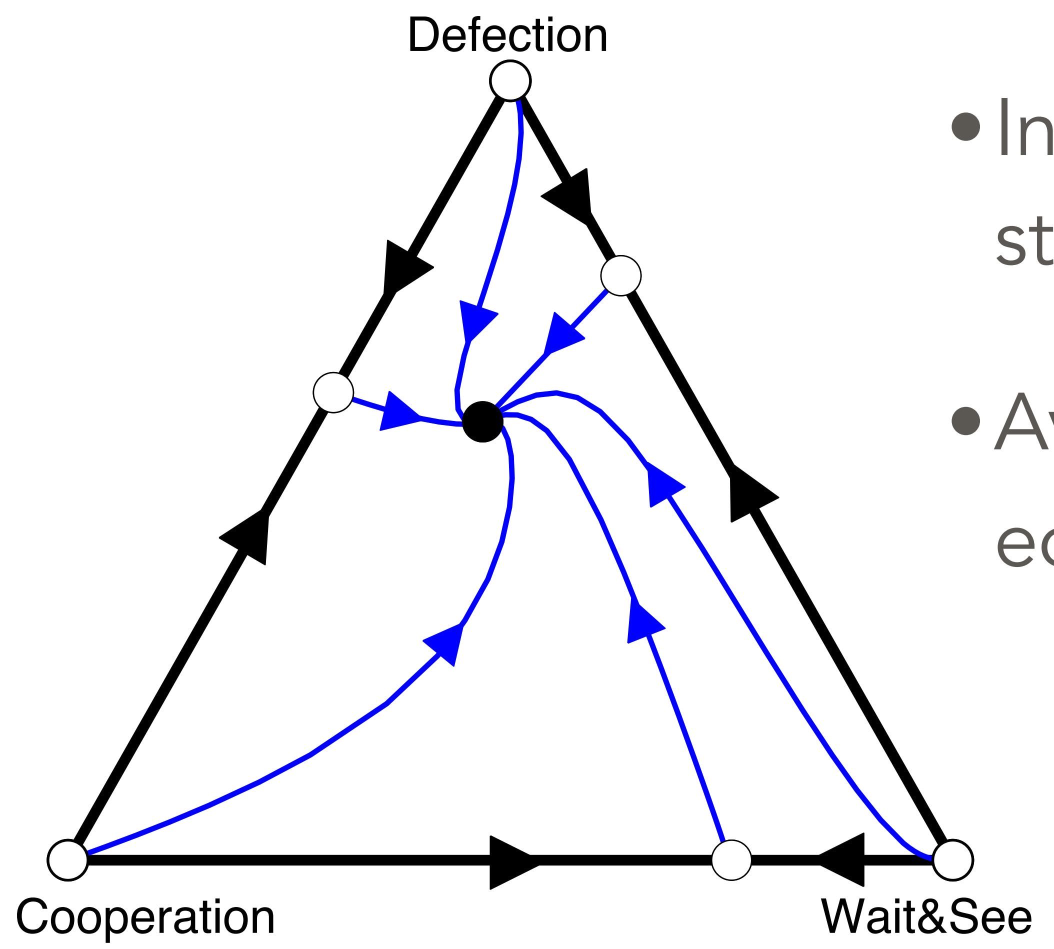

- In the end, all three strategies coexist.
- Average fitness in this equilibrium: $\bar{f} = 2$

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

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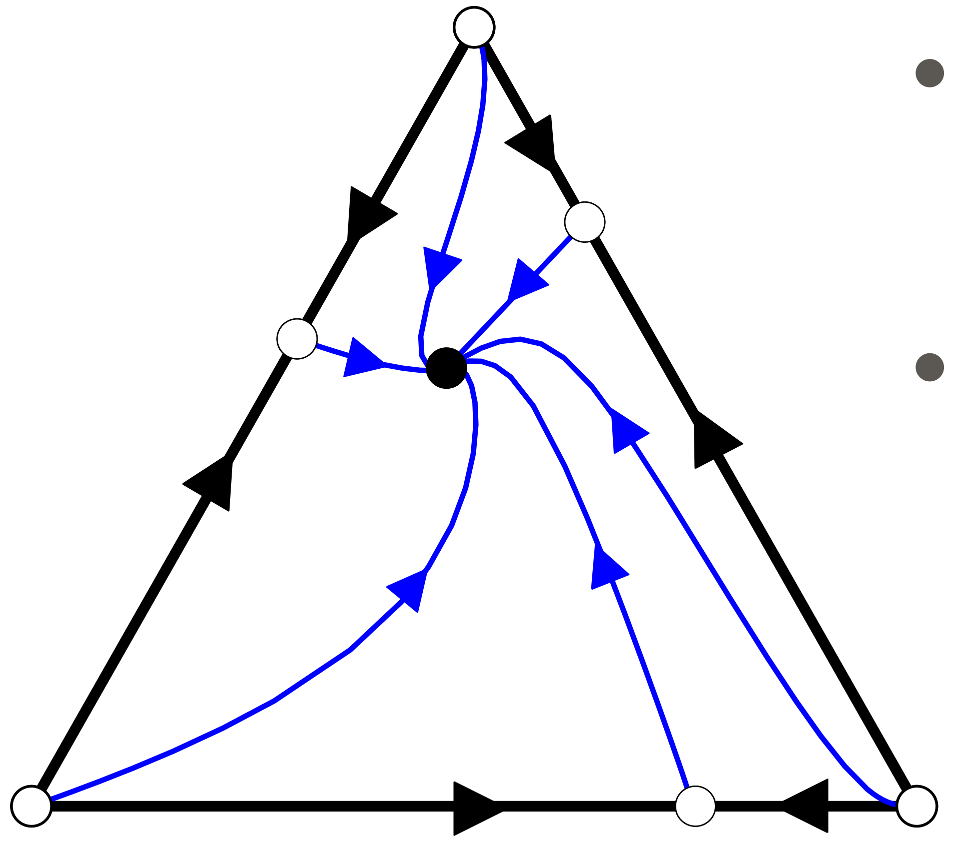

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Example 1.10. Rock Paper Scissors

Consider the following generalised version of rock paper scissors.

