El juego de la evolución

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Sumario

(1) Teoría de Juegos

(2) La evolución como un juego

(3) Ejemplos de la biología

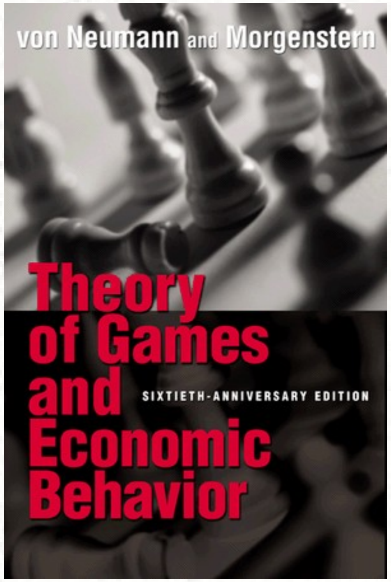
(4) La evolución de la cooperación

Teoría de Juegos

Origen

Von Neumann
(1903-1957)

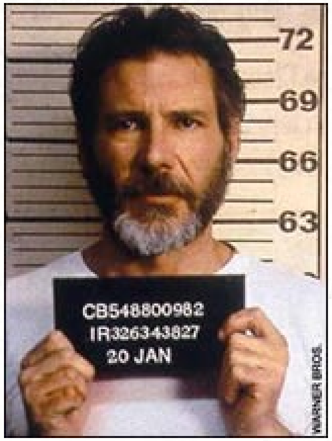
Morgenstern
(1902-1977)



