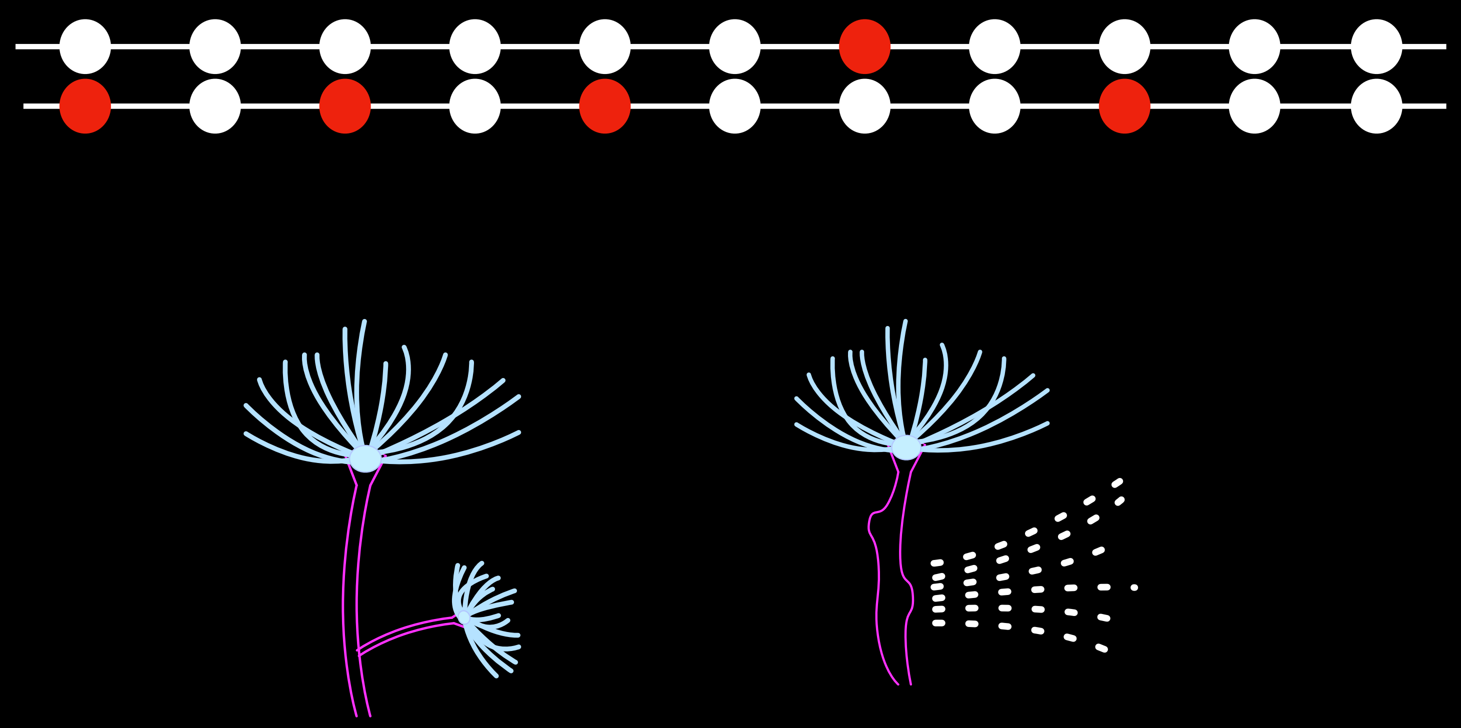
Reciprocity and punishment in the evolution of cooperation

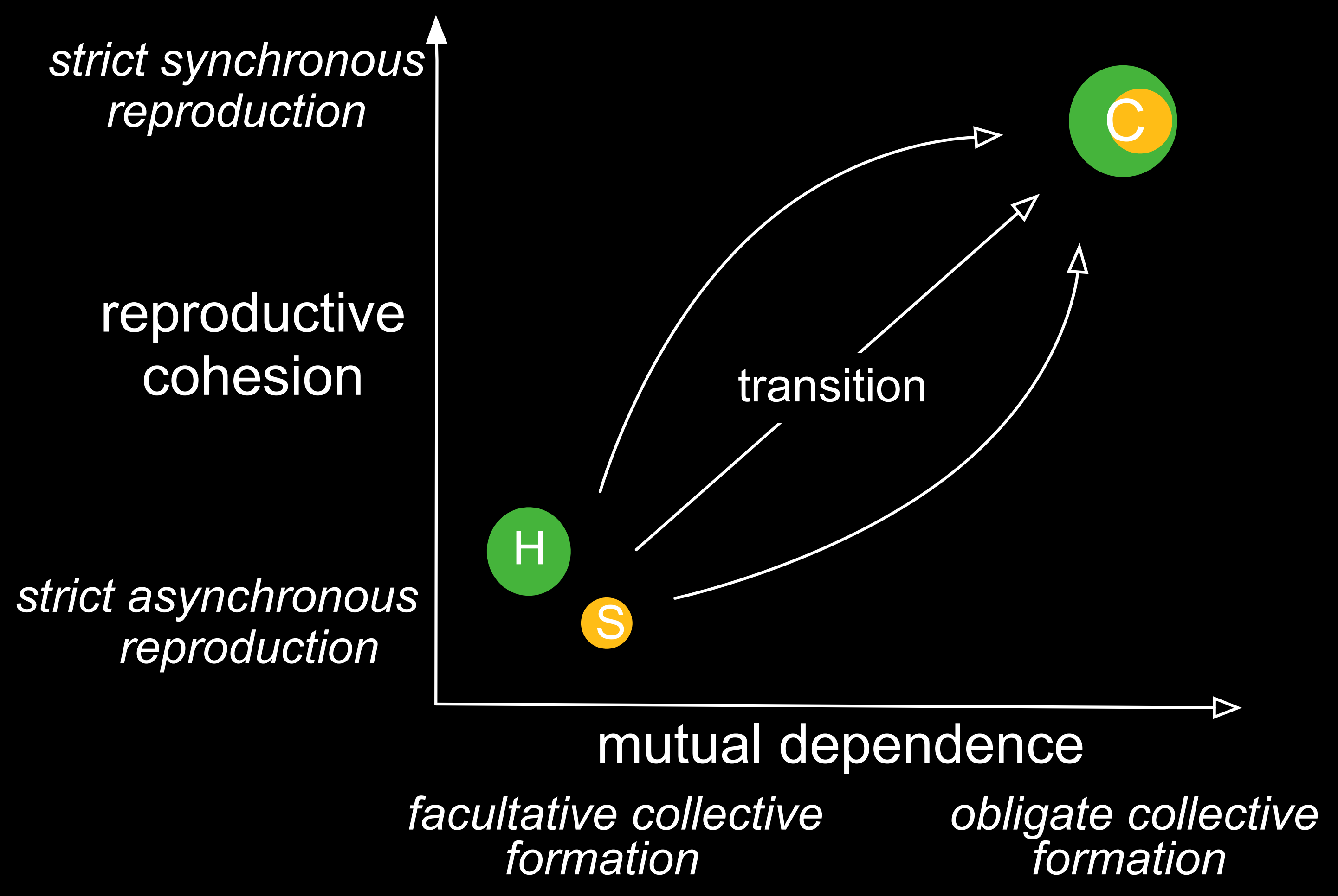
Gaurav Athreya

me



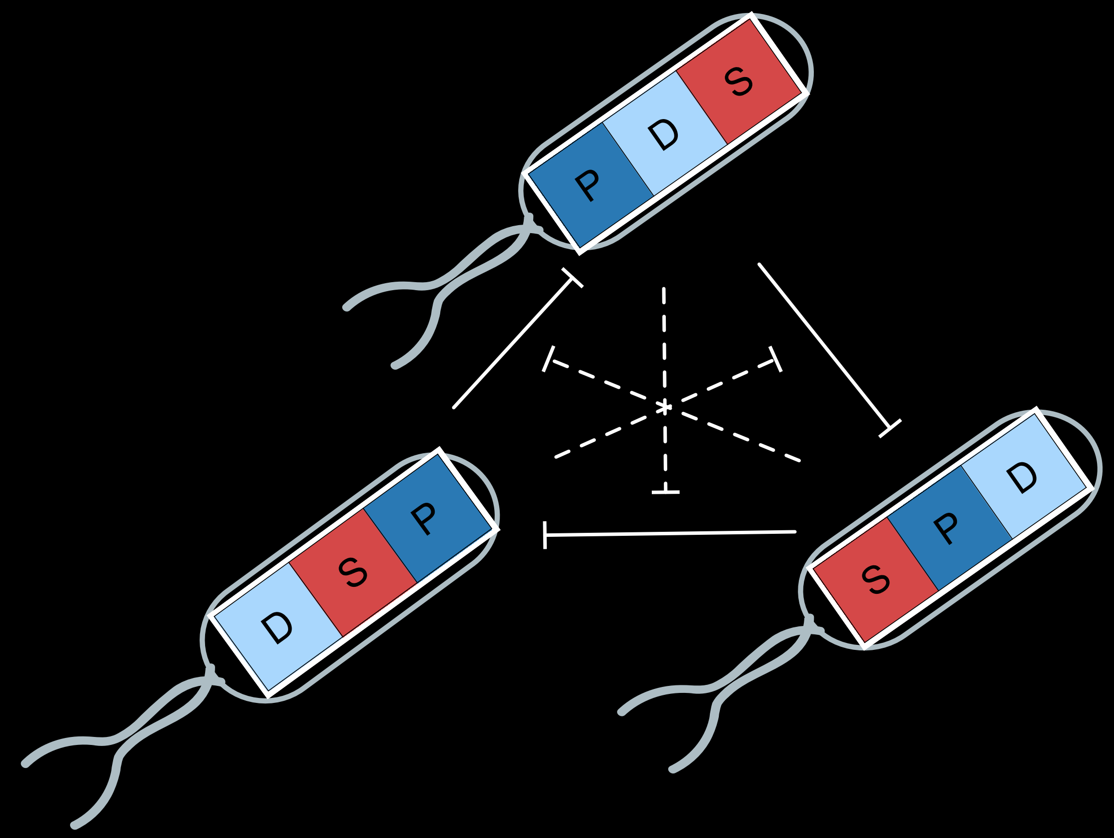
Cartoon *Hydra oligactis* budding (left) and producing gametes (right)

