EVOLUTIONARY DYNAMICS

Jose Cuesta

Grupo Interdisciplinar de Sistemas Complejos

Departamento de Matemáticas

Universidad Carlos III de Madrid

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(6) Evolutionary game theory

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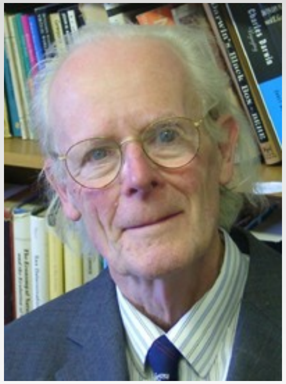
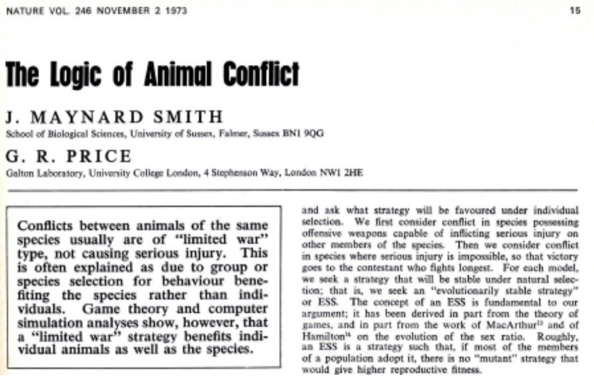
Evolutionary game theory

Evolutionary game theory


John Maynard Smith
(1920 - 2004)


George Price
(1922 - 1975)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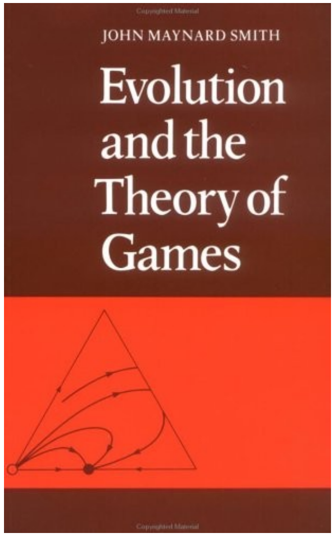
The Logic of Animal Conflict

J. MAYNARD SMITH
School of Biological Sciences, University of Sussex, Falmer, Sussex BN1 9QG

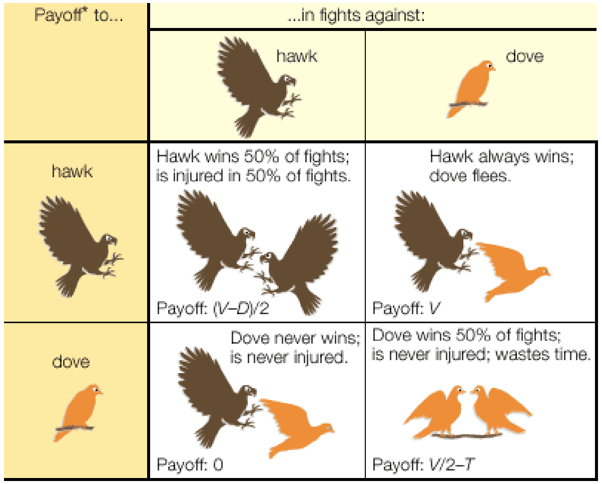
G. R. PRICE
Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE

Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur[13] and of Hamilton[14] on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.



Hawk-Dove Model: Costs and Benefits of Fighting over Resources



Payoff* to...	...in fights against: hawk	dove
hawk	Hawk wins 50% of fights; is injured in 50% of fights. Payoff: $(V–D)/2$	Hawk always wins; dove flees. Payoff: V
dove	Dove never wins; is never injured. Payoff: 0	Dove wins 50% of fights; is never injured; wastes time. Payoff: $V/2–T$

*V = fitness value of winning resources in fight
D = fitness costs of injury
T = fitness costs of wasting time

Hawks and doves

R = resource (food)
D = damage received in conflict

D > R

		individual 2	
		hawk	**dove**
individual 1	**hawk**	(R–D) / 2	R
	dove	0	R / 2

Hawks and doves

$$[\text{hawks}] = x \qquad [\text{doves}] = 1 - x$$

Accumulated payoffs are proportional to:

$$W_{\text{hawk}}(x) = \frac{R-D}{2}x + R(1-x)$$

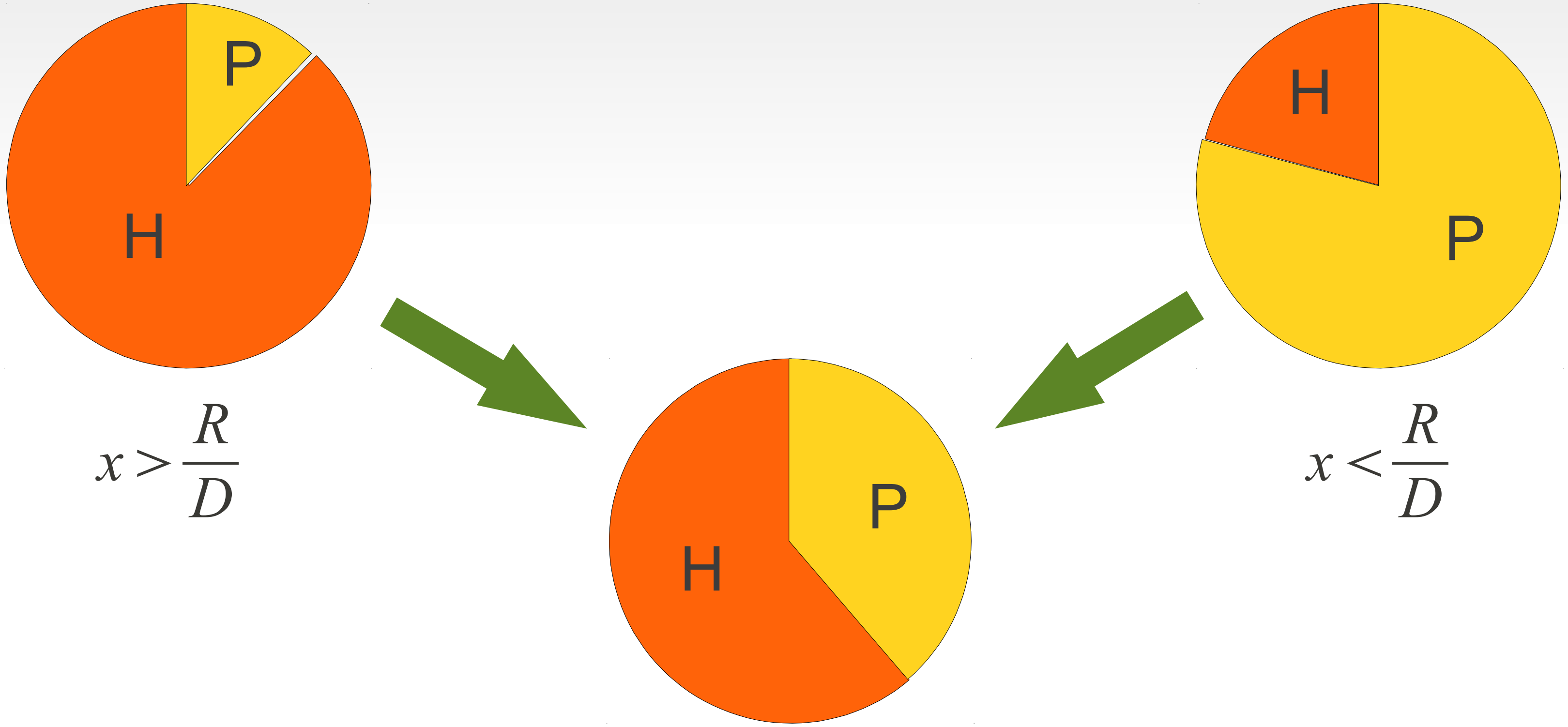
$$W_{\text{dove}}(x) = \frac{R}{2}(1-x)$$

Evolutionary assumption:

$$f_i(\boldsymbol{x}) = \mathscr{F}(W_i(\boldsymbol{x})) \qquad \mathscr{F}'(w) > 0$$