	Rock	Paper	Scissors
Rock	0	$-a_2$	b_3
Paper	b_1	0	$-a_3$
Scissors	$-a_1$	b_2	0

Evolutionary game theory: An example of a 3x3 game

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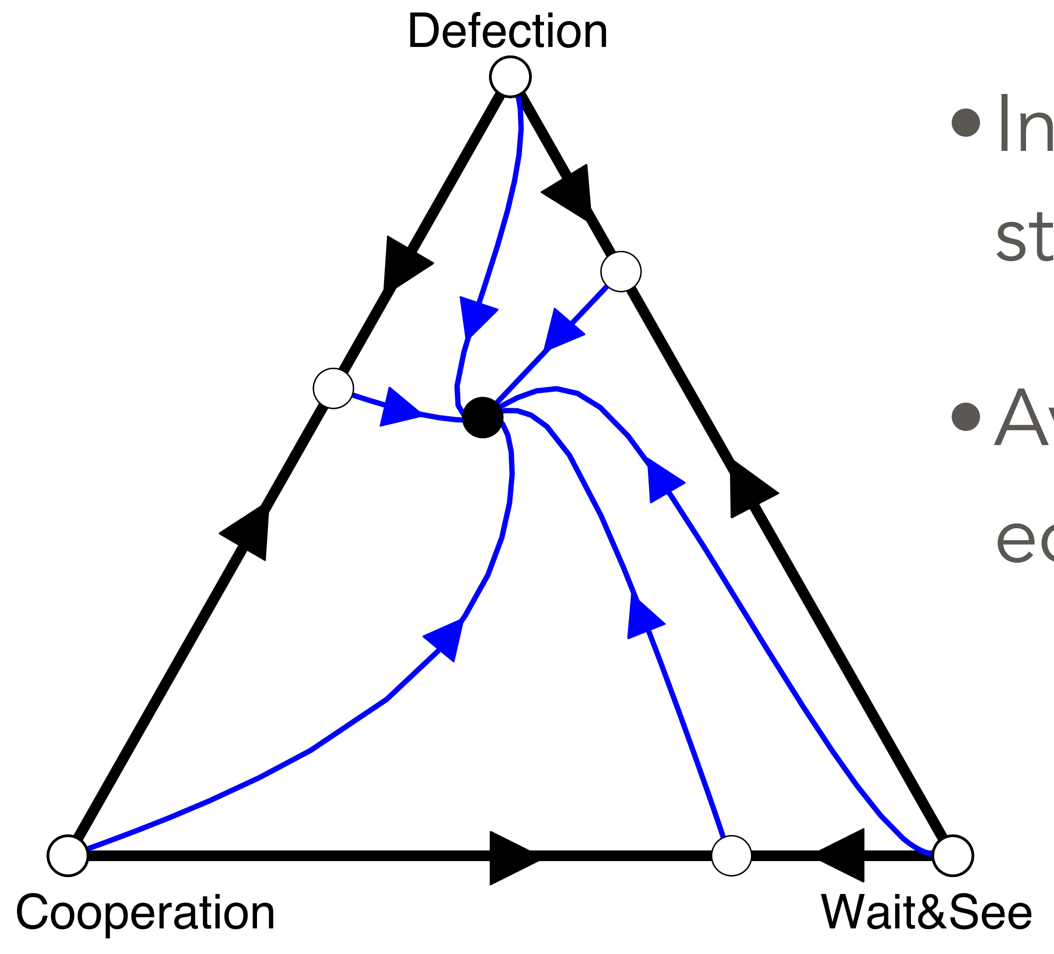

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It turns out there are three possible dynamics.

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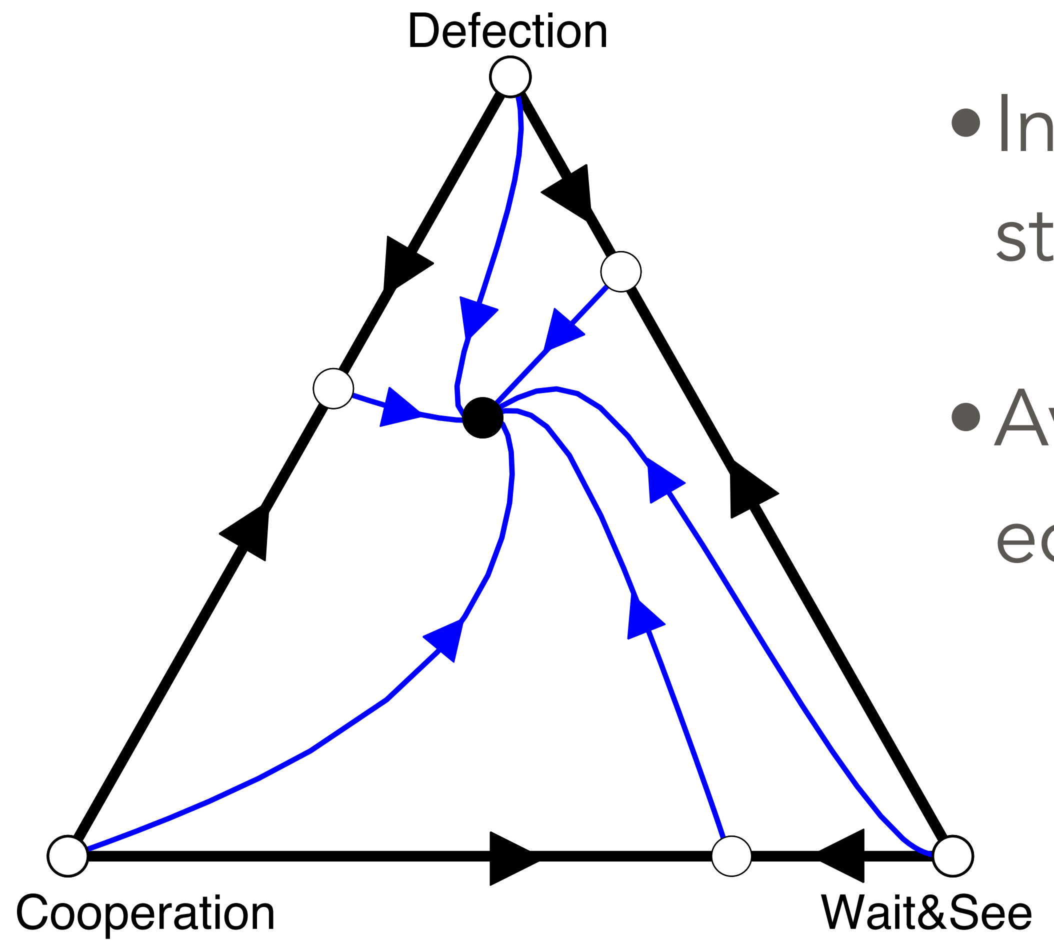