The evolution of sex



Formalising the notion of a between-species ETI

Evolutionary Transitions in Individuality



Interaction graph of a certain kind of microbial community

Community ecology

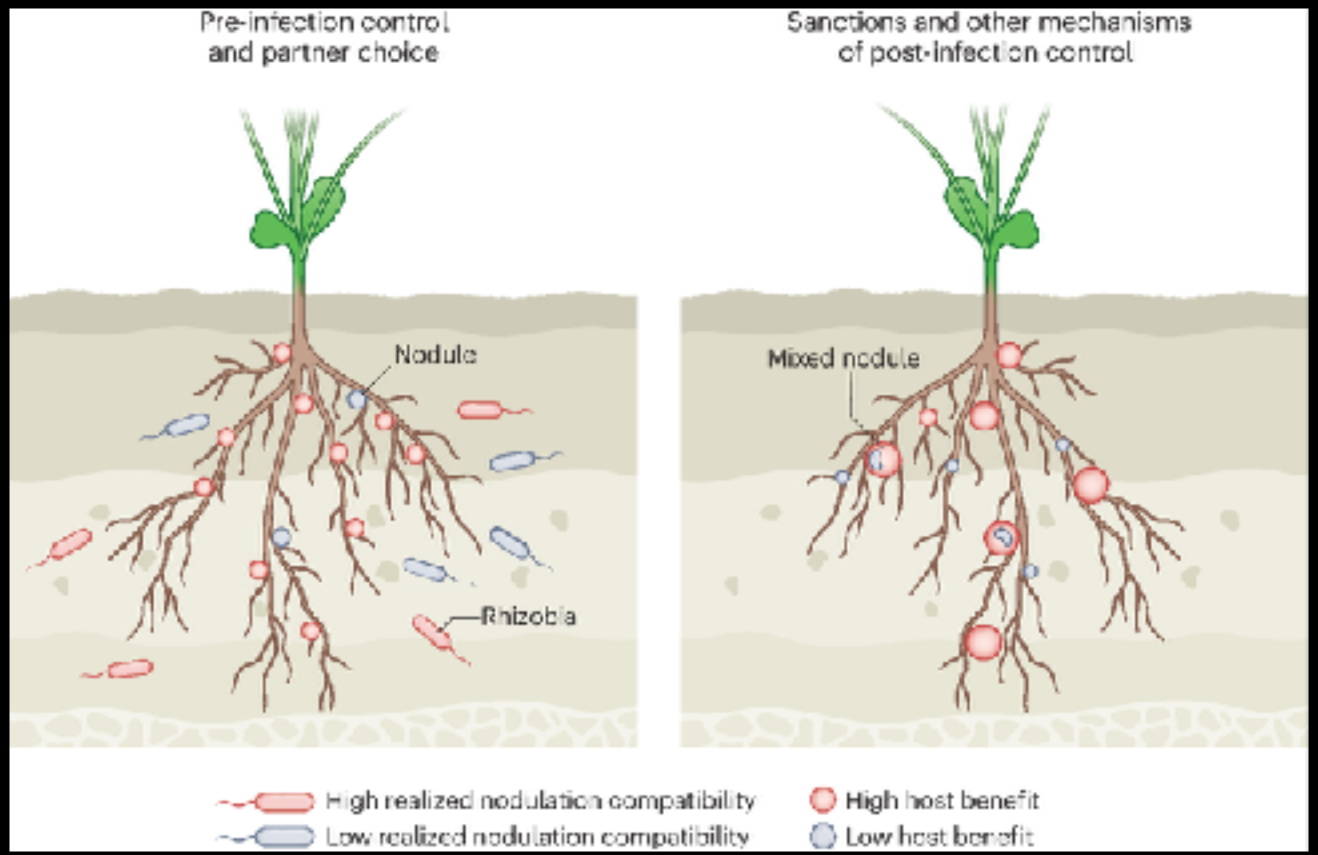
The evolution of cooperation

P. nigripilosus, a cheater of the ant-acacia mutualism

Two vervet monkeys grooming each other

meerkat alarm calls

Bloodsharing in vampire bats



Nitrogen fixation in the legume-rhizobium mutualism

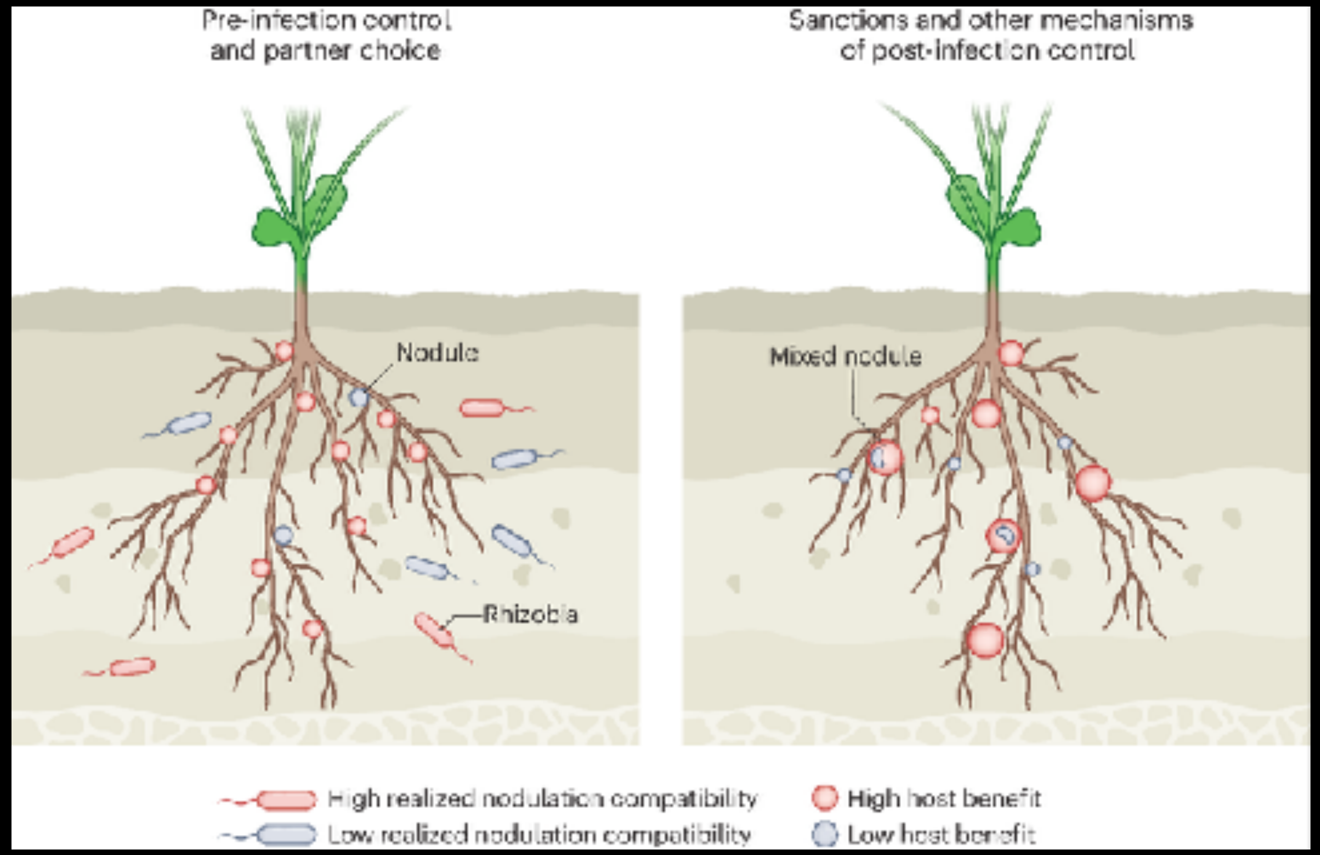
The evolution of cooperation

P. nigripilosus, a cheater of the ant-acacia mutualism

Two vervet monkeys grooming each other

meerkat alarm calls

Bloodsharing in vampire bats



Nitrogen fixation in the legume-rhizobium mutualism

cooperation
vs.
altruism
vs.
mutualism?