Hawks and doves

$$W_{\text{hawk}}(x) - W_{\text{dove}}(x) = \frac{1}{2}(R - D\,x)$$



$x > \frac{R}{D}$

$x < \frac{R}{D}$

$x = \frac{R}{D}$

Symmetric games

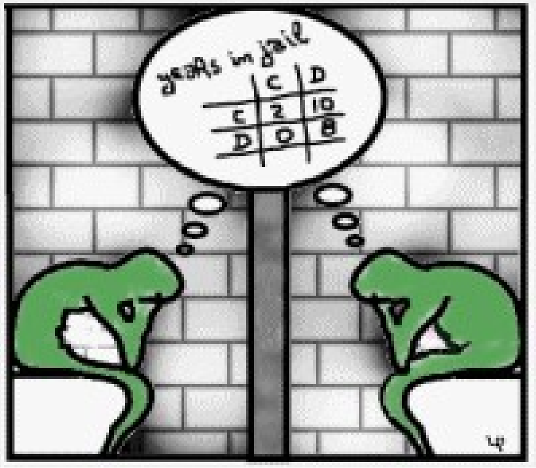
- Individuals confronting each other (players): n
- Species (strategies): $i = 1, \dots , r$
- Payoffs: $\Pi(i, j_2, \dots, j_n)$
- Mean payoffs in a population $\boldsymbol{x}$:

$$W_i(\boldsymbol{x}) = \sum_{j_2=1}^{r} \cdots \sum_{j_n=1}^{r} \Pi(i, j_2, \dots, j_n) x_{j_2} \cdots x_{j_n}$$