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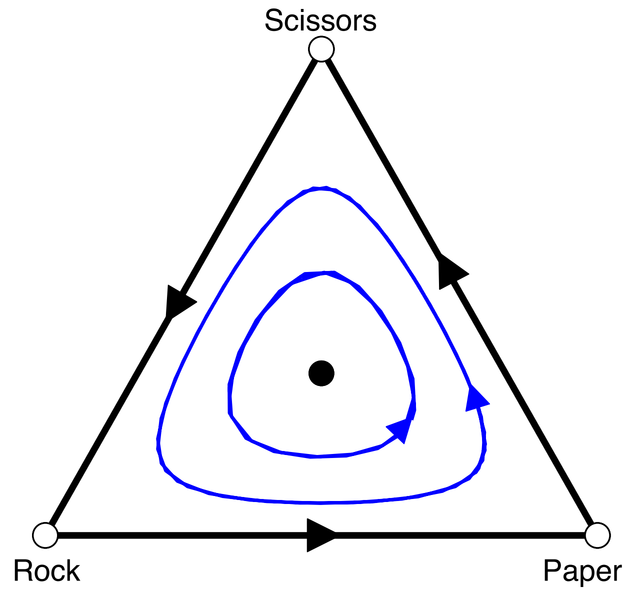

Evolutionary game theory: An example of a 3x3 game

Example 1.9. The volunteer's timing dilemma (continued)

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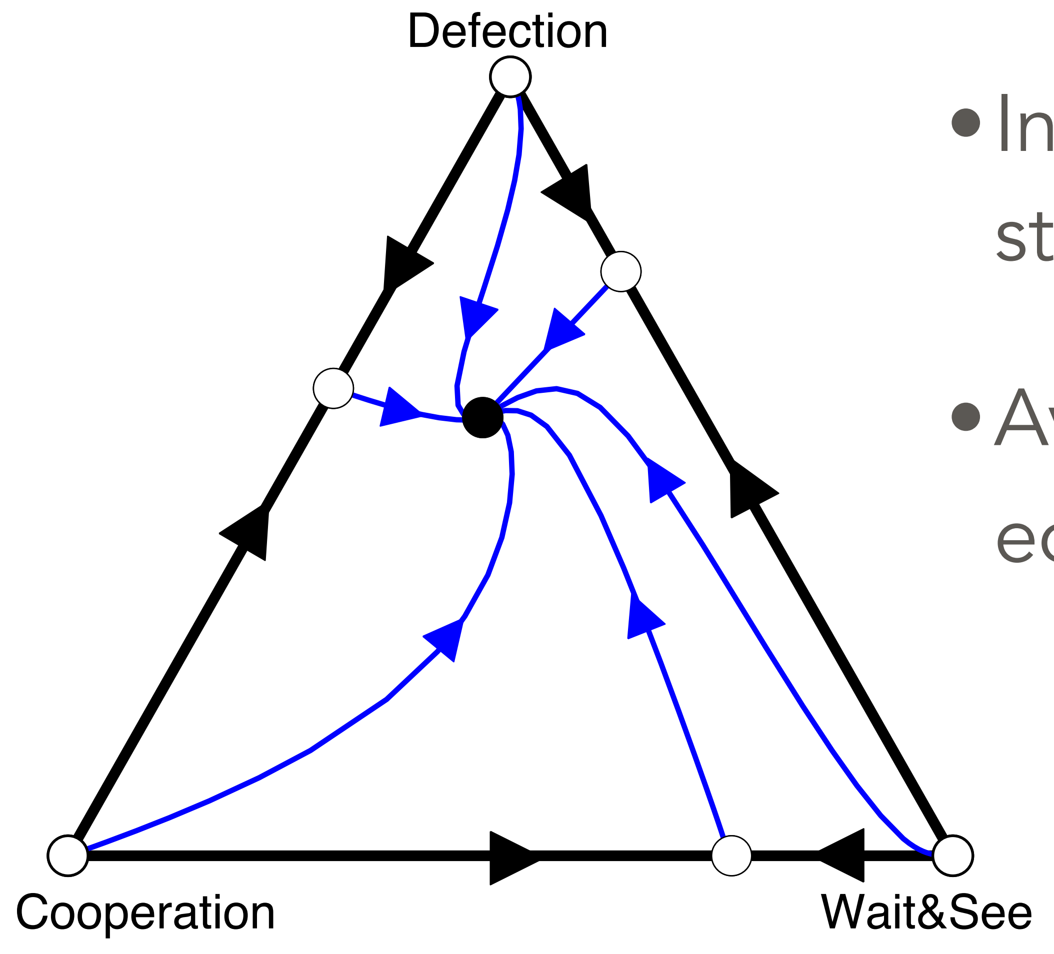

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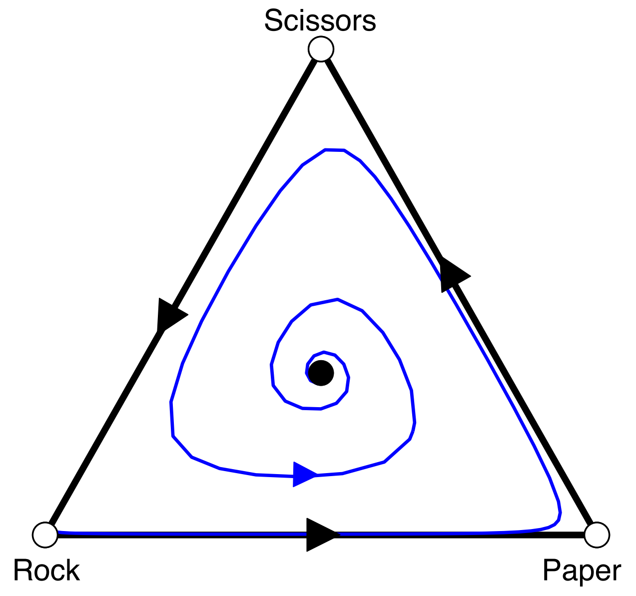