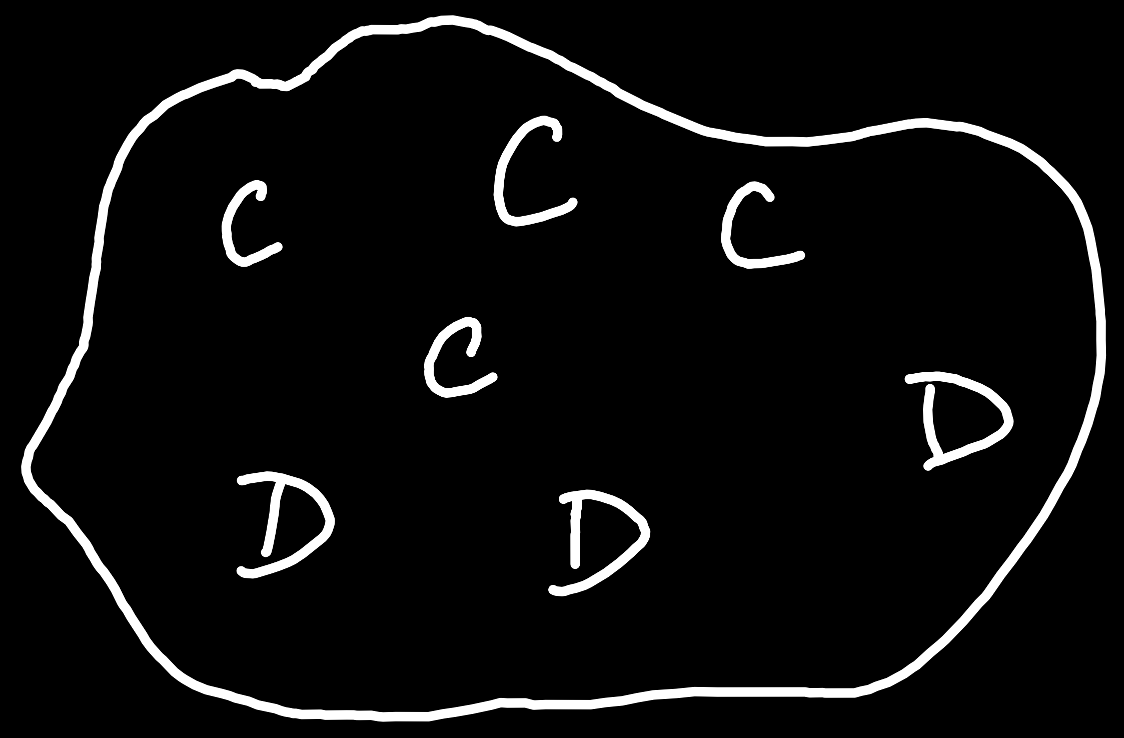
The prisoner's dilemma

payoff to "row player"	C	D
C	$b-c$	$-c$
D	b	0

$$\dot{p} = p(1-p)(\pi_C - \pi_D)$$

$$\pi_C > \pi_D \Rightarrow \dot{p} > 0$$

Cooperation? Positive assortment



groups of size N, each C or D, $\# C = k$, $\frac{b}{N} - c > 0$

payoff

$$\Pi_C : \frac{kb}{N} - c = \frac{b}{N} - c + \frac{(k-1)b}{N}$$

$$\Pi_D : \frac{kb}{N} = 0 + \frac{kb}{N}$$

average interaction environment: e_C, e_D

$$\Pi_C = \frac{b}{N} - c + \frac{e_C b}{N}$$

$$\Pi_D = 0 + \frac{e_D b}{N}$$

when is $\Pi_C > \Pi_D$?

$$e_C - e_D > \frac{cN}{b} - 1 > 0$$

Fletcher and Doebeli, 2009

Cooperation? Positive assortment

well-mixed : $\mathbb{P}(\#\text{ coop} = k) = \binom{N}{k} p^k (1-p)^{N-k}$ $\quad e_C = e_D = Np$

or, cooperators increase in freq $\Rightarrow$ $\exists$ positive assortment

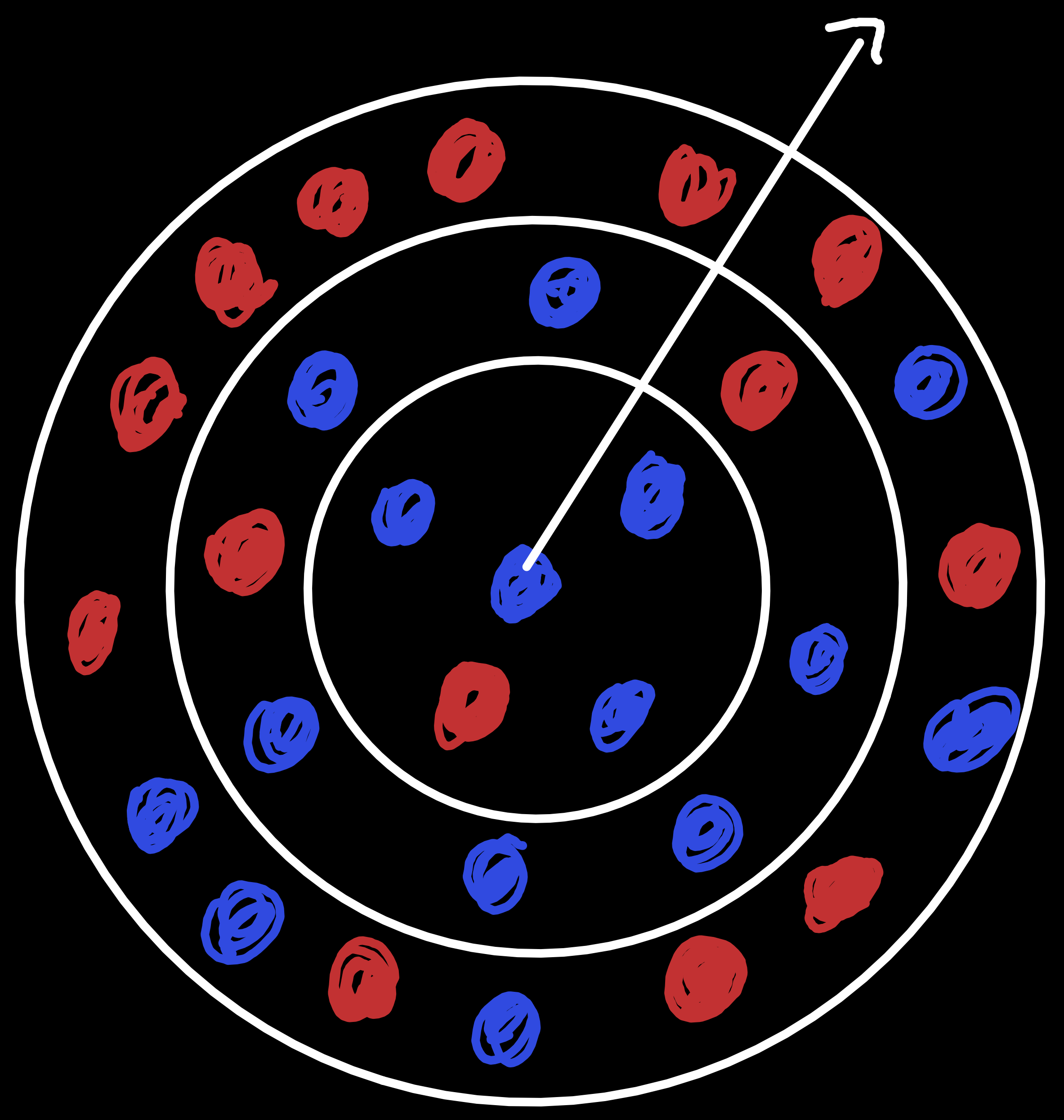
$$\left(\frac{e_C + 1}{N} - \frac{e_D}{N}\right) b > c$$

A kind of Hamilton's rule!

do cooperators receive more help or defectors ?