$$i = 1, \dots, r$$

Classic games

prisoner's dilemma



prisoner 2

		coop.	defect
prisoner 1	coop.	3	0
	defect	4	1

Classic games

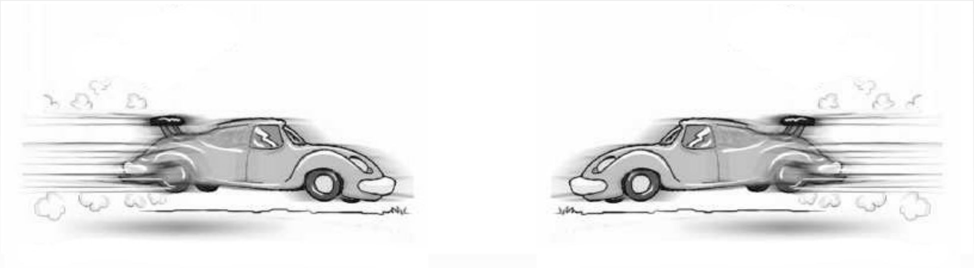
stag-hunt

hunter 2

		stag	hare
hunter 1	**stag**	3	0
	hare	2	1

Classic games

chicken / snowdrift



player 2

		stay	quit
player 1	**stay**	–1	2
	quit	0	0

Classic games

rock, paper, scissors

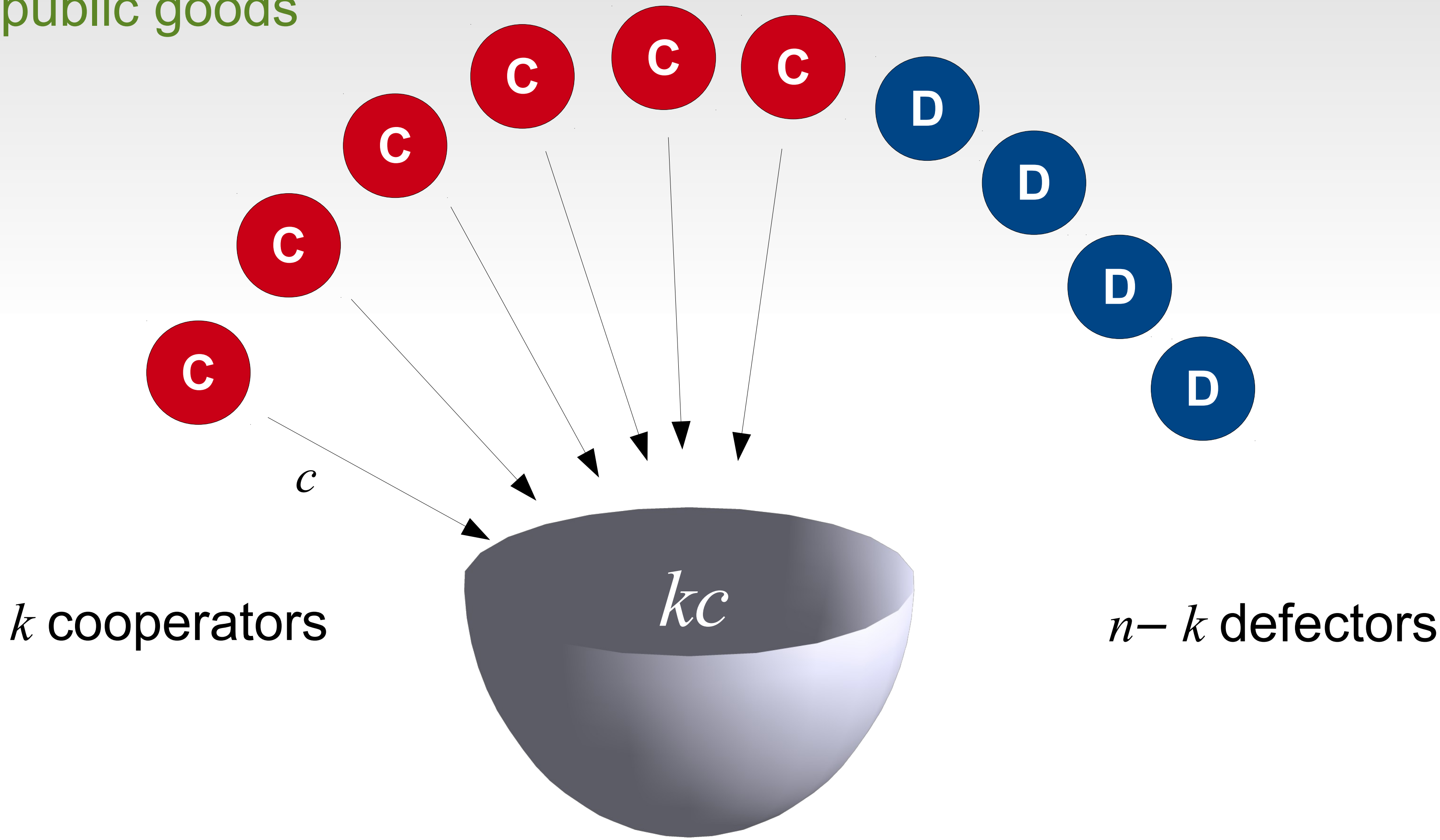
player 2

player 1

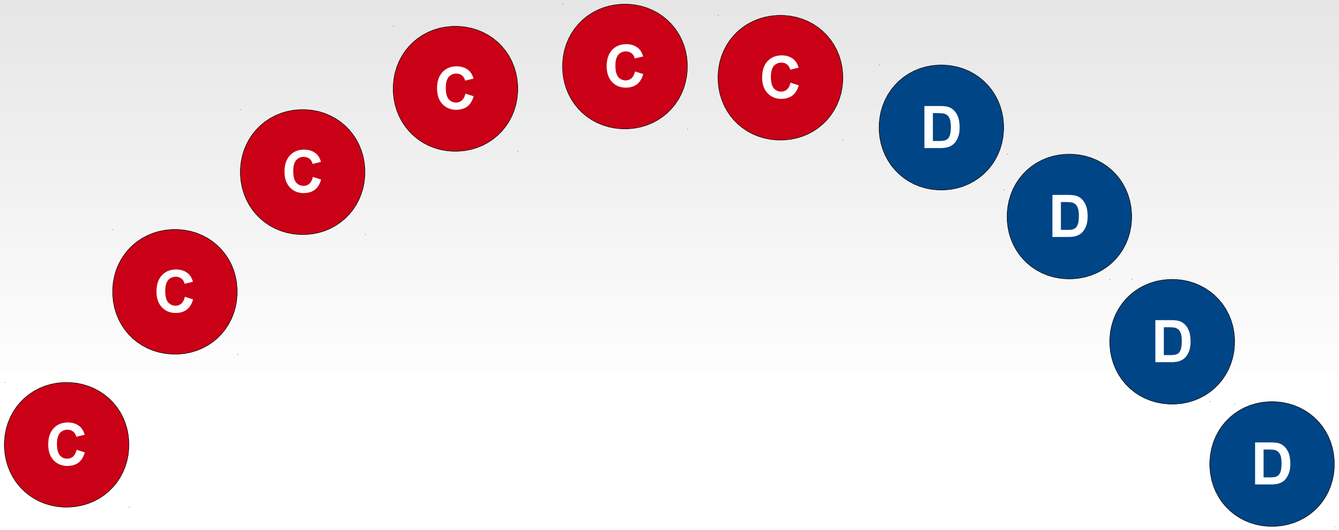
	r	p	s
r	0	–1	1
p	1	0	–1
s	–1	1	0

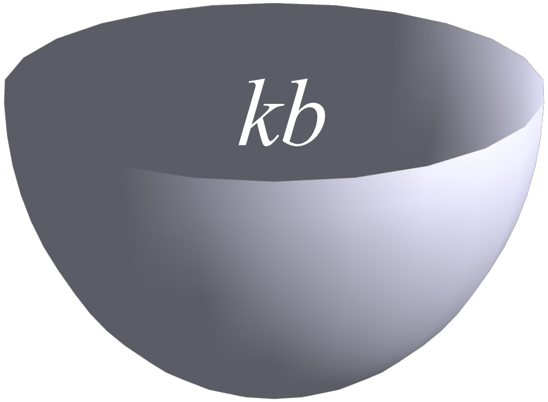
Classic games

public goods



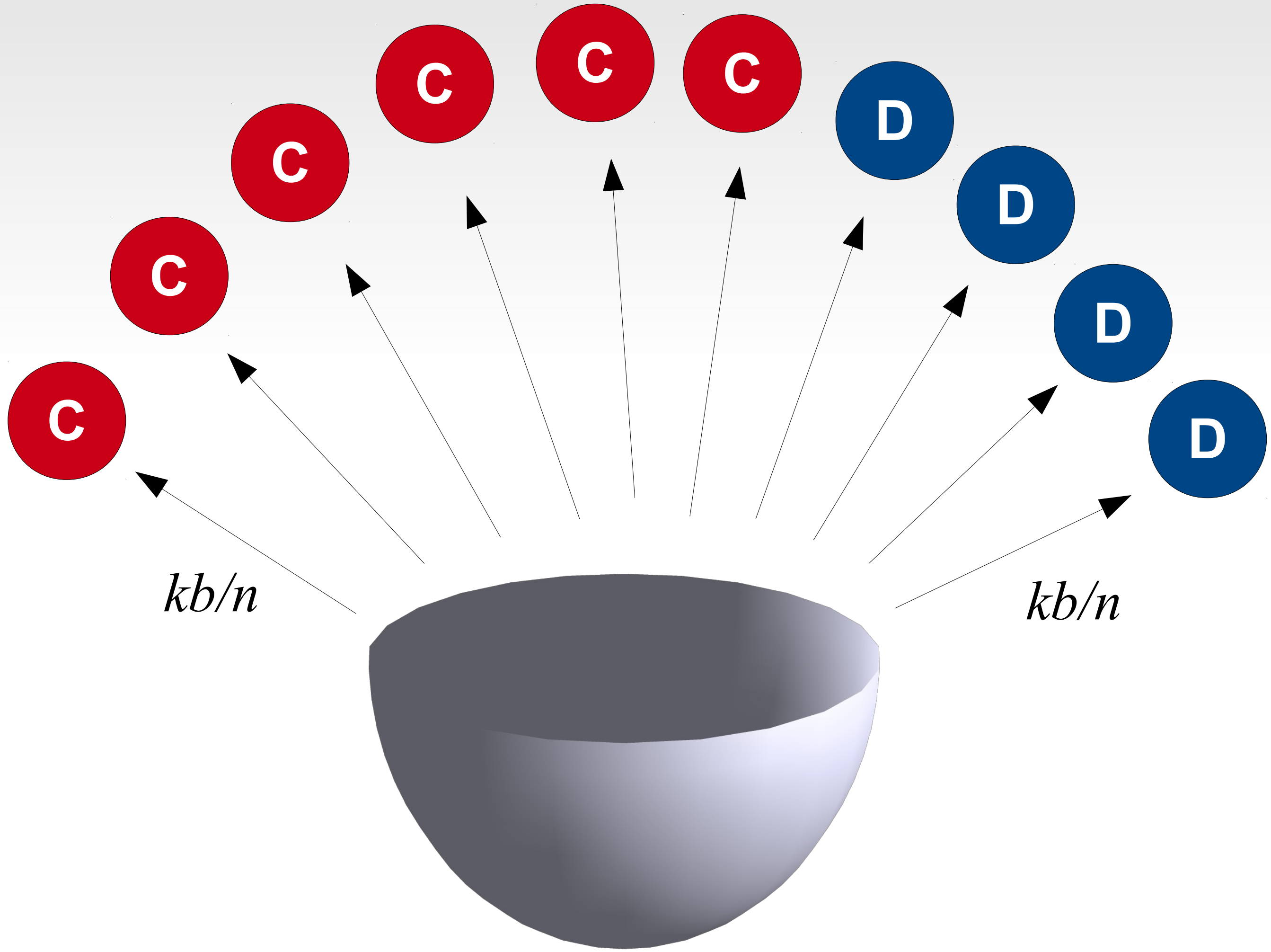
Classic games



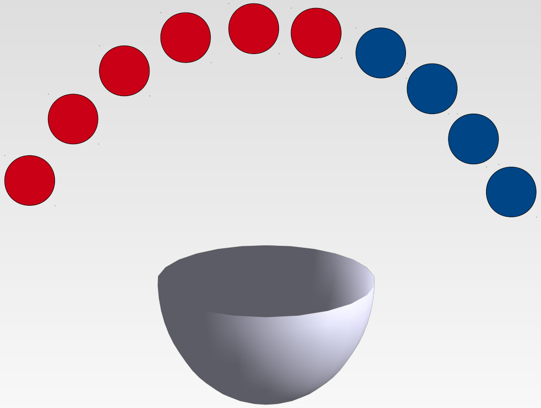


$b > c$

Classic games



Classic games



public goods

remaining $n-1$ players

	# C →	**0**	**1**	**2**	**…**	$n-1$
player 1	**C**	$b/n-c$	$2b/n-c$	$3b/n-c$	…	$b-c$
	D	0	b/n	$2b/n$	…	$(n-1)b/n$

Replicator equation

Simplest relation between fitness and payoff:

$$\mathscr{F}(w)=\alpha w+\gamma$$

$$\frac{d x_i}{d t}=x_i\left(f_i(\boldsymbol{x})-\boldsymbol{x}\cdot\boldsymbol{f}(\boldsymbol{x})\right)$$

$$\frac{d x_i}{d(\alpha t)}=x_i\left(W_i(\boldsymbol{x})-\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right)$$