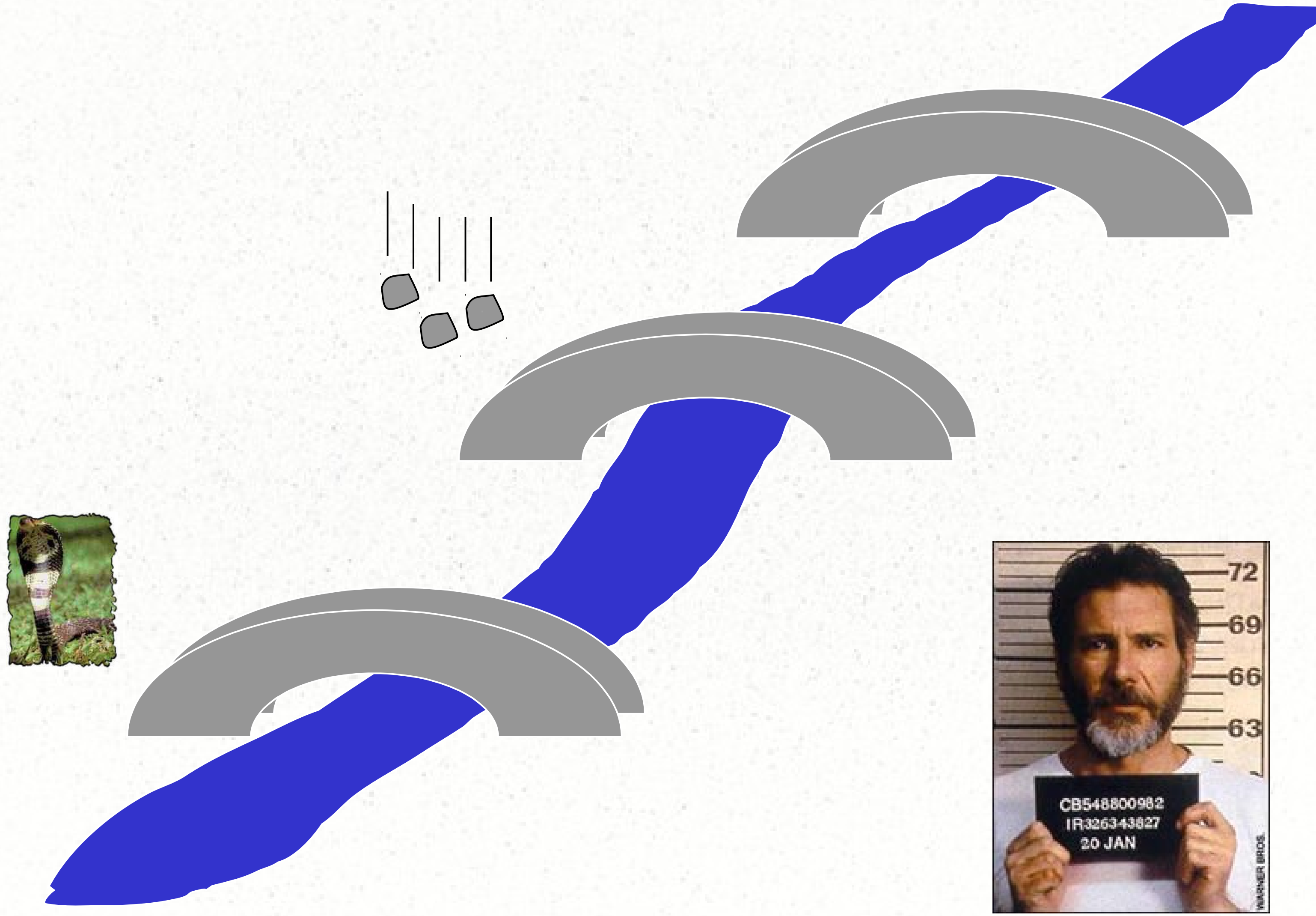
1944

Un problema de decisión

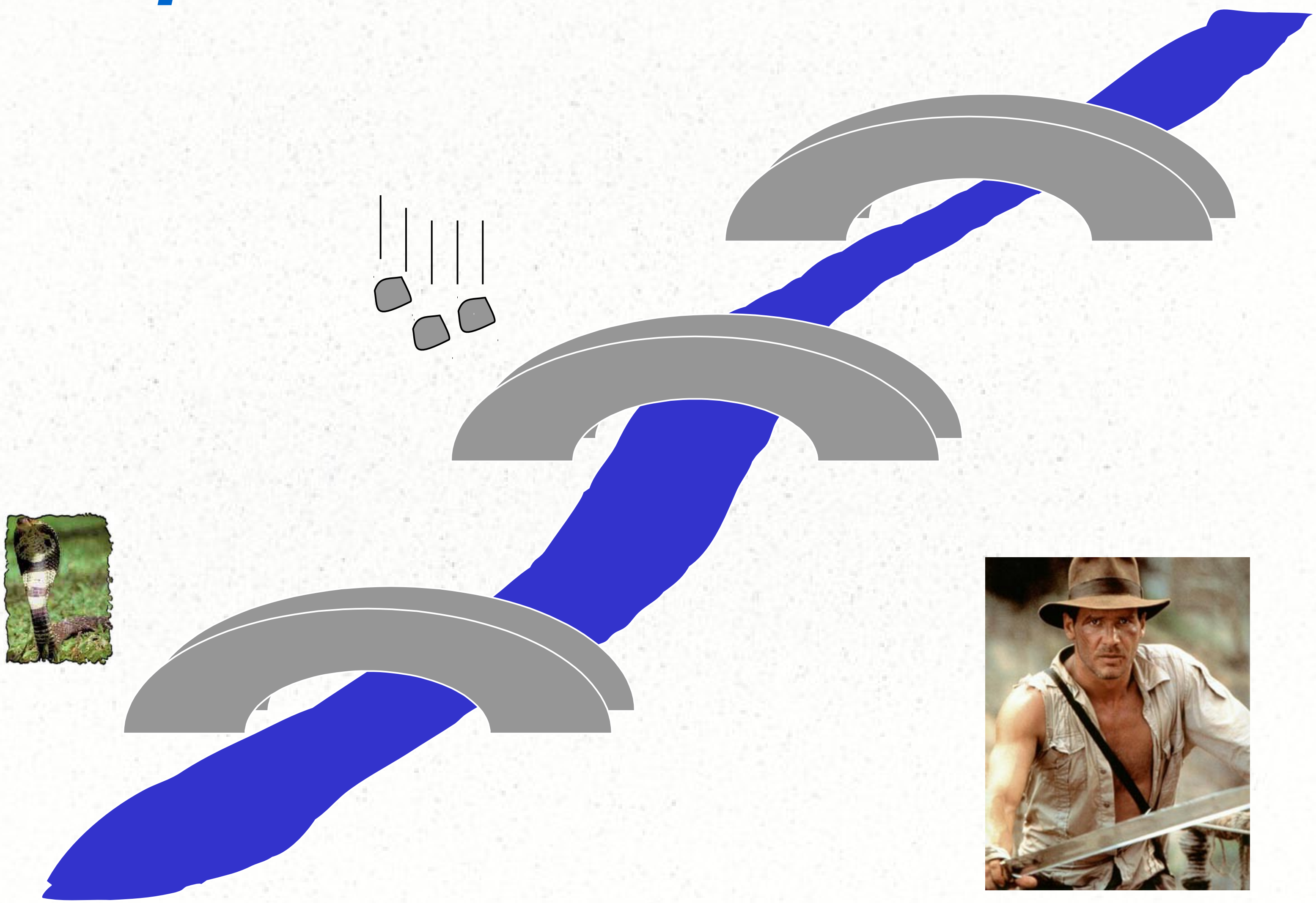