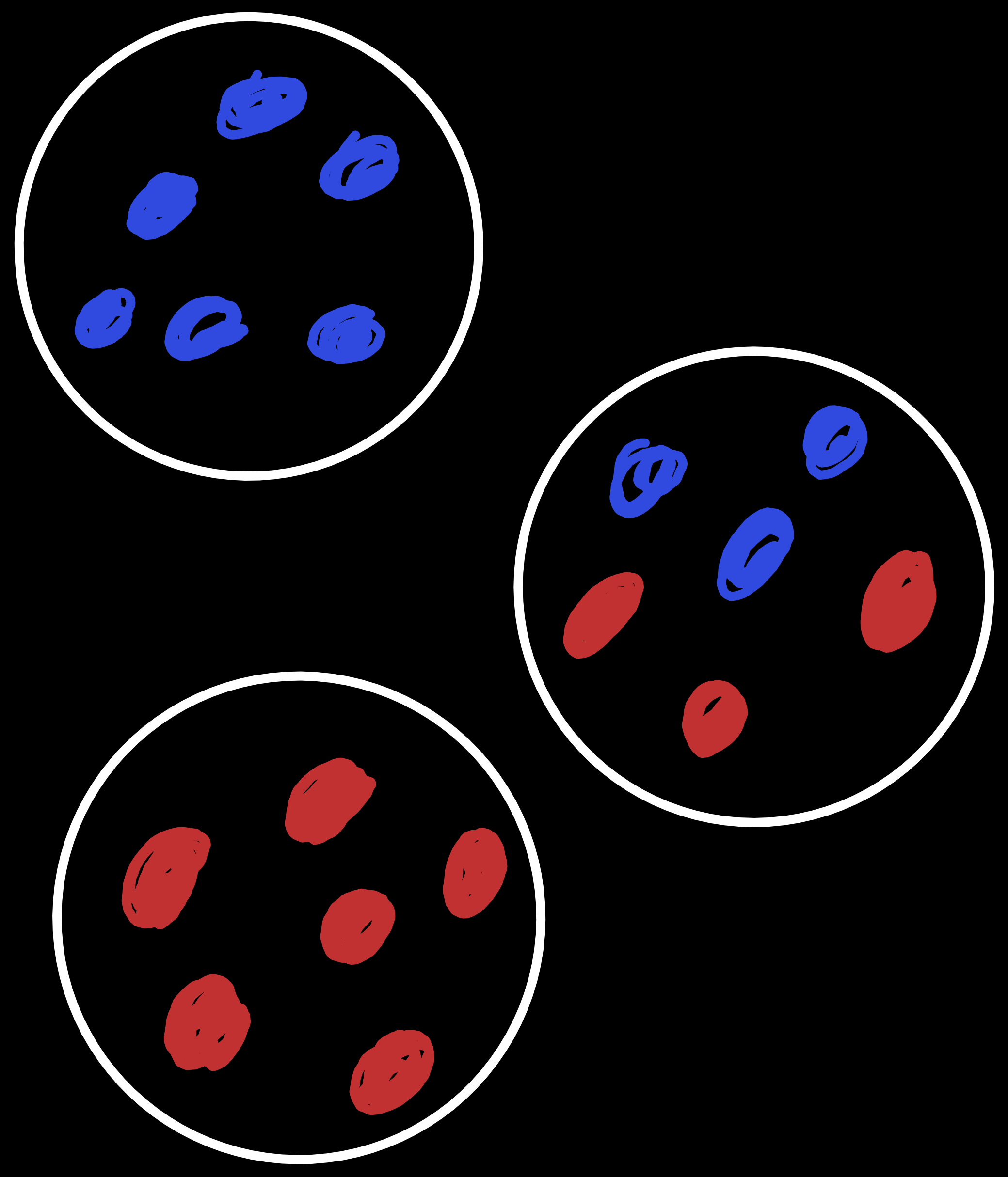
Fletcher and Doebeli, 2009

Routes to positive assortment

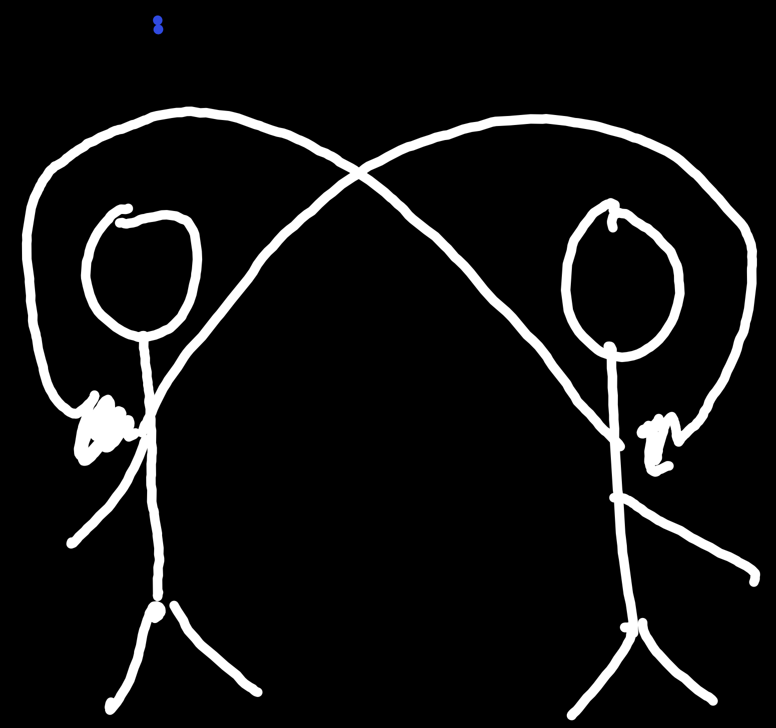


Limited dispersal /
"population viscosity" /
spatial structure

Kin recognition



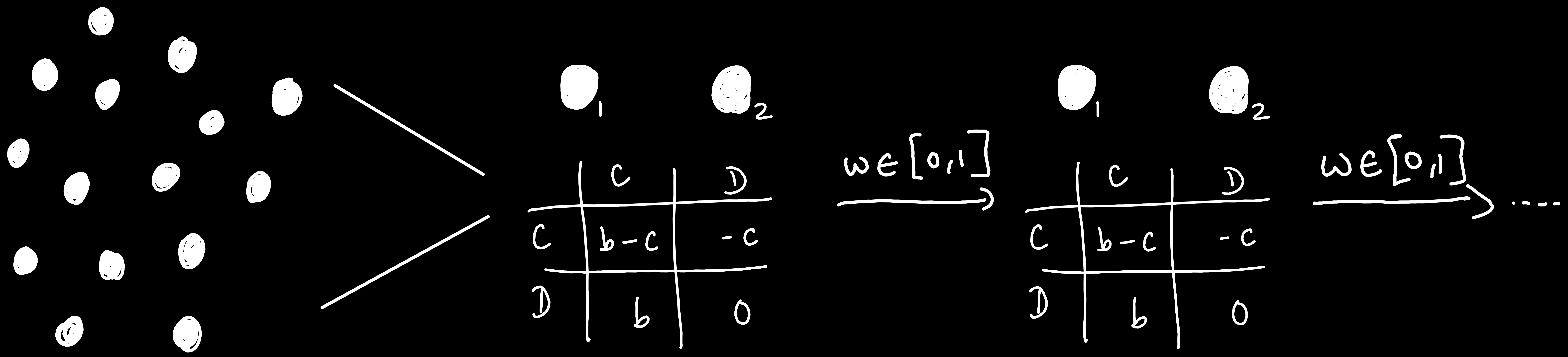
Multilevel selection



Conditional behaviour

The iterated prisoner's dilemma

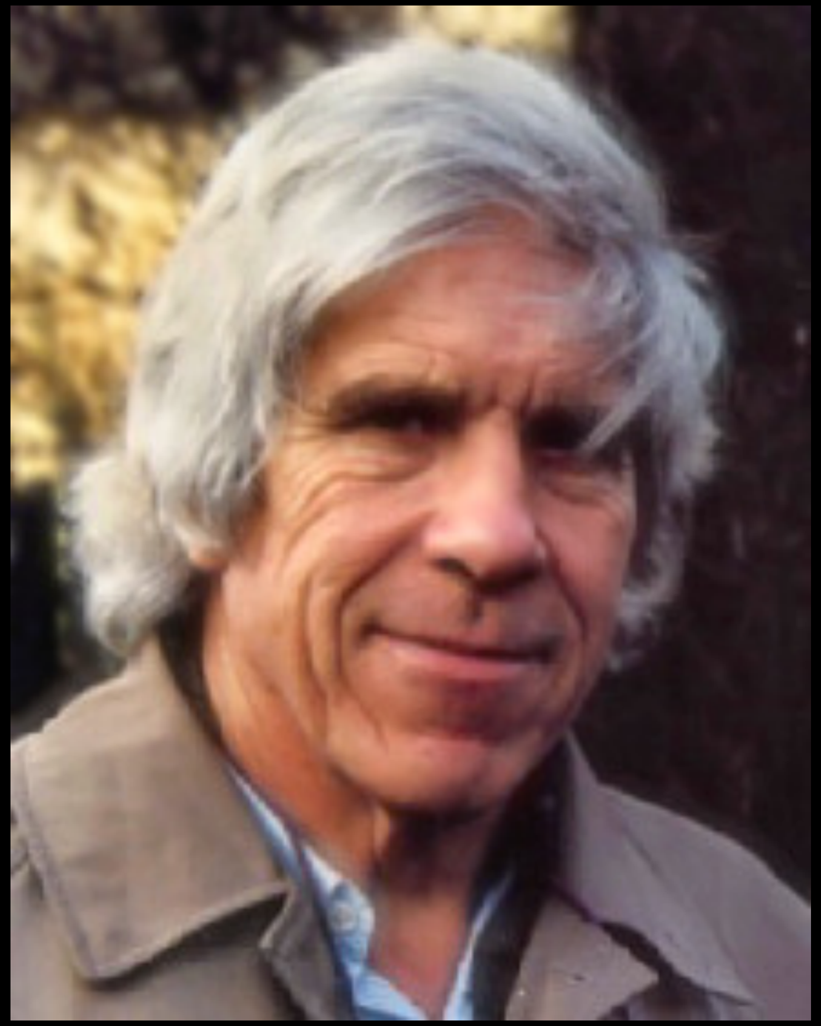
- remember interaction history
- change behaviour based on this information



Why not a fixed number *N* of rounds of interaction?

History of the iterated Prisoner's Dilemma

Trivers, 1971



"To see what type of strategy can thrive in a variegated environment of more or less sophisticated strategies, one of us (R.A.) conducted a computer tournament for the Prisoner's Dilemma. The strategies were submitted by game theorists in economics, sociology, political science, and mathematics."

R. Axelrod (left) and W. D. Hamilton (right), 1981

Direct reciprocity: *Tit-for-Tat* (TFT)

conditional cooperation :

$$\mathbb{P}(C \mid C) = 1$$
$$\mathbb{P}(D \mid D) = 1$$