equilibria are independent of α and γ

Replicator equation

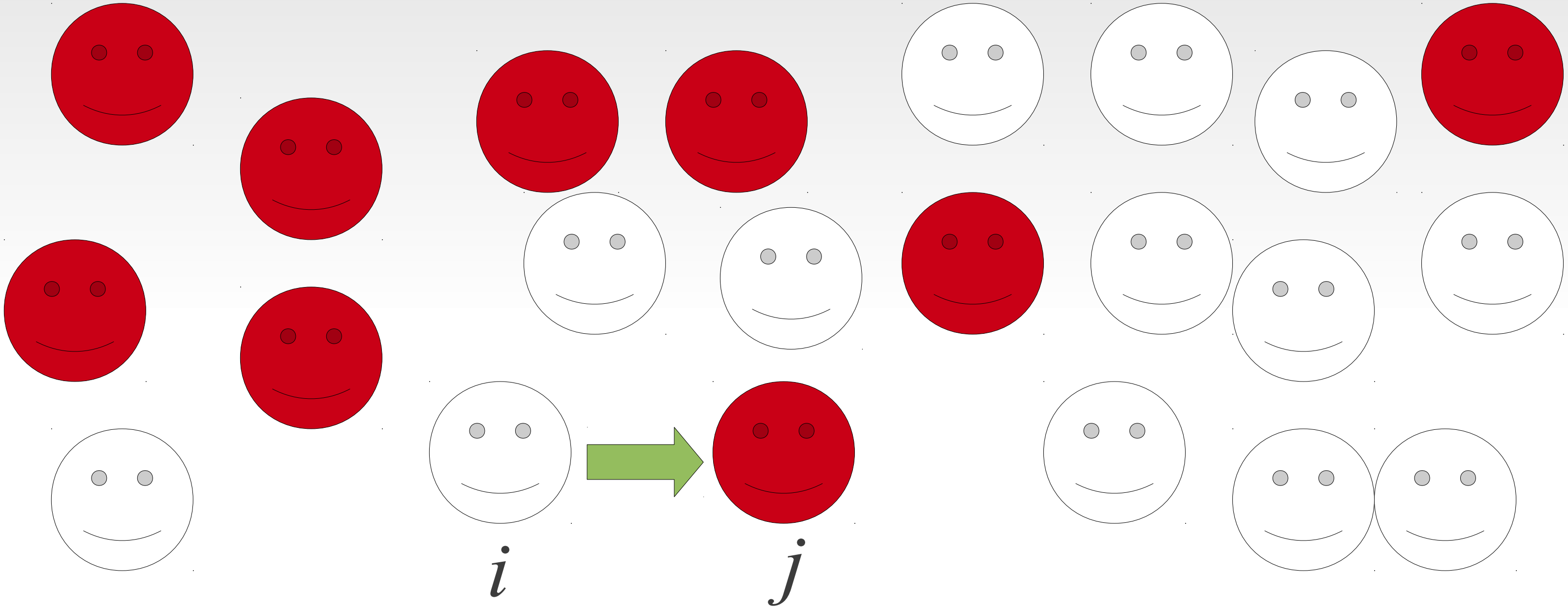
Common choice:

$$\mathcal{F}(w)=w$$

$$\boxed{\frac{dx_i}{dt}=x_i\left(W_i(\boldsymbol{x})-\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right)}$$

replicator equation

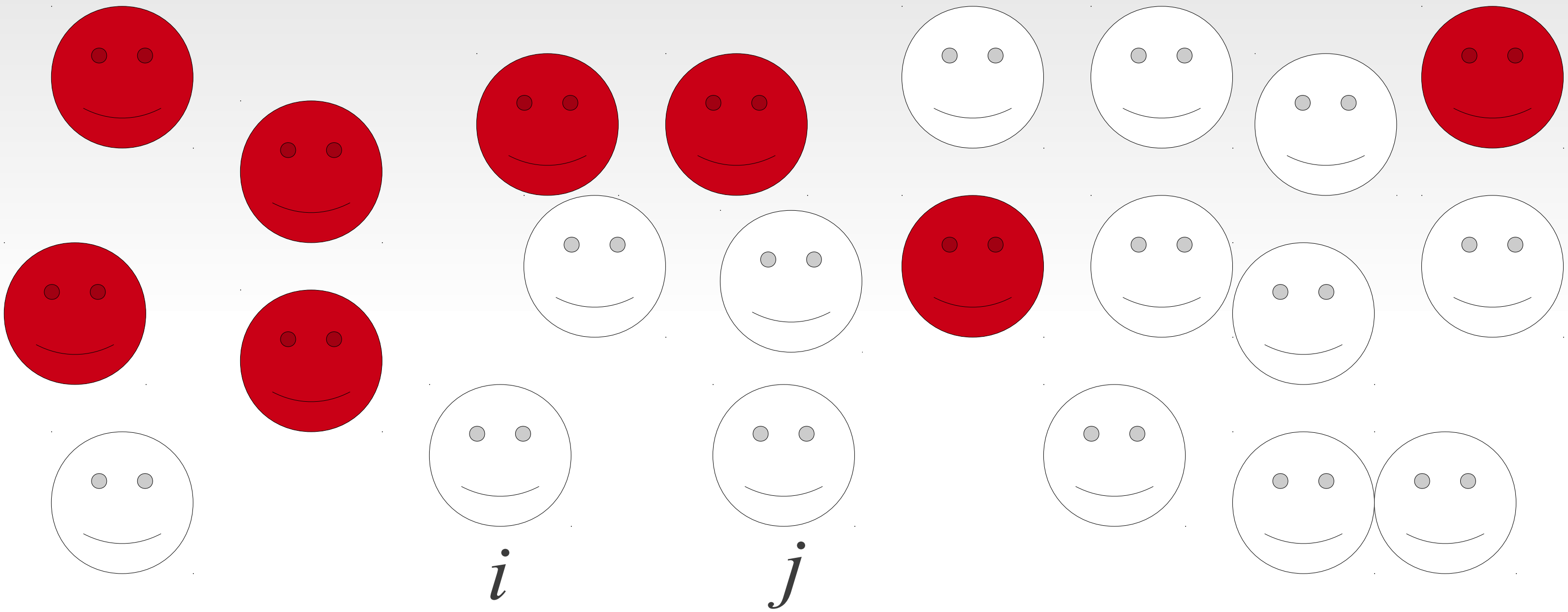
Social dynamics: imitation



$$T_{j \to i} = f_{i,j}(\boldsymbol{x})$$

imitation probability

Social dynamics: imitation



$$\frac{d\,x_i}{d\,t} = \sum_{j=1}^{r} \left[f_{i,j}(\boldsymbol{x}) - f_{j,i}(\boldsymbol{x}) \right] \underbrace{x_i\, x_j}_{\text{meeting probability}}$$

Social dynamics: imitation

Assumptions:

① $f_{i,j}(\boldsymbol{x}) = F(W_i(\boldsymbol{x}), W_j(\boldsymbol{x}))$

② $F(u, v) = \varphi(u - v)$

③ $\psi(z) \equiv \varphi(z) - \varphi(-z)$

$$\frac{d x_i}{d t} = x_i \sum_{j=1}^{n} \psi[W_i(\boldsymbol{x}) - W_j(\boldsymbol{x})] x_j$$

Social dynamics: imitation

$$\varphi(z) = (z)_+ \qquad \Rightarrow \qquad \psi(z) = z$$

$$\frac{dx_i}{dt} = x_i\left(W_i(\boldsymbol{x}) - \boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right)$$

Equilibria

$$\frac{d\,x_i}{d\,t}=x_i\left(W_i(\boldsymbol{x})-\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right)$$

$x_i=0$ or $W_i(\boldsymbol{x})=\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})$

↕

all species present in an equilibrium earn the same payoff

2 species, 2 players

$$\Pi = \begin{array}{cc} \mathrm{A} & \mathrm{B} \\ \end{array}$$

$$\Pi = \begin{array}{cc|c} \mathrm{A} & \mathrm{B} & \\ a & b & \mathrm{A} \\ c & d & \mathrm{B} \end{array}$$

$$[\mathrm{A}] = x \qquad [\mathrm{B}] = 1 - x$$

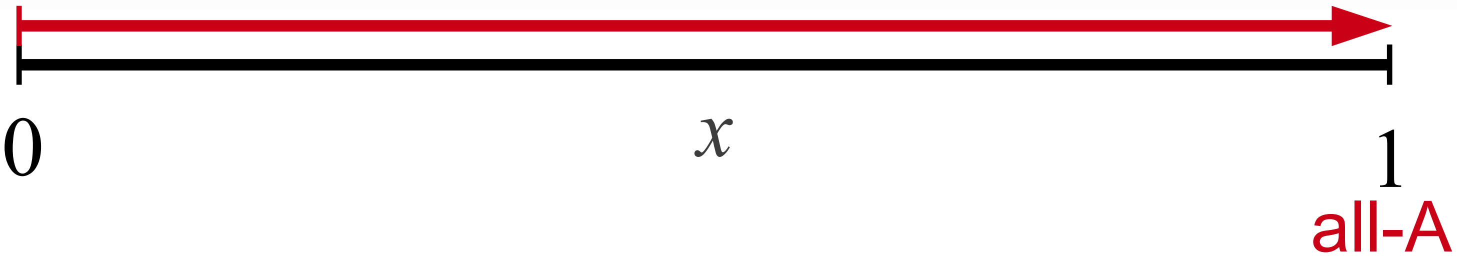
$$f_{\mathrm{A}}(x) = a\,x + b(1 - x)$$
$$f_{\mathrm{B}}(x) = c\,x + d(1 - x)$$