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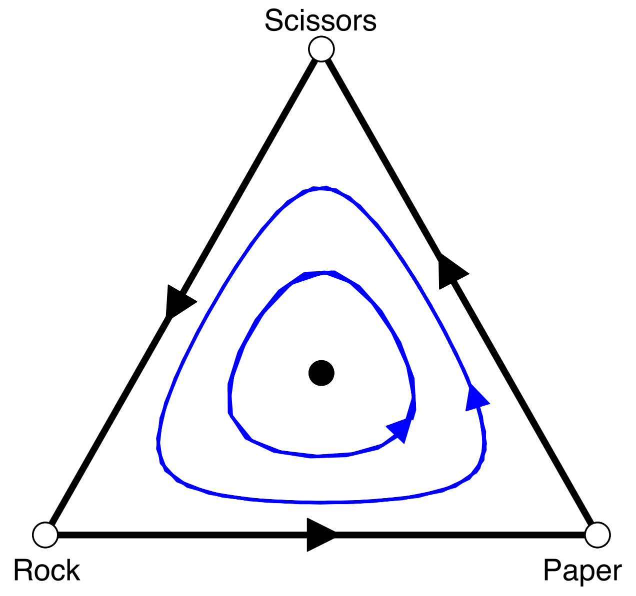

Evolutionary game theory: An example of a 3x3 game

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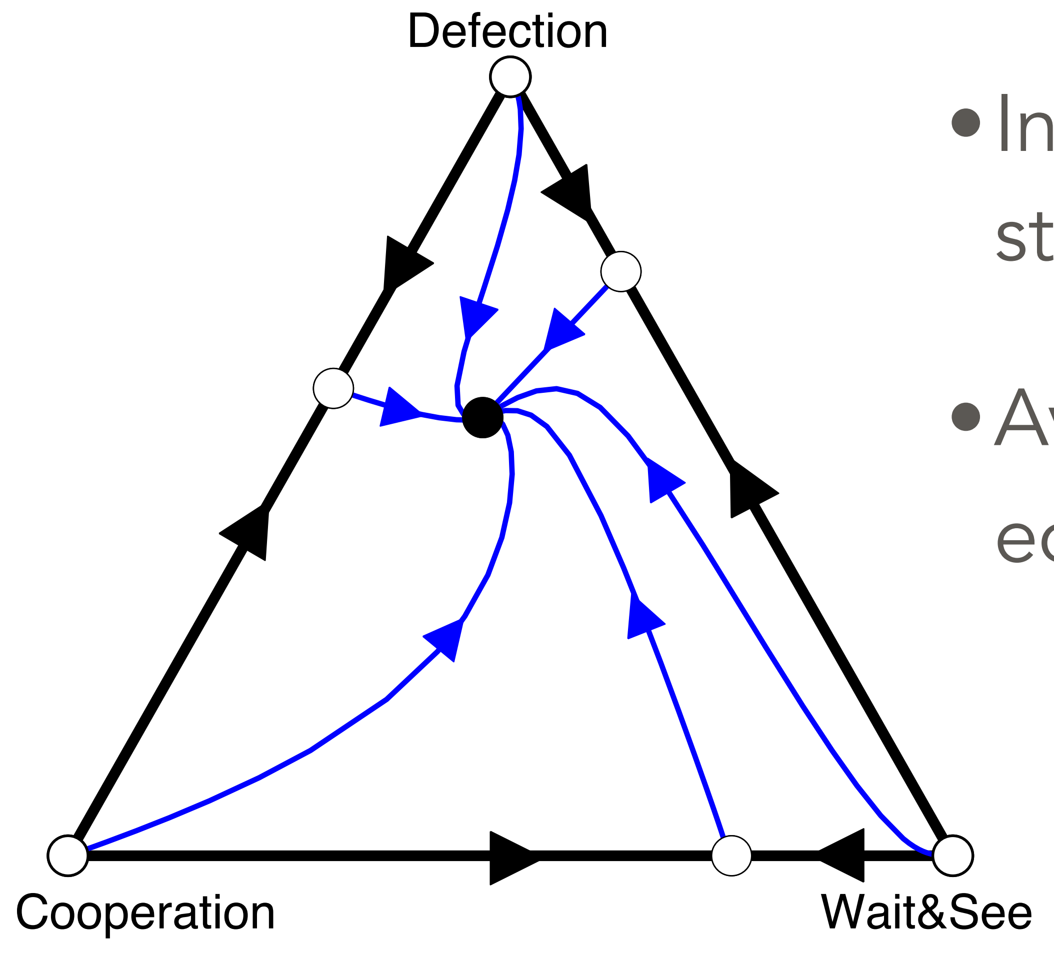

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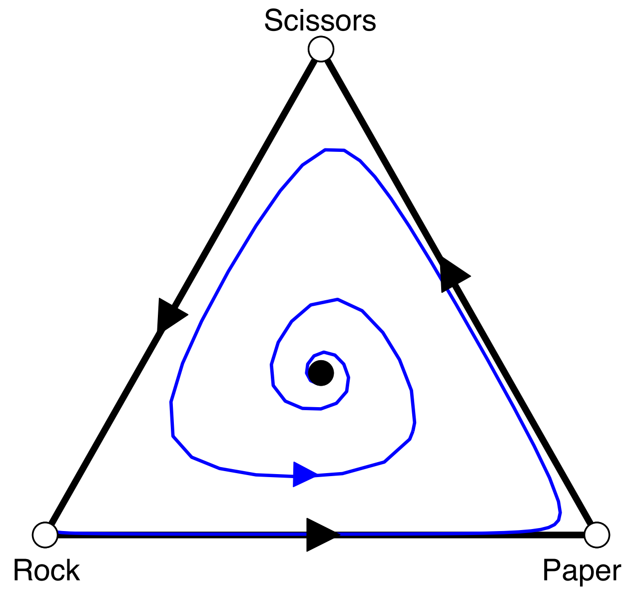