Un problema de decisión



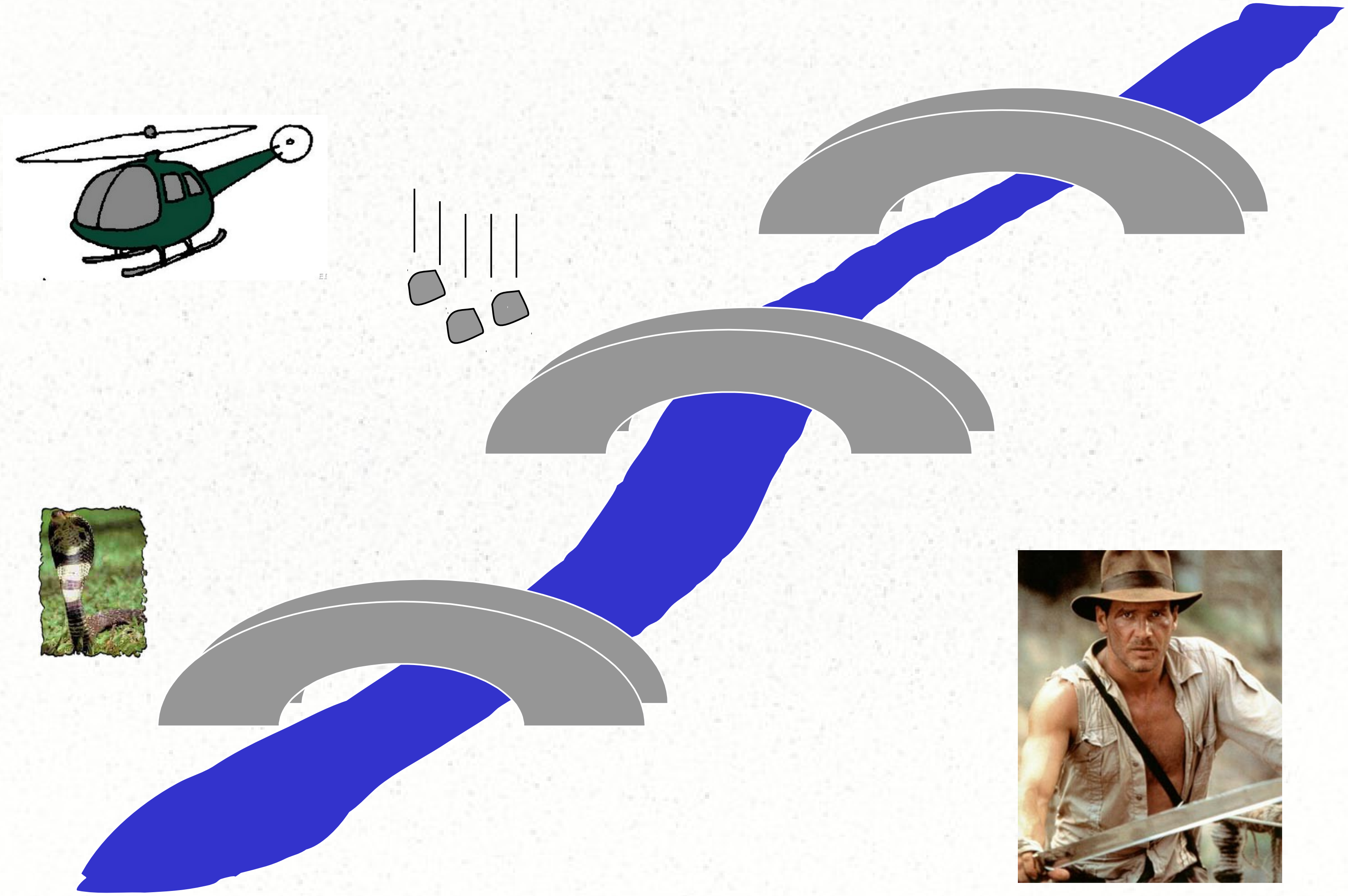
Un problema de decisión



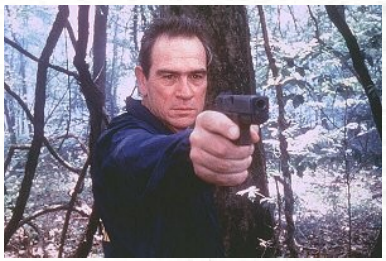