$$\pi(TFT \mid TFT) = 1.(\quad\cdot\quad) + w.(\quad) + w^2(\quad) + w^3(\quad)\ldots$$

$$= \frac{b-c}{1-w}$$

$$\pi(ALLC \mid TFT) = 1.(b-c) + w(b-c) + \ldots$$

$$= \frac{b-c}{1-w} \quad !$$

positive assortment ?

Tit-for-Tat is an ESS, sort of

$$\pi(\text{ALLD} \mid \text{TFT}) = 1 \cdot b + w \cdot 0 + w^2(0) + \cdots$$
$$= b$$

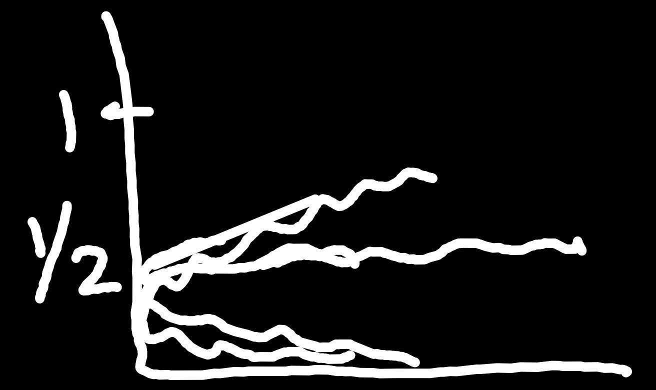
$$\pi(\text{TFT} \mid \text{TFT}) > \pi(\text{ALLD} \mid \text{TFT}) \quad \text{when} \quad \frac{b-c}{1-w} > b$$
$$\Rightarrow \boxed{wb > c}$$

$$\pi(\text{DCDCDC}\ldots \mid \text{TFT}) = b + w(-c) + w^2 b + w^3(-c) + \cdots$$
$$= \frac{b - wc}{1 - w^2}$$

$$\frac{b-c}{1-w} > \frac{b-wc}{1-w^2} \Rightarrow \boxed{w > \frac{b}{c}}$$

Tit-for-Tat is an ESS, sort of

ALLC arises as a mutant



$$\Pi(\text{ALLD} \mid \text{TFT}) \cdot q + \Pi(\text{ALLD} \mid \text{ALLC})(1-q) > V(\text{TFT}/\text{TFT})$$

$$q \cdot \frac{b}{1-\omega} + (1-q)\, b > \frac{b-c}{1-\omega}$$

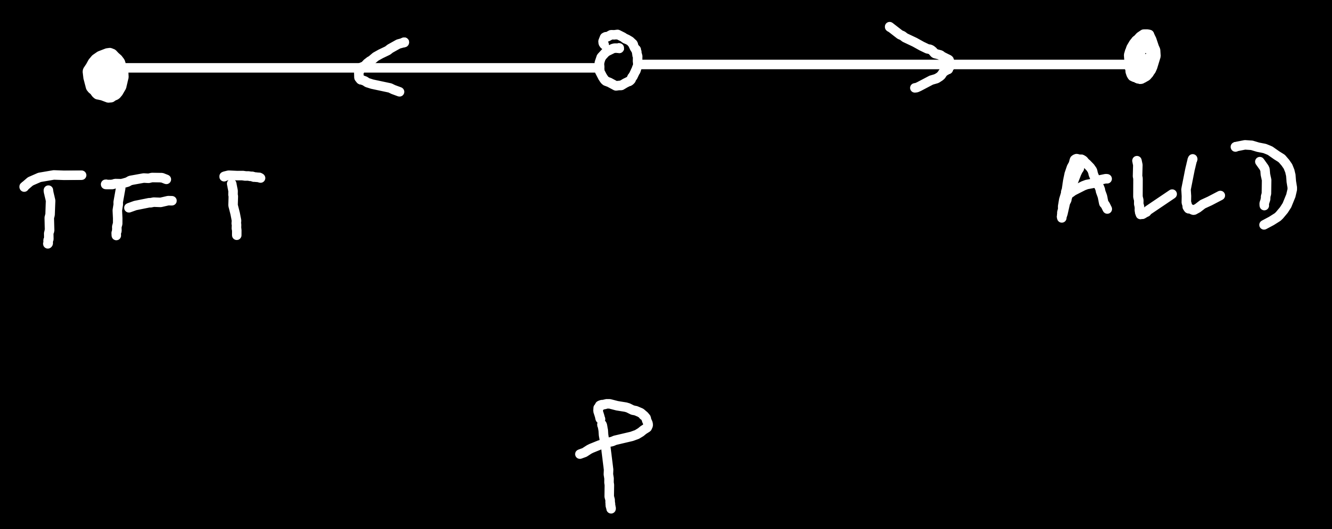
$q > 1 - \frac{c}{\omega b}$ ALLD invades and goes to fixation

Any strategy can be destabilised (Boyd & Lorberbaum 1987)