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

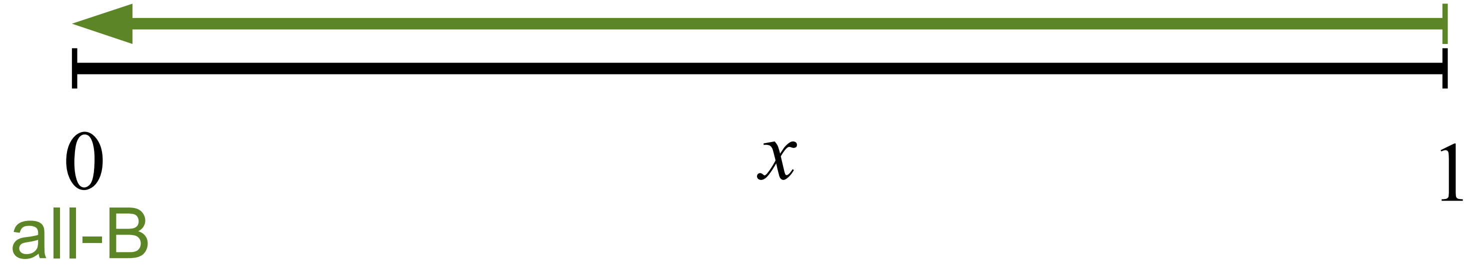
2 species, 2 players

$(b-d)(c-a)<0$ ⇔ 1 species dominates

$b-d>0$



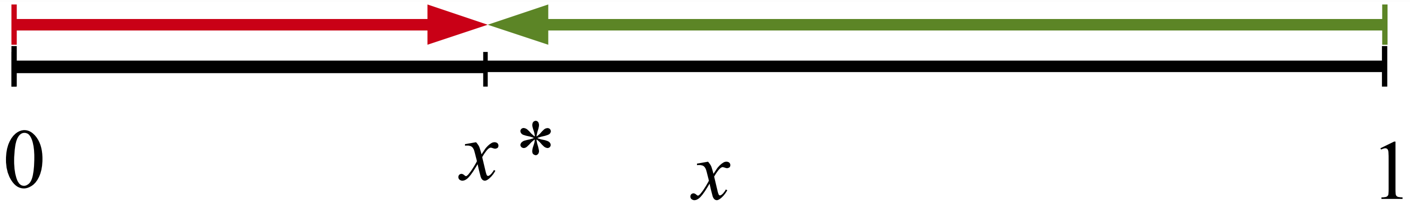
$b-d<0$



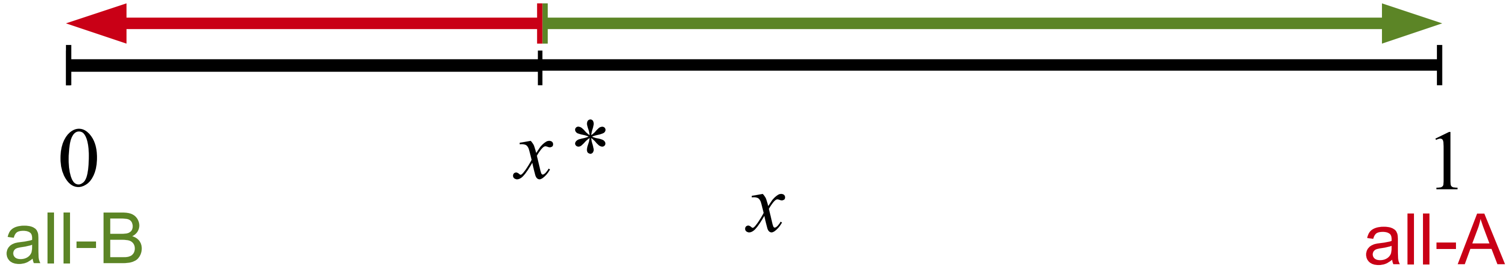
2 species, 2 players

$$(b-d)(c-a)>0 \quad \Leftrightarrow \quad x^*=\frac{b-d}{b-d+c-a}$$

$$b-d>0$$

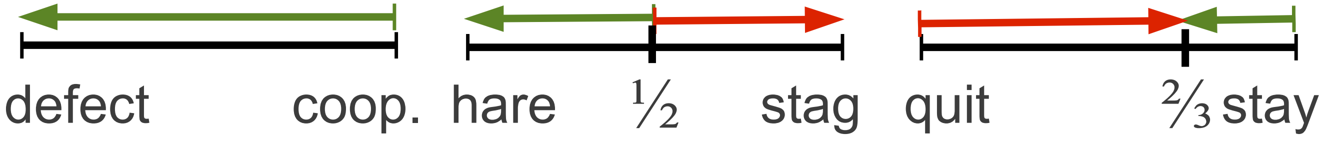


$$b-d<0$$



2 species, 2 players

	prisoner's dilemma	stag hunt	chicken / snowdrift
a	3	3	–1
b	0	0	2
c	4	2	0
d	1	1	0
$c - a$	1	–1	1
$b - d$	–1	–1	2
$(b - d)(c - a)$	–1	1	2



2 species, *n* players (public goods)

$$[\mathrm{C}]=x$$

$$W_{\mathrm{D}}(x)=\sum_{k=0}^{n-1}\binom{n-1}{k}x^{k}(1-x)^{n-1-k}\frac{b}{n}k$$

$$=b\frac{n-1}{n}x$$

$$W_{\mathrm{C}}(x)=\sum_{k=0}^{n-1}\binom{n-1}{k}x^{k}(1-x)^{n-1-k}\left(\frac{b}{n}(k+1)-c\right)$$

$$=b\frac{n-1}{n}x+\frac{b}{n}-c$$

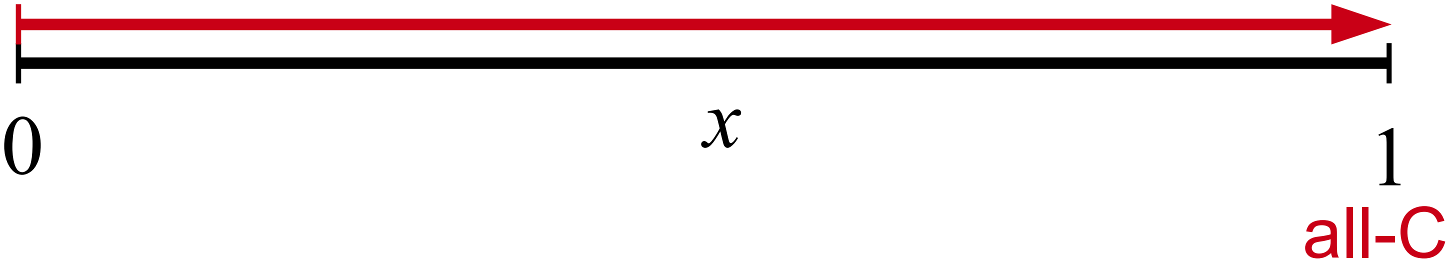
2 species, *n* players (public goods)