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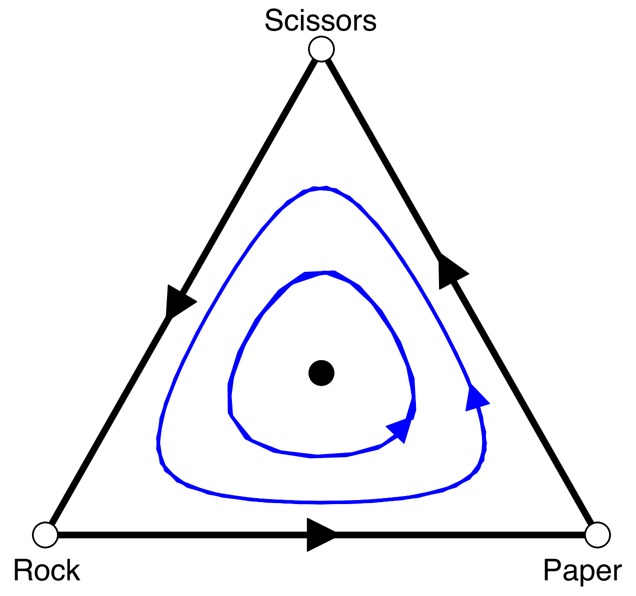

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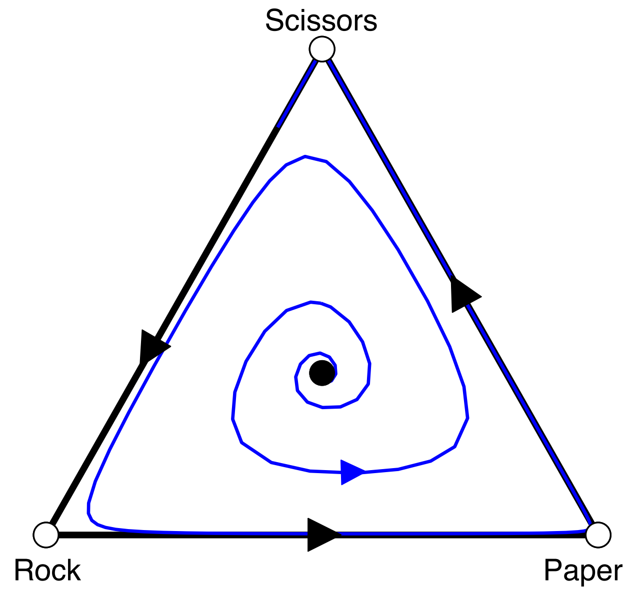

Evolutionary game theory: Non-transitive game in nature

Example 1.11. Non-transitive games in nature

1. Mating behavior in lizards (Sinervo & Lively 1996)

Three male morphs in side-blotched lizards:

- Males with orange throats defend large territories
- Males with blue throats defend smaller territories
- Males with yellow throats are sneakers without territory

The rock–paper–scissors game and the evolution of alternative male strategies

B. Sinervo & C. M. Lively

Department of Biology and Center for the Integrative Study of Animal Behavior, Indiana University, Bloomington, Indiana 47405, USA

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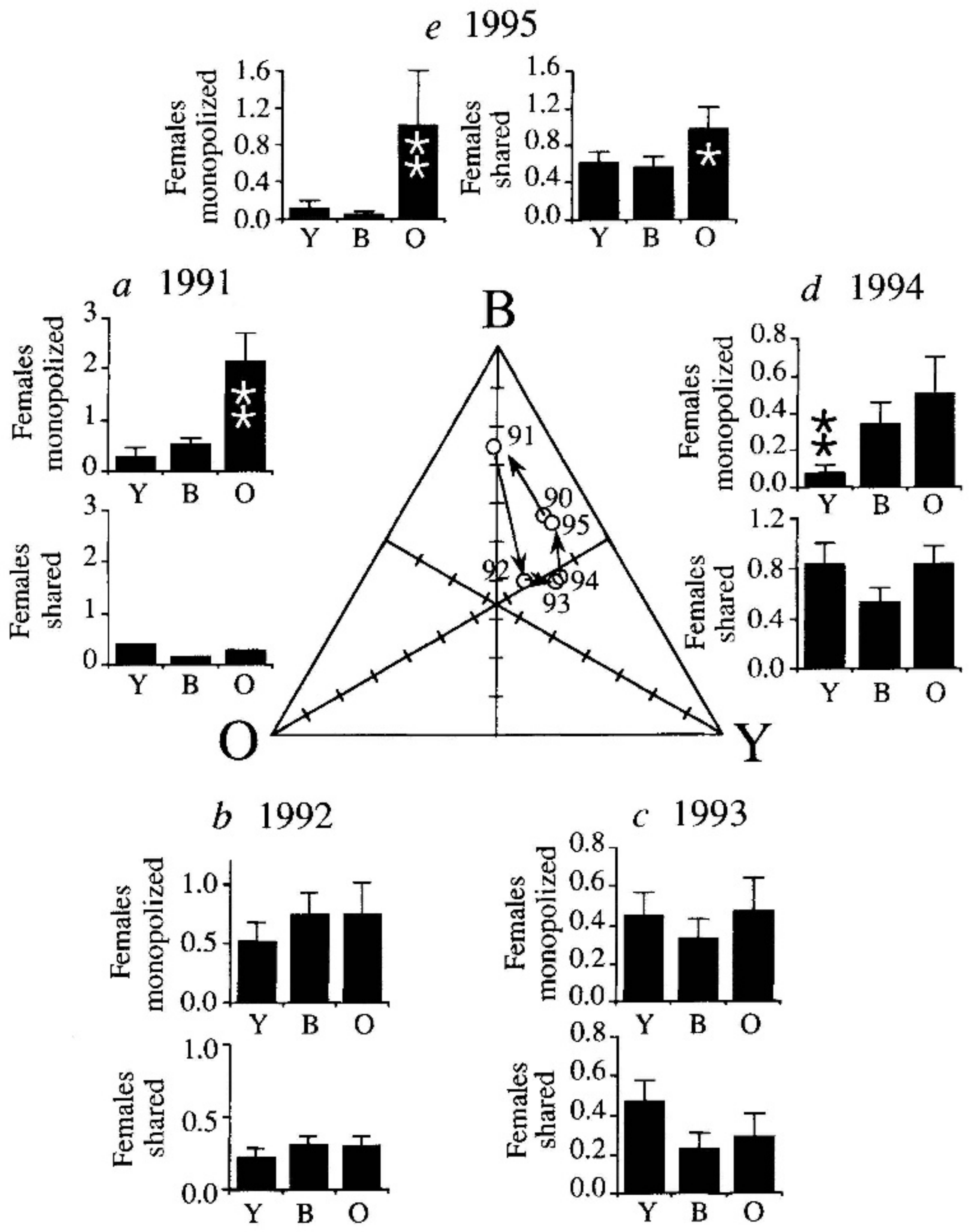

Evolutionary game theory: Non-transitive game in nature

Example 1.11. Non-transitive games in nature (continued)

2. Competition among E. Coli (Kerr et al, 2002)

Three strains of E. Coli

- Colicin-producing strain (C)
- Sensitive strain (S)
- Resistant strain (R)

Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors

Benjamin Kerr*, Margaret A. Riley†, Marcus W. Feldman*
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S is invaded by C, C is invaded by R, R is invaded by S.