Un problema de decisión

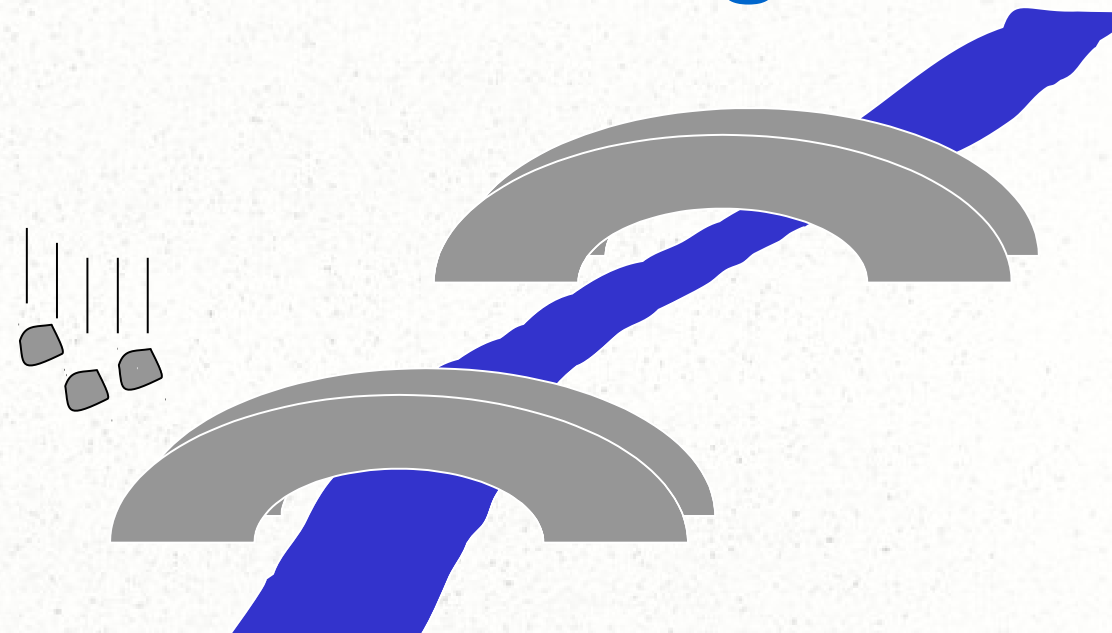
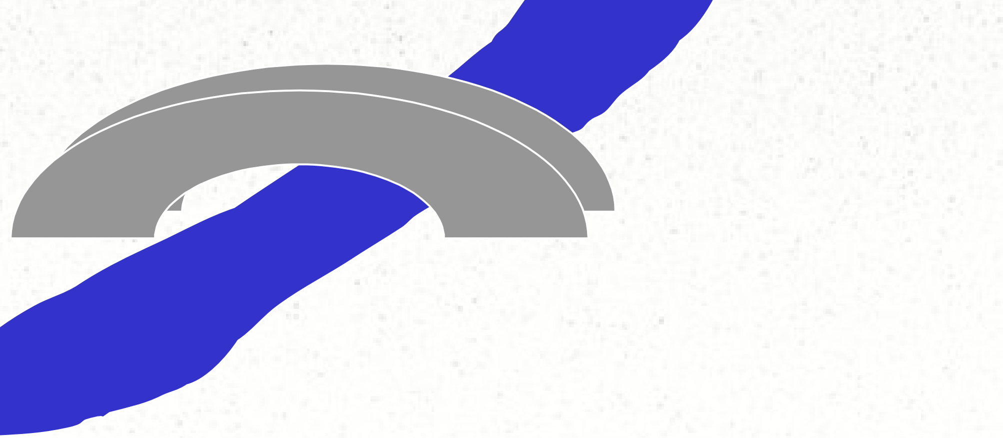