$$\frac{dx}{dt} = x(1-x)\left[W_{\mathrm{C}}(x) - W_{\mathrm{D}}(x)\right]$$

$$= x(1-x)\left(\frac{b}{n} - c\right)$$

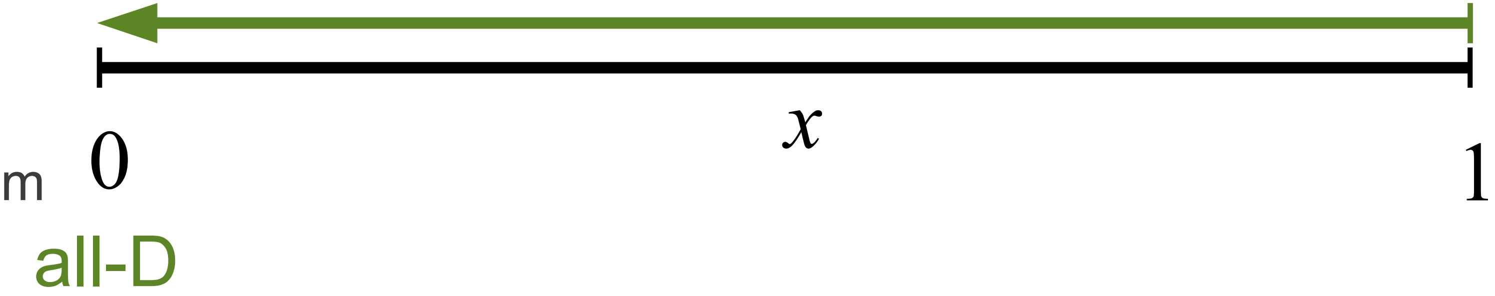
$b > nc$

weak altruism



$b < nc$

strong altruism



Replicator eq.: properties

①

$$\boldsymbol{e}_i = (0,\ldots,0,\underset{(i)}{1},0,\ldots,0)$$

$$W_i(\boldsymbol{x}) = \boldsymbol{e}_i \cdot \boldsymbol{W}(\boldsymbol{x}) \qquad \forall\, \boldsymbol{x}$$

$\boldsymbol{e}_1, \ldots, \boldsymbol{e}_r$ are equilibria of the replicator equation

Replicator eq.: properties

② $\widetilde{\Pi}(i, j_2, \ldots, j_n) = \Pi(i, j_2, \ldots, j_n) + \xi(j_2, \ldots, j_n)$

$$\Omega(\boldsymbol{x}) = \sum_{j_2=1}^{r} \cdots \sum_{j_n=1}^{r} \xi(j_2, \ldots, j_n) x_{j_2} \cdots x_{j_n}$$

$$\widetilde{W}_i(\boldsymbol{x}) = W_i(\boldsymbol{x}) + \Omega(\boldsymbol{x})$$

$$\boxed{\frac{d x_i}{d t} = x_i \left[\widetilde{W}_i(\boldsymbol{x}) - \boldsymbol{x} \cdot \widetilde{\boldsymbol{W}}(\boldsymbol{x})\right] = x_i \left[W_i(\boldsymbol{x}) - \boldsymbol{x} \cdot \boldsymbol{W}(\boldsymbol{x})\right]}$$

Replicator eq.: properties

③

$$V(\boldsymbol{x}) \equiv \prod_{i=1}^{r} x_i^{p_i}$$

$$\boxed{\frac{dV}{dt} = V(\boldsymbol{x})\left[\boldsymbol{p}\cdot\boldsymbol{W}(\boldsymbol{x}) - (\boldsymbol{p}\cdot\boldsymbol{1})\,\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right]}$$

in particular:

$$\frac{d}{dt}\left(\frac{x_i}{x_j}\right) = \left(\frac{x_i}{x_j}\right)\left[W_i(\boldsymbol{x}) - W_j(\boldsymbol{x})\right]$$

Rock, paper, scissors

$$\Pi = \begin{array}{cccc} \mathrm{R} & \mathrm{P} & \mathrm{S} & \\ \left(\begin{array}{ccc} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{array}\right. & & \left.\right) & \begin{array}{c} \mathrm{R} \\ \mathrm{P} \\ \mathrm{S} \end{array} \end{array}$$

$$\Pi = -\Pi^T \quad \Rightarrow \quad \boldsymbol{x} \cdot \boldsymbol{W}(\boldsymbol{x}) = \boldsymbol{x}\,\Pi\,\boldsymbol{x} = 0$$

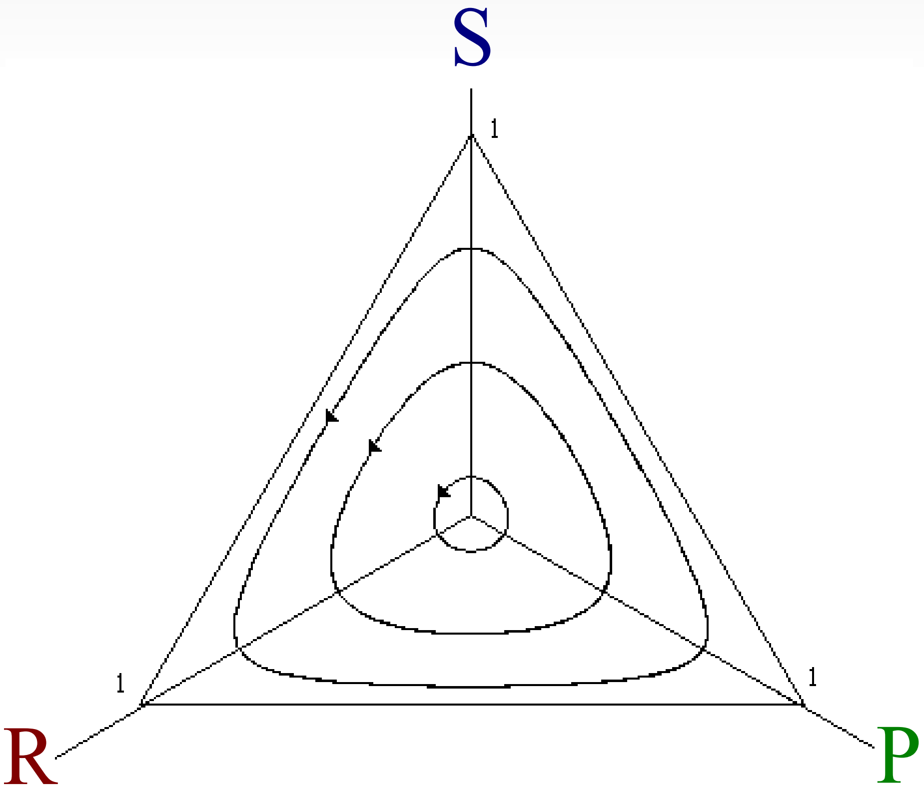
$$\boldsymbol{p} = \left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right) \quad \Rightarrow \quad \boldsymbol{W}(\boldsymbol{p}) = \mathbf{0}$$

$\boldsymbol{p}$ is an interior equilibrium

Rock, paper, scissors

$$V(\boldsymbol{x}) \equiv x_1 x_2 x_3 \quad \Rightarrow \quad \frac{dV}{dt} = V(\boldsymbol{x}) 3 \boldsymbol{p} \cdot \boldsymbol{W}(\boldsymbol{x}) = 0$$

$$x_1 x_2 x_3 = c \leqslant \frac{1}{27}$$ orbits



Generalized RPS

$$\Pi = \begin{array}{c} \\ \\ \\ \end{array}\begin{array}{ccc|c} R & P & S & \\ \hline 0 & -a & 1 & R \\ 1 & 0 & -a & P \\ -a & 1 & 0 & S \end{array}$$

$$\boldsymbol{W}(\boldsymbol{p}) = \frac{1-a}{3}\mathbf{1} \qquad \boldsymbol{p}\cdot\boldsymbol{W}(\boldsymbol{p}) = \frac{1-a}{3}$$

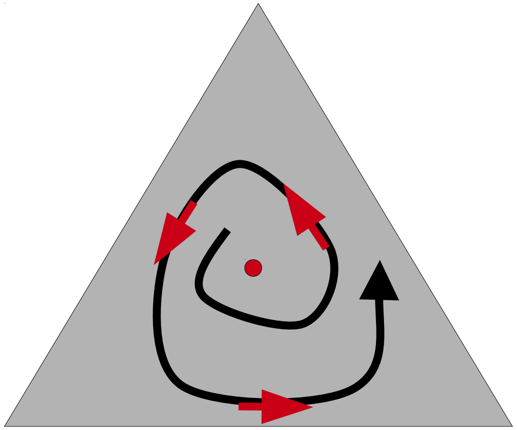
$\boldsymbol{p}$ is an interior equilibrium