Always-Defect is also an ESS, sort of

$$\pi(ALLD \mid ALLD) = 0$$

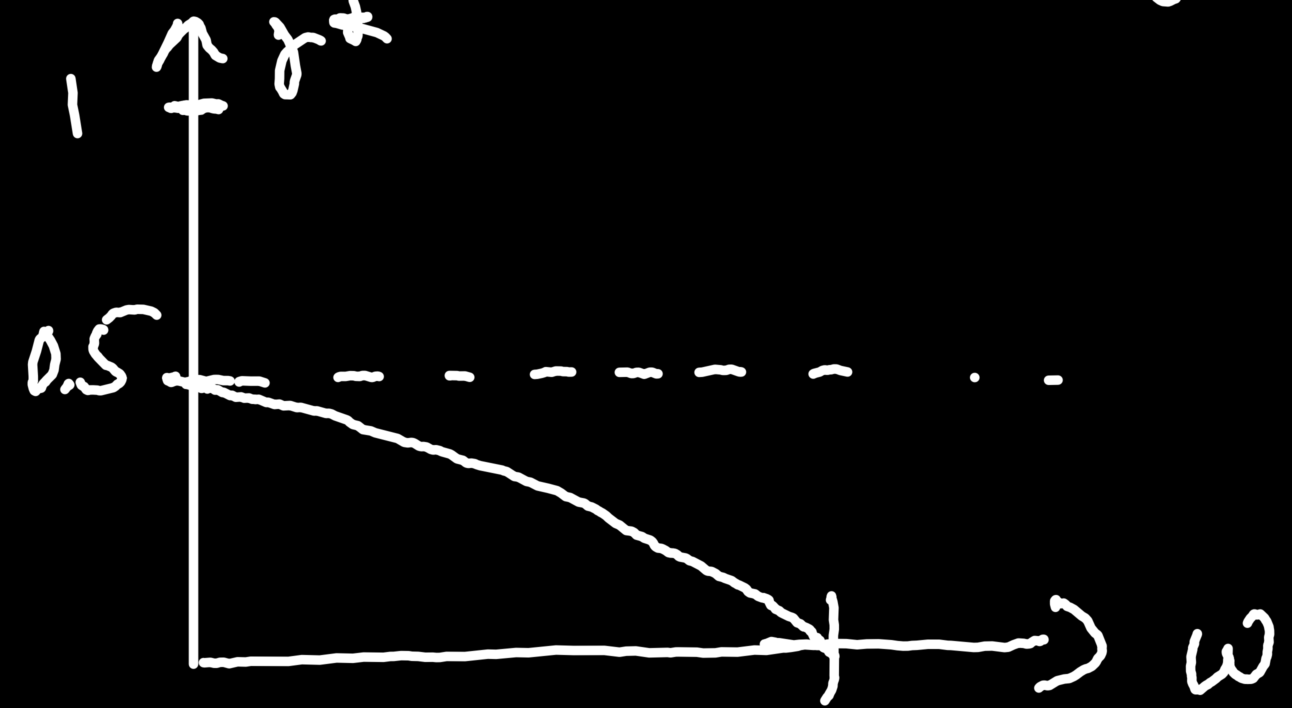
$$\pi(TFT \mid ALLD) = -c$$

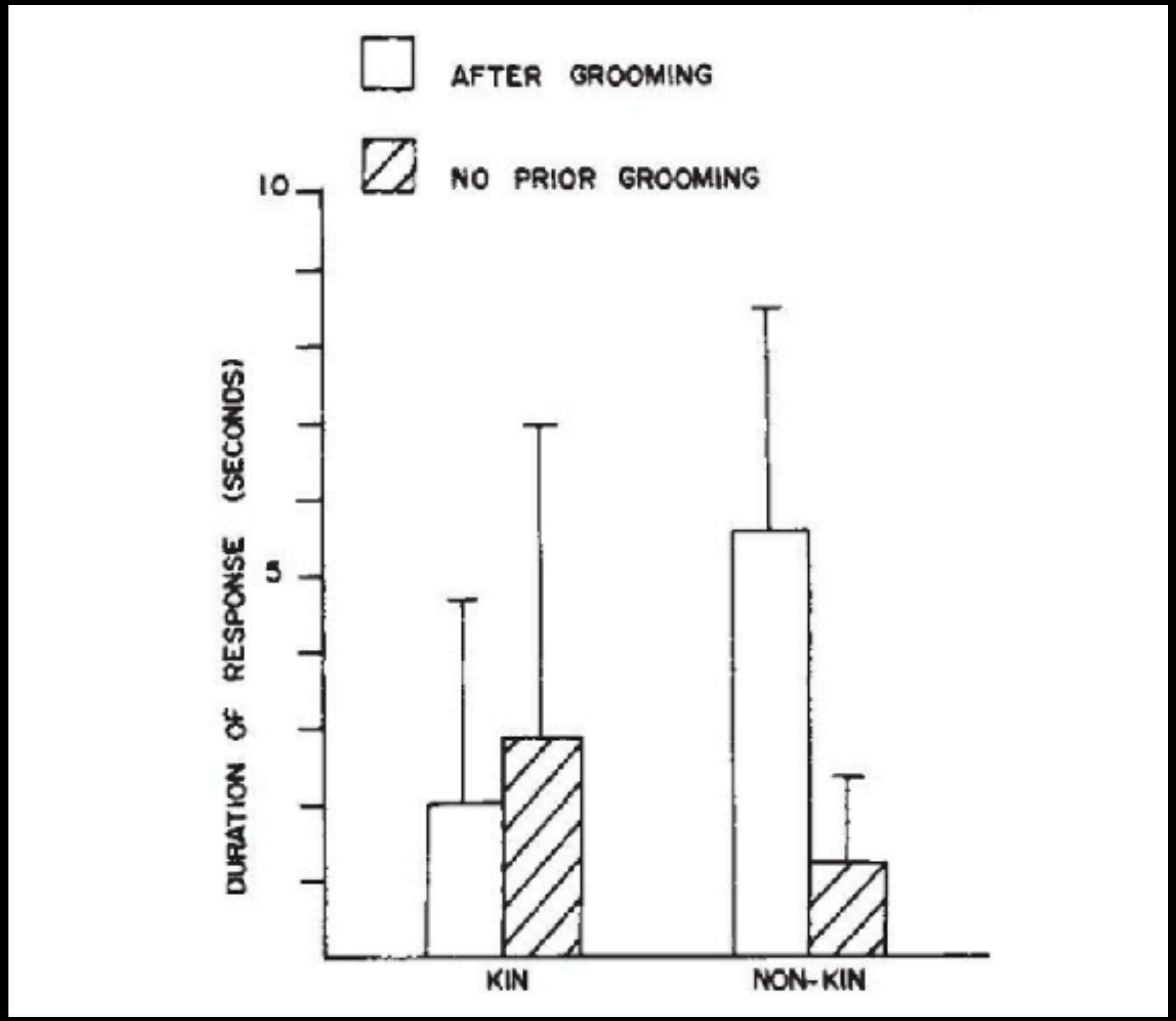


$$0 > -c$$

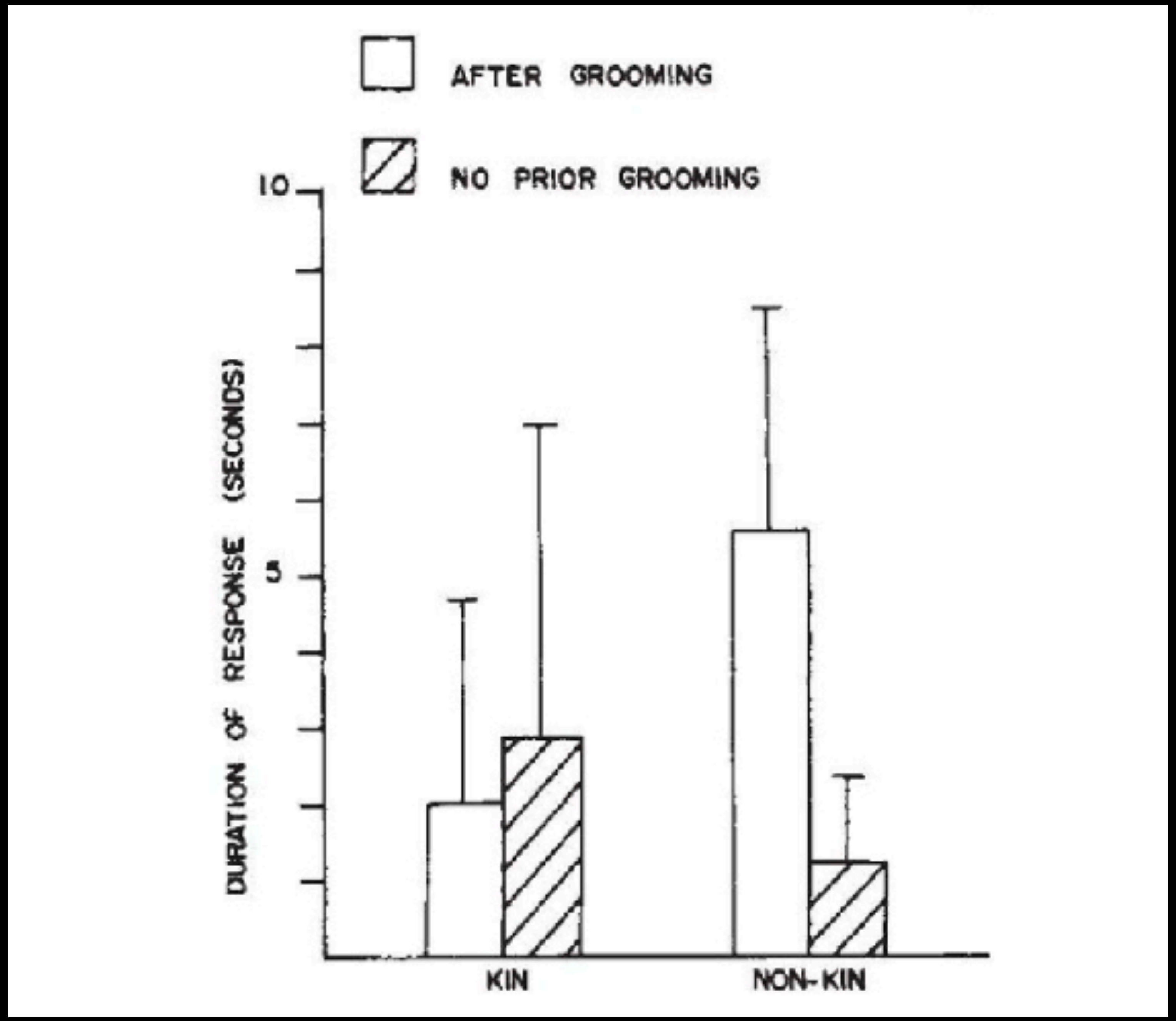
BUT! If interacting partners have an additional assortation mechanism, TFT can invade ALLD if