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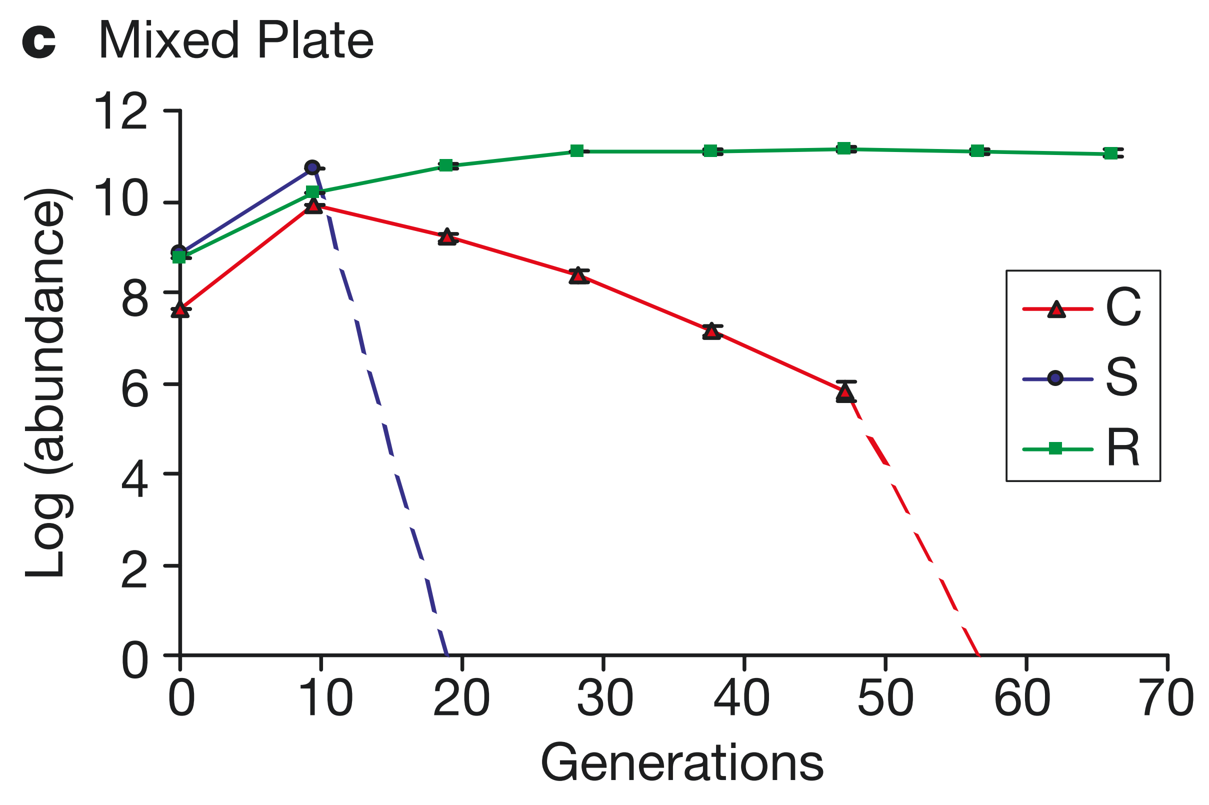