Generalized RPS

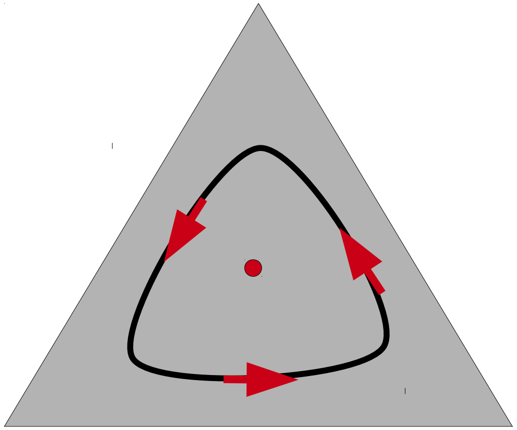
$$\frac{dV}{dt} = V(\boldsymbol{x})\left[\mathbf{1}\cdot\boldsymbol{W}(\boldsymbol{x}) - 3\,\boldsymbol{x}\cdot\boldsymbol{W}(\boldsymbol{x})\right]$$

$$= V(\boldsymbol{x})(1-a)\left[1-3\left(x_1 x_2 + x_2 x_3 + x_3 x_1\right)\right]$$

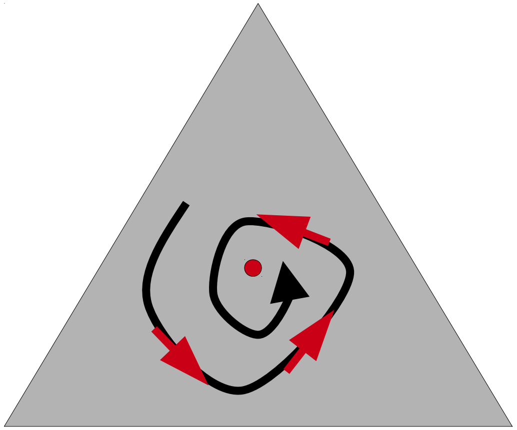
$$= V(\boldsymbol{x})\frac{3}{2}(1-a)\left[x_1^2 + x_2^2 + x_3^2 - \frac{1}{3}\right]$$



$a > 1$



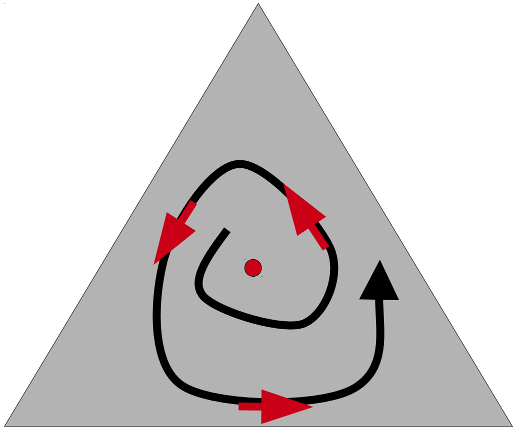
$a = 1$



$a < 1$

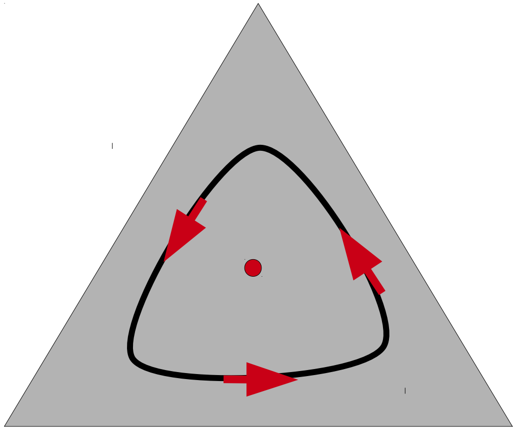
Generalized RPS

$$\Pi = \begin{array}{cc} \begin{matrix} \mathrm{R} & \mathrm{P} & \mathrm{S} \end{matrix} & \\ \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix} & \begin{matrix} \mathrm{R} \\ \mathrm{P} \\ \mathrm{S} \end{matrix} \end{array}$$



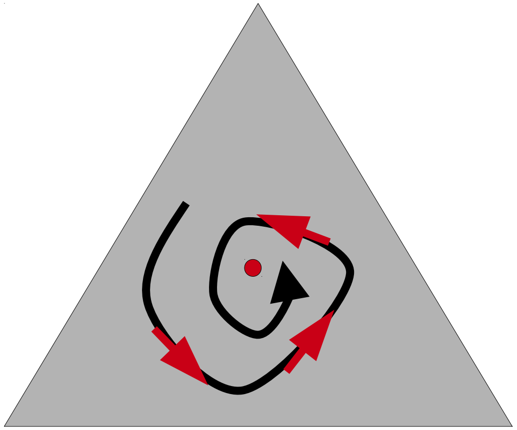
$\det \Pi < 0$

$(a_1 a_2 a_3 > b_1 b_2 b_3)$



$\det \Pi = 0$

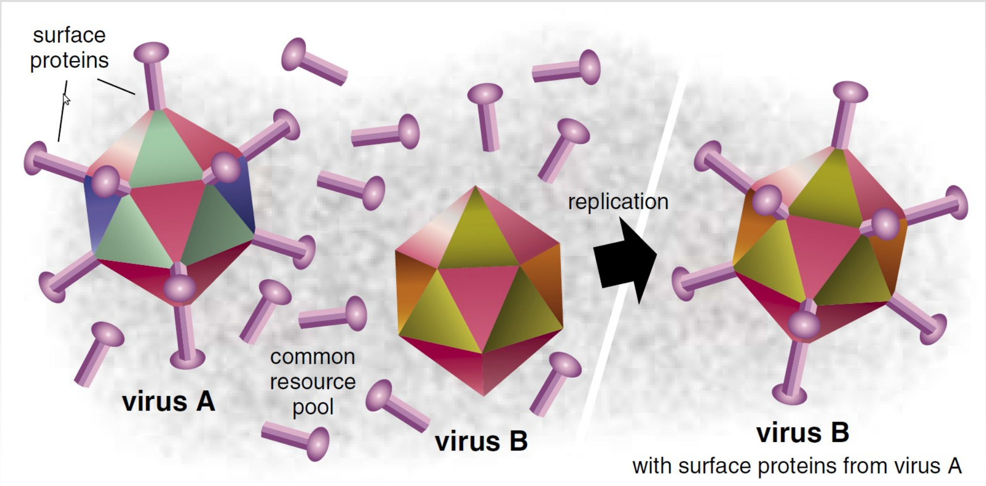
$(a_1 a_2 a_3 = b_1 b_2 b_3)$

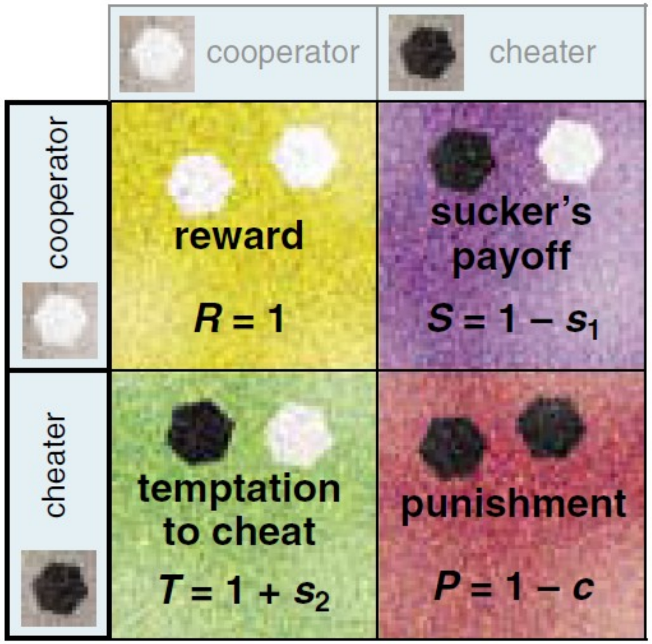


$\det \Pi > 0$

$(a_1 a_2 a_3 < b_1 b_2 b_3)$

Hyperparasites





	cooperator	cheater
cooperator	**reward** $R = 1$	**sucker's payoff** $S = 1 - s_1$
cheater	**temptation to cheat** $T = 1 + s_2$	**punishment** $P = 1 - c$