$$r > \frac{1-w}{\frac{b}{c}-w}$$

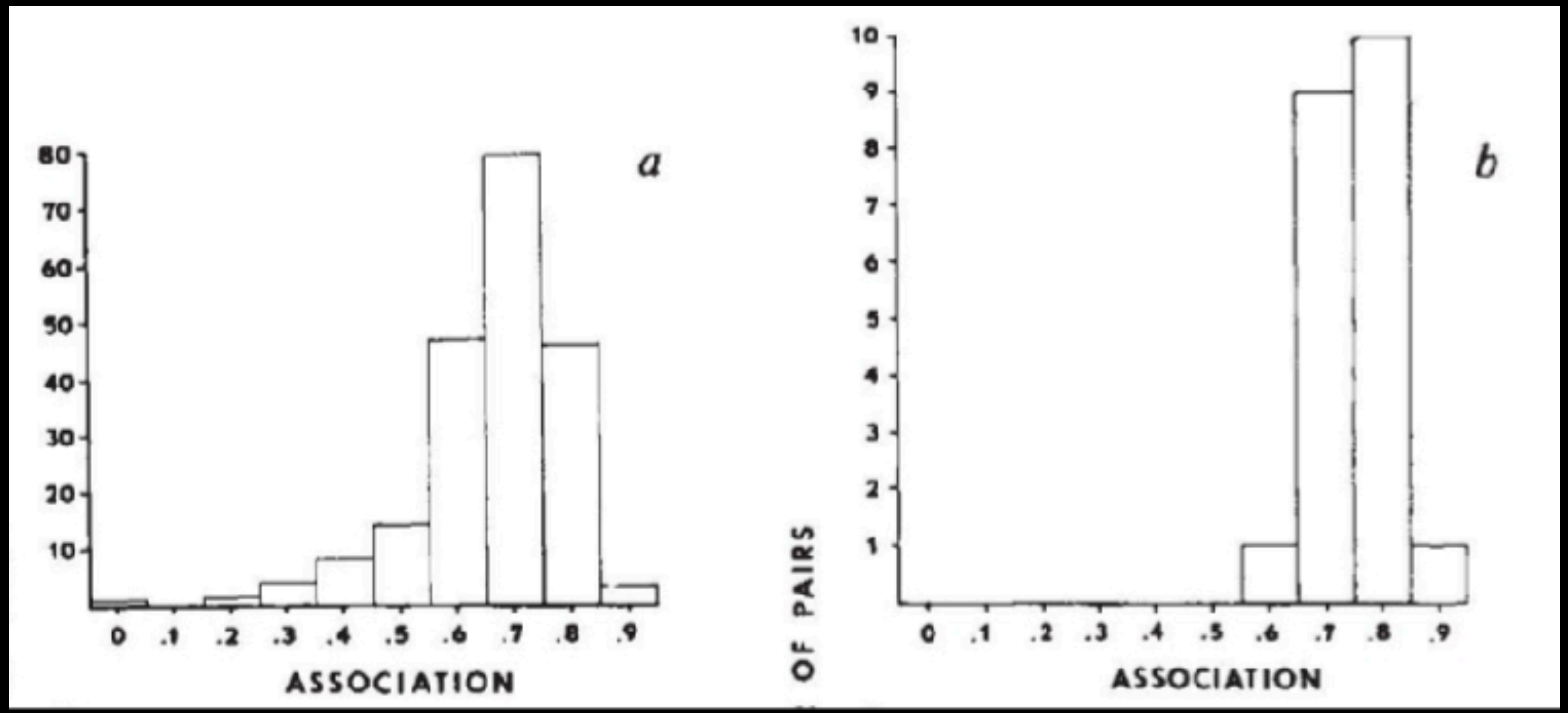




Seyfarth and Cheney, 1984



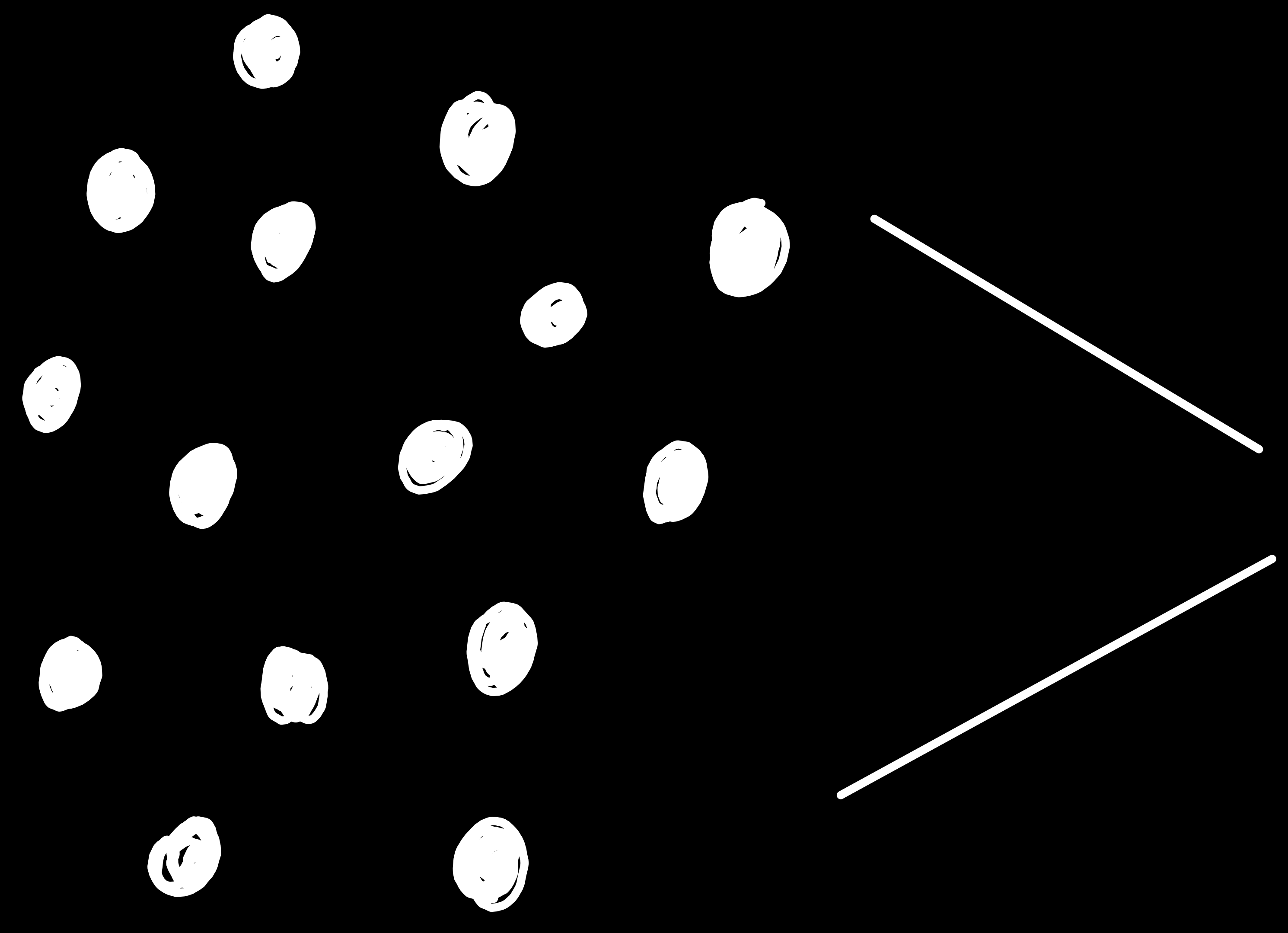
Seyfarth and Cheney, 1984



Wilkinson, 1984

Indirect reciprocity: *Discriminator*

- also remember all individuals



$1 \quad 2$

	C	D
C	$b-c$	$-c$
D	b	0

$\xrightarrow{w \in [0,1]}$

$1 \quad 3$

	C	D
C	$b-c$	$-c$
D	b	0

$\xrightarrow{w \in [0,1]} \ldots$

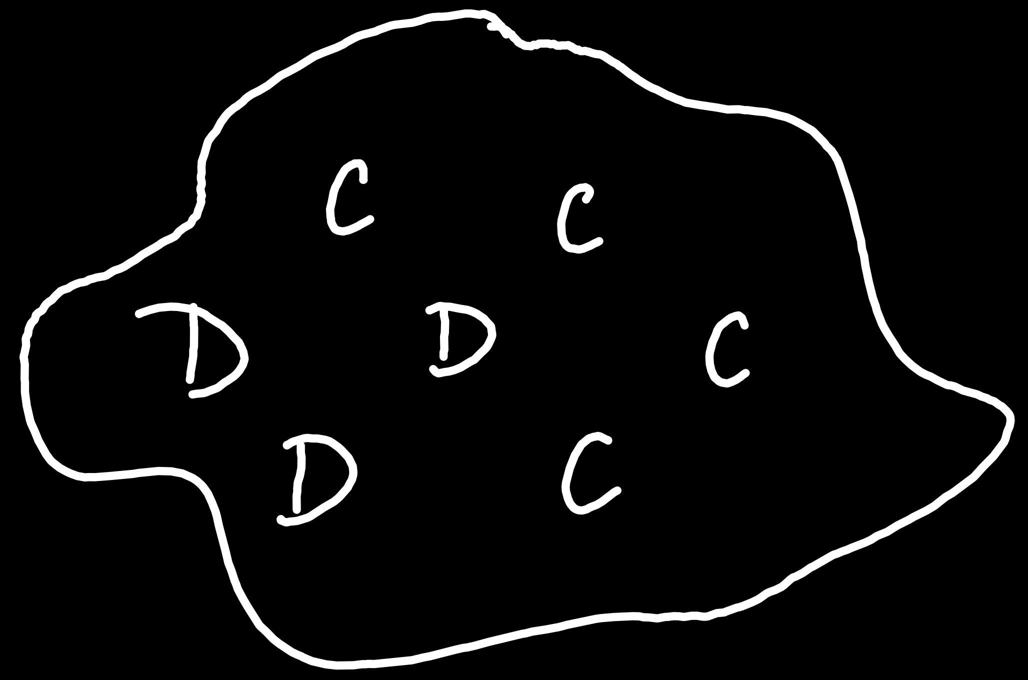
$$\pi(\text{Discriminator} \mid \text{Discriminator}) = (b-c)\cdot 1 + (b-c)w + (b-c)w^2 + \ldots\ldots$$

$$= \frac{b-c}{1-w}$$

$$\pi(\text{ALLD} \mid \text{Discriminator}) = b \cdot 1 + 0 \cdot w + 0 \cdot w^2 + \ldots\ldots$$

$$= b$$

Large groups and insufficient reciprocity



groups of size N, each C or D, # coop $= k$

payoffs $\pi_C = \frac{kb}{N} - c$ $\quad \pi_D = \frac{kb}{N}$

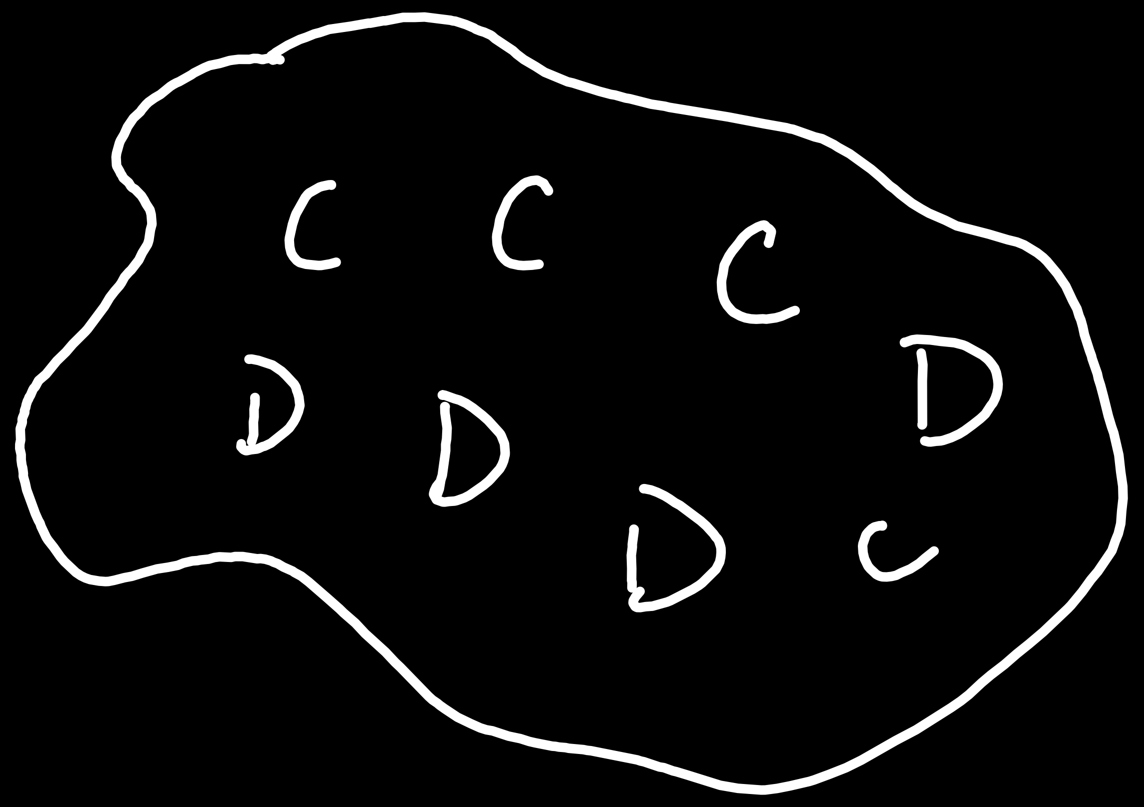
strategy $(T_i)_{i=0}^{N-1}$:= cooperate only if i <u>others</u> cooperate

$$\pi(T_{N-1} \mid N-1) = \frac{b-c}{1-w}, \quad \pi(\mathrm{ALLD} \mid N-1) = \frac{n-1}{n} b$$

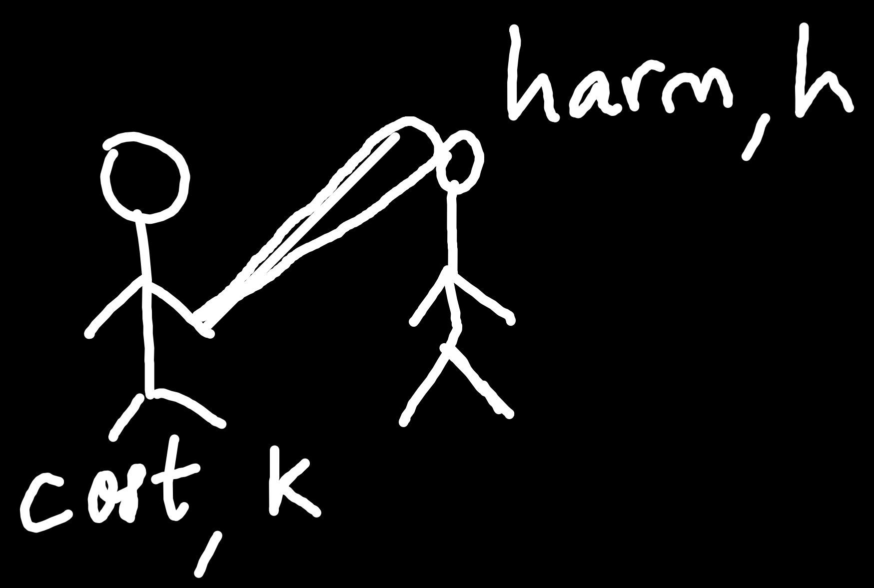
T_{N-1} is an ESS if $\frac{b-c}{1-w} > \frac{n-1}{n} b$, T_{N-1} cannot invade ALLD

T_{N-m} $\forall\, m > 1$ not an ESS, and kinship is not as useful.