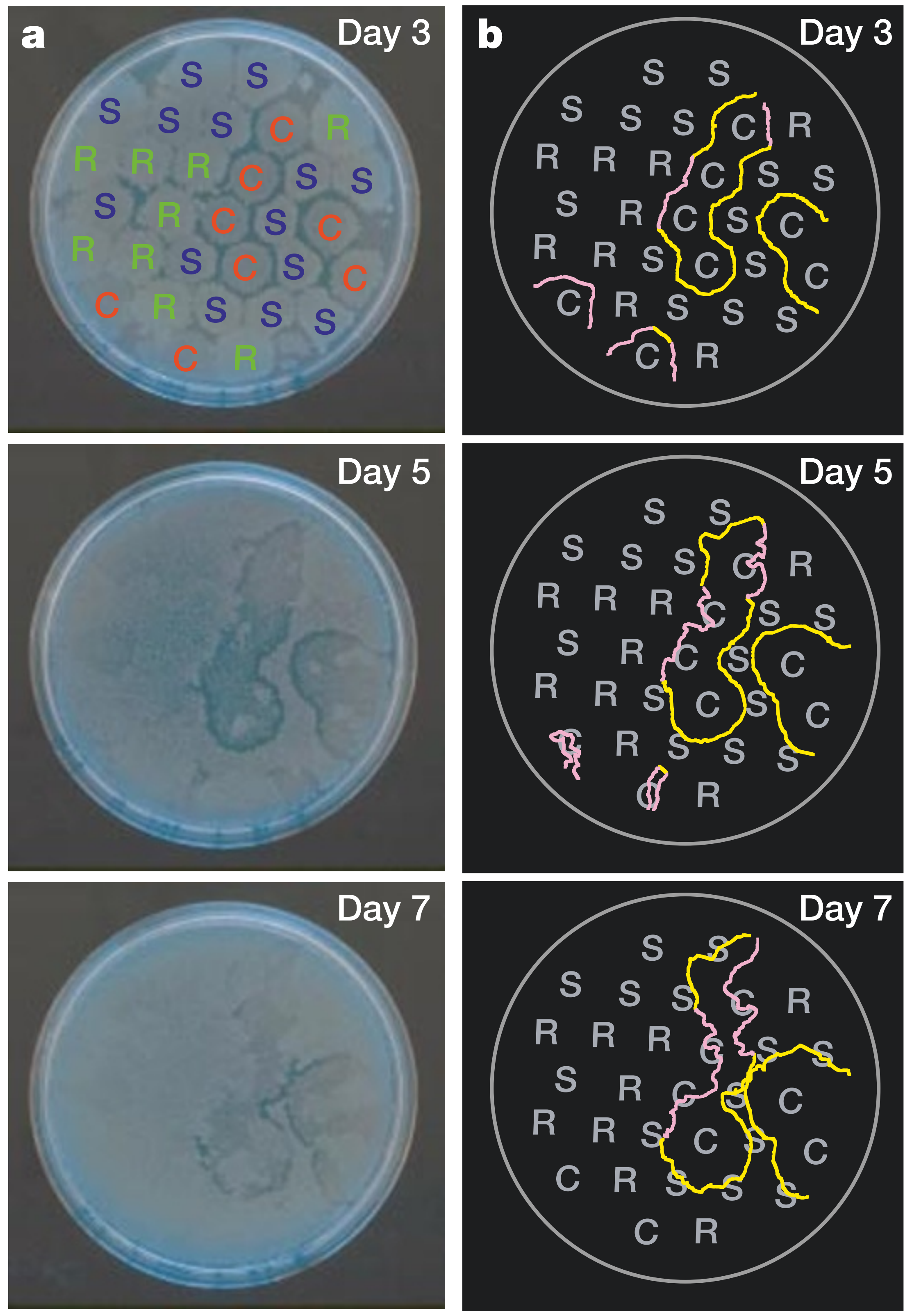

Evolutionary game theory: Replicator dynamics versus classical game theory

Remark 1.12. Replicator dynamics vs Nash equilibrium

In the examples we have seen so far, the outcome "predicted" by replicator dynamics often had a close relationship to the (symmetric) Nash equilibria of the game. This is not a coincidence; instead one can show the following results.

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4. There are beautiful connections to the concepts of classical game theory, without making any strong assumptions on the rationality of individuals. (How is this possible?)

Evolutionary game theory: Replicator dynamics versus classical game theory

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Replicator dynamics might be both considered as a model of biological evolution, or of cultural evolution (imitation). However, it is also important to stress that replicator dynamics is one out of many evolutionary dynamics to consider. The optimal model depends on the applications one has in mind.

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One might want to consider other models, for example, if one is interested in games in finite populations (e.g., Nowak et al, Nature 2004), games in structured populations (e.g., Ohtsuki et al, Nature 2006), or games with continuous traits (e.g., Geritz et al, Evol Ecol Res 1998).

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To provide some intuition for how other models look like, I briefly discuss in the following the case of finite populations.

Evolutionary game theory: Games in finite populations

Remark 2.15. Basic Setup of the Moran process

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$$\pi_1(i) = \frac{i-1}{N-1}a + \frac{N-i}{N-1}b$$

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$$T_i^+ = \frac{if_1(i)}{if_1(i) + (N-i)f_2(i)} \cdot \frac{N-i}{N}$$

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- One can show (Nowak et al, 2004):

$$\varphi_1 \approx \frac{1}{N} + \frac{6}{N}\Big(N(a + 2b - c - 2d) - (2a + b + c - 4d)\Big)w$$

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Remark 2.18. One-third rule

- In the special case that the game is a coordination game like stag-hunt ($a > c,\ d > b$), condition (2.17.1) is equivalent to $x^* < 1/3$, where

$$x^* = \frac{d-b}{a-b-c+d}.$$

Evolutionary game theory: Games in finite populations

Remark 2.17. Fixation under weak selection

- To further simplify the expression for φ_1, we can do a Taylor expansion when selection is weak, $w \to 0$.

- One can show (Nowak et al, 2004):

$$\varphi_1 \approx \frac{1}{N} + \frac{6}{N}\Big(N(a + 2b - c - 2d) - (2a + b + c - 4d)\Big)w$$

- We say that strategy i is favored to invade if its fixation probability φ_i is larger than the neutral $1/N$.

- For large N, we conclude that strategy i is favored if

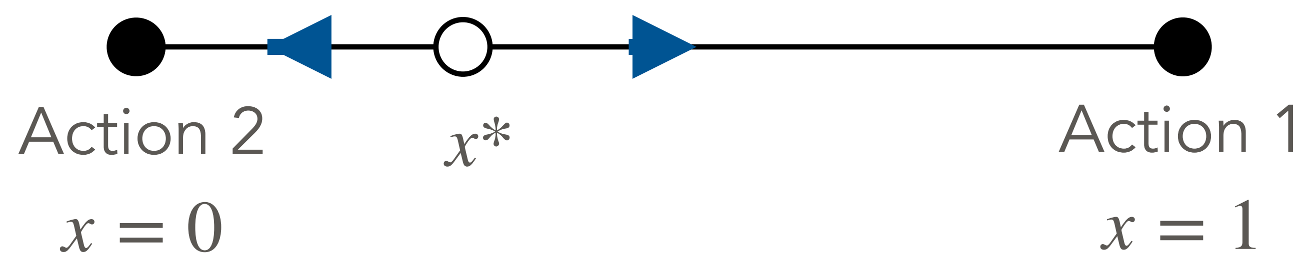
$$a + 2b > c + 2d \qquad (2.17.1)$$

Remark 2.18. One-third rule

- In the special case that the game is a coordination game like stag-hunt ($a > c$, $d > b$), condition (2.17.1) is equivalent to $x^* < 1/3$, where

$$x^* = \frac{d - b}{a - b - c + d}.$$

This x^* is precisely the interior fixed point according to replicator dynamics.