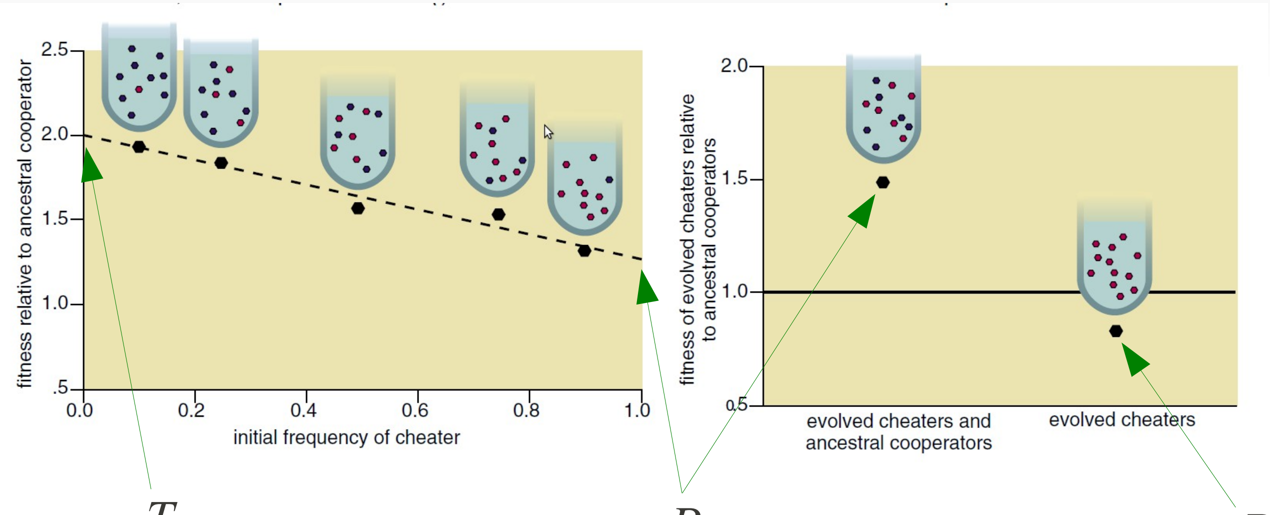
$$[\text{cheater}] = x$$

$$W_{\text{cheater}}(x) = T(1-x) + P\,x$$
$$W_{\text{cooper.}}(x) = R(1-x) + S\,x$$

Turner & Chao, Nature **398**, 441-443 (1999)

Hyperparasites

$$\frac{W_{\text{cheater}}(x)}{W_{\text{cooper.}}(x)} = \frac{T(1-x)+P\,x}{R(1-x)+S\,x}$$

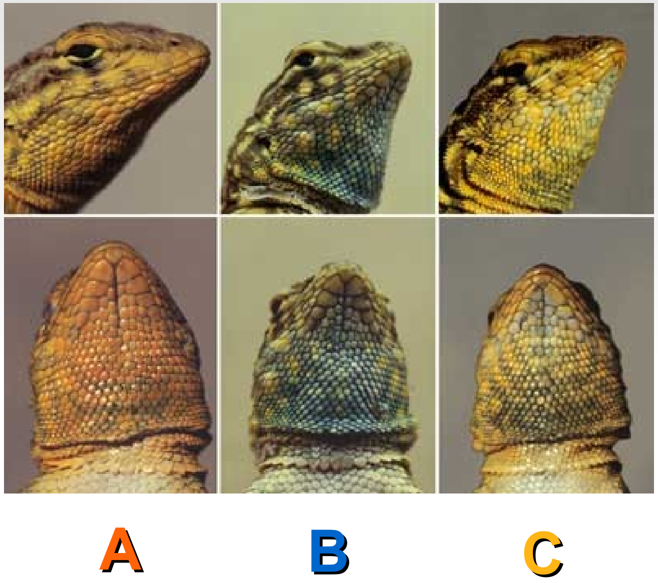


$\frac{T}{R}$ $\frac{P}{S}$ P

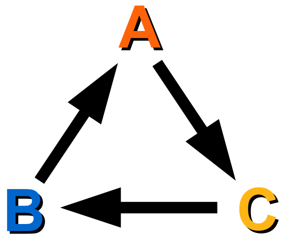
Turner & Chao, Nature **398**, 441-443 (1999)

Lizard's mating habits

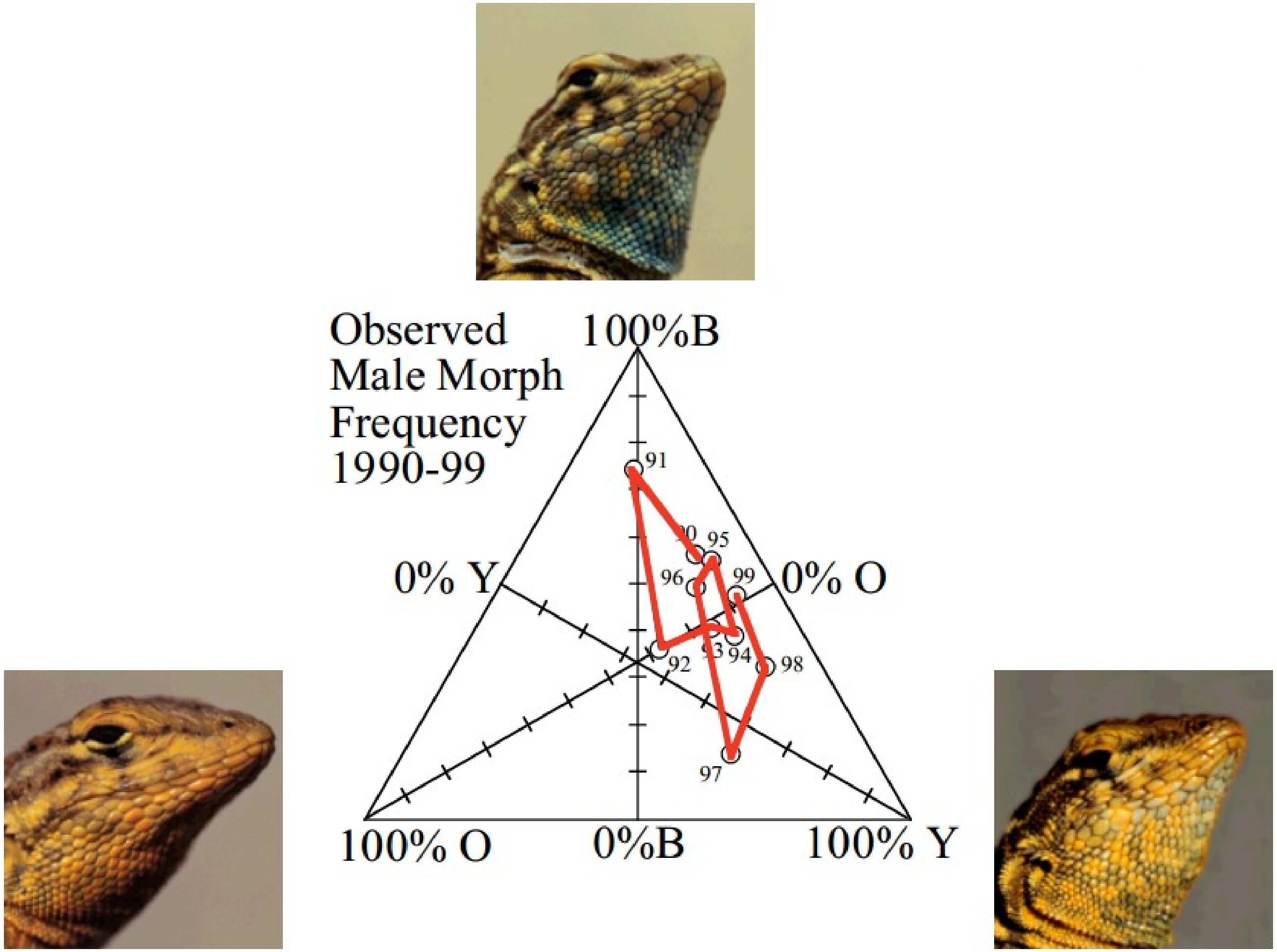
Uta stansburiana



A monogamous and jelous
B polygamous
C sneaky



Lizard's mating habits



Zamudio & Sinervo, PNAS **97**, 14427-14432 (2000)