Un problema de decisión



Un problema estratégico



Elementos de un juego

jugadores

Elementos de un juego

estrategias

Elementos de un juego

preferencias

Elementos de un juego

utilidad

0 50 100

Ejemplo de utilidad

- Resultados:

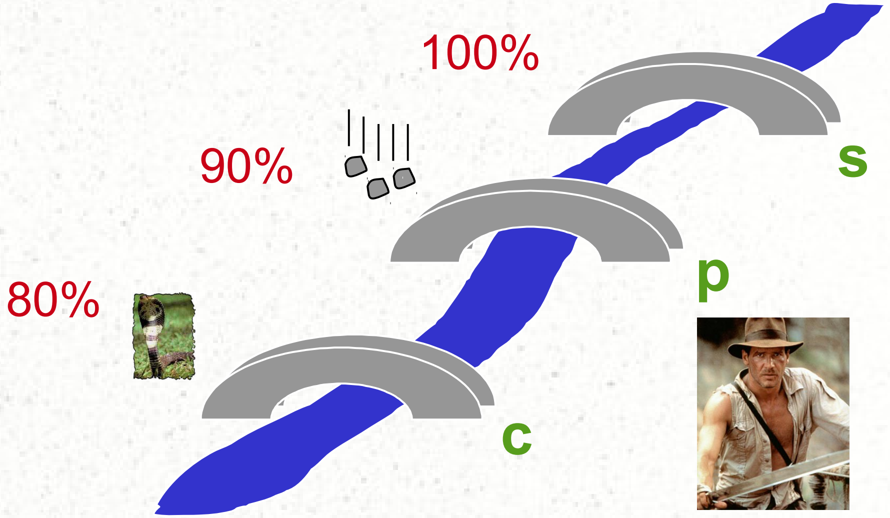
  vivir ($u = 1$) / morir ($u = 0$)

- Estrategias:

  seguro / **p**iedras / **c**obras

- Utilidad:

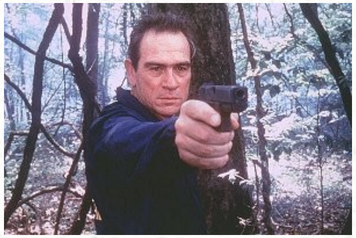
  $u(\mathbf{s}) = 1.0$ / $u(\mathbf{p}) = 0.9$ / $u(\mathbf{c}) = 0.8$



Forma estratégica

	s	p	c
s	0	1	1
p	0.9	0	0.9
c	0.8	0.8	0

Forma estratégica



	s	p	c
s	1	0	0
p	0.1	1	0.1
c	0.2	0.2	1

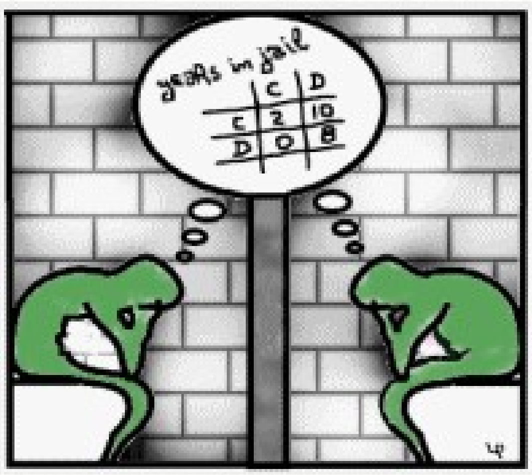
Principio de racionalidad

El objetivo de todo jugador es maximizar su utilidad

Conocimiento común

Juegos clásicos

dilema del prisionero



prisionero 2

prisionero 1		coop.	traic.
	coop.	3	0
	traic.	4	1

Juegos clásicos

piedra, papel, tijeras

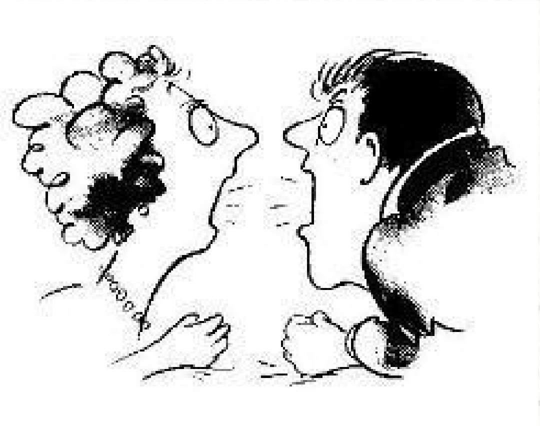
jugador 2

jugador 1

	pi	pa	ti
pi	0	-1	1
pa	1	0	-1
ti	-1	1	0

Juegos clásicos

la batalla de los sexos

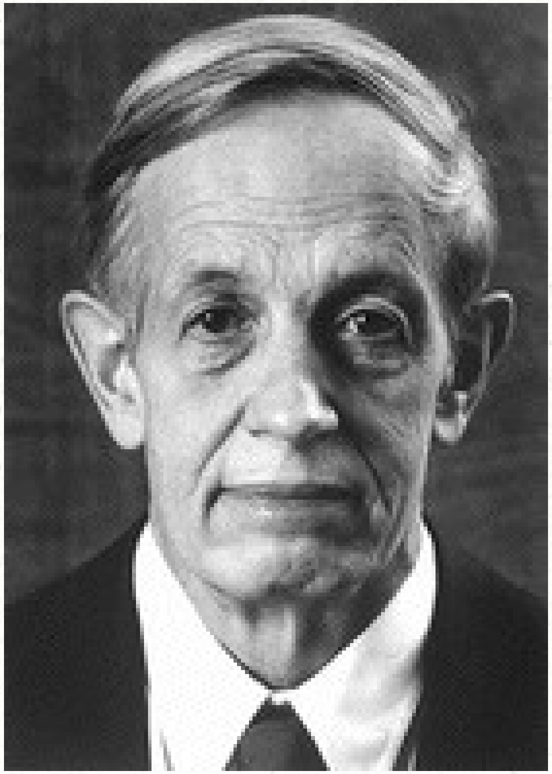


ÉL

ELLA

	ópera	fútbol
ópera	1 / 2	0 / 0
fútbol	0 / 0	2 / 1

Equilibrio de Nash



Nash (1928-)

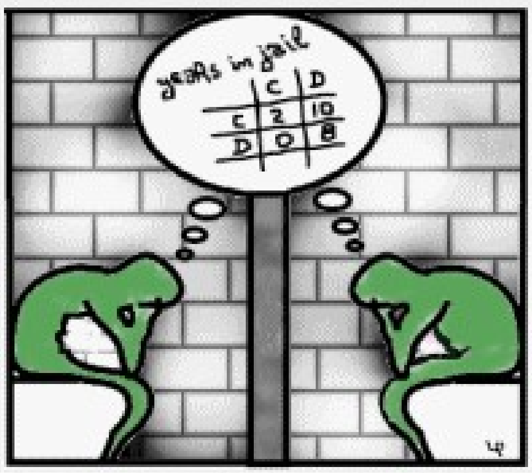
tesis de máster: 1949 - premio Nobel de Economía: 1994

Equilibrio de Nash

Una elección de estrategias de los jugadores es **equilibrio de Nash** si ninguno puede mejorar su ganancia cambiando <u>unilateralmente</u> de estrategia

Equilibrio único

dilema del prisionero



prisionero 2

prisionero 1		coop.	traic.
	coop.	3	0
	traic.	4	1

Sin equilibrio

piedra, papel, tijeras

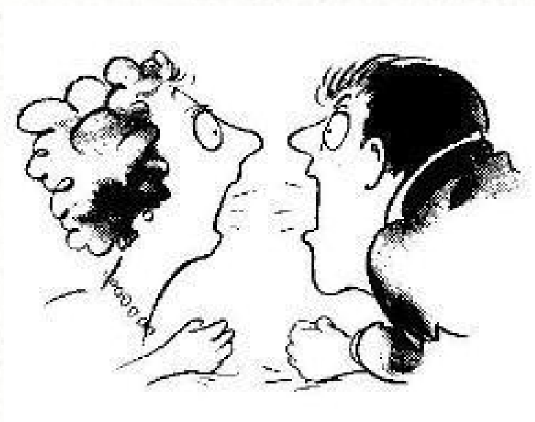
jugador 2

jugador 1

	pi	pa	ti
pi	0	-1	1
pa	1	0	-1
ti	-1	1	0

Varios equilibrios

la batalla de los sexos



ÉL

ELLA

	ópera	fútbol
ópera	1 / 2	0 / 0
fútbol	0 / 0	2 / 1