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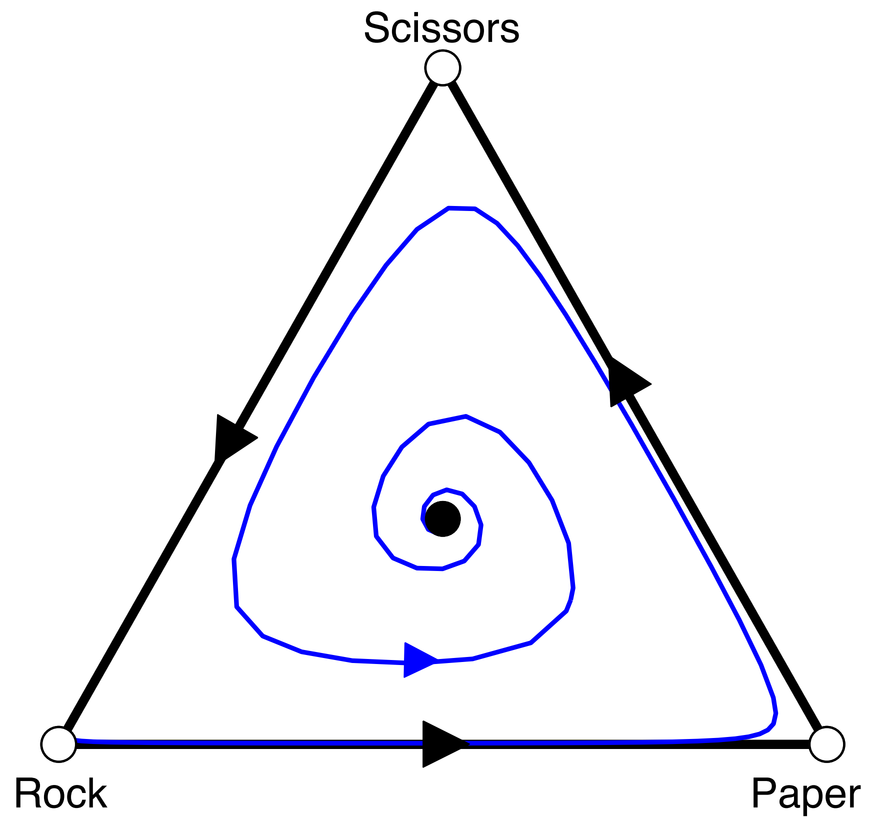

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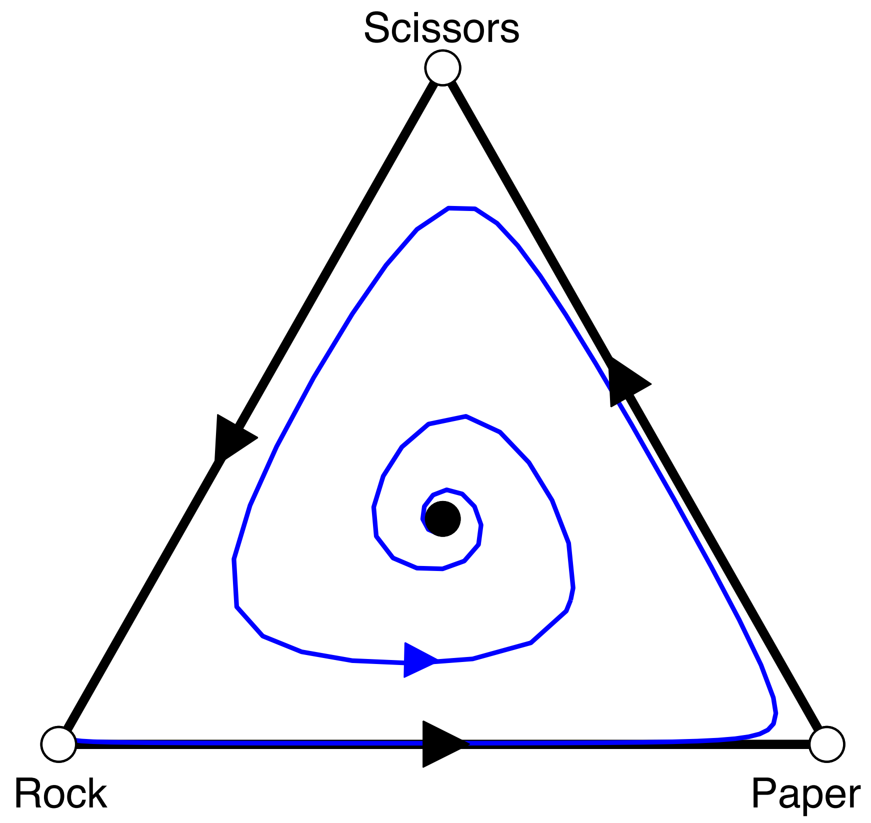

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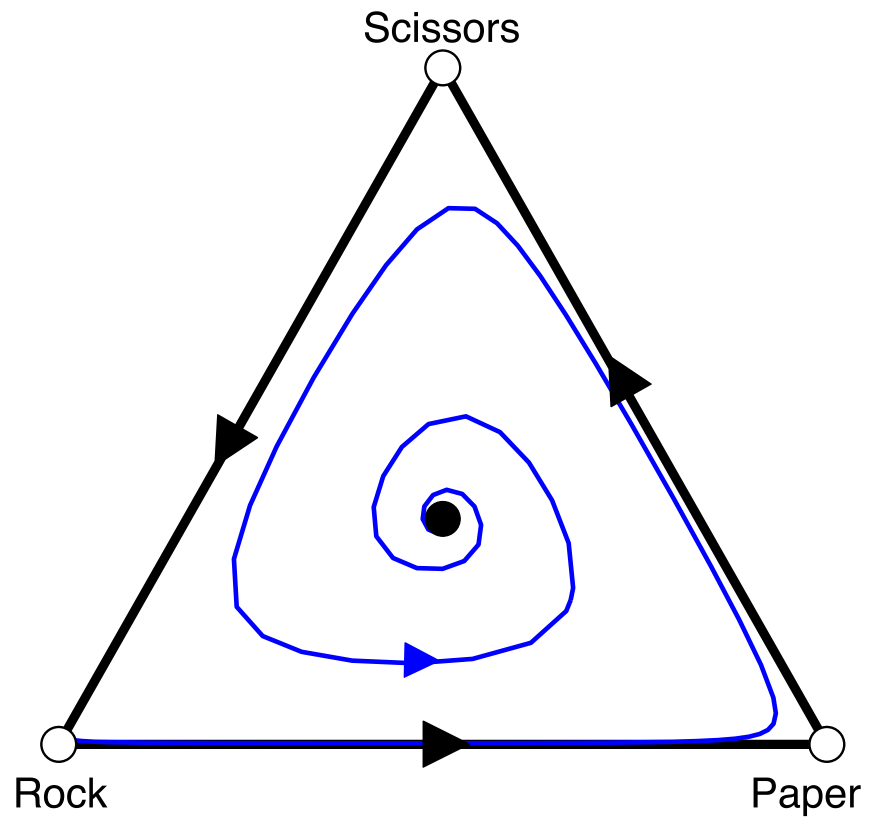

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3. Tomorrow, we will use such models of evolutionary dynamics to address one particular problem in evolutionary biology: why do individuals cooperate?