Punishment



+



Altruistic punisher (AP)

Reluctant cooperator (RC)
(cooperate only after being punished)

$$\pi(AP \mid x \text{ other APs}) = (x+1)\frac{b}{N} - c - (N-x-1)k + \omega \cdot \frac{b-c}{1-\omega}$$

$$\pi(RC \mid x \text{ other APs}) = \begin{cases} \frac{xb}{N} - xh + \frac{\omega}{1-\omega}(b-c) & x > 0 \\ 0 & x = 0 \end{cases}$$

AP is an ESS when $(N-1)h > c - \frac{b}{N}$

AP can invade RC when $\omega \frac{b-c}{1-\omega} - (N-1)k > c - \frac{b}{N}$

Group-foraging chimpanzees,
de Waal 1982

Worker punishment in naked mole rats (a eusocial mammal!),
Reeve 1992

cooperatively breeding superb fairywrens,
Mulder and Langmore 1993

Clutton-Brock and Parker, 1995

What have we learnt?

- Cooperation? Positive assortment
- Reciprocity can lead to long-lasting cooperation, but in principle it is not always evolutionarily stable
- When groups are large, reciprocity is not efficient
- Punishment can solve the problem of cooperation in large groups

Extensions and more recent work

The second order free-rider problem

The leading eight: social norms for indirect reciprocity

Memory-*n* strategies (aka reactive-*n*). What is the maximum necessary memory?

Price equation & Hamilton's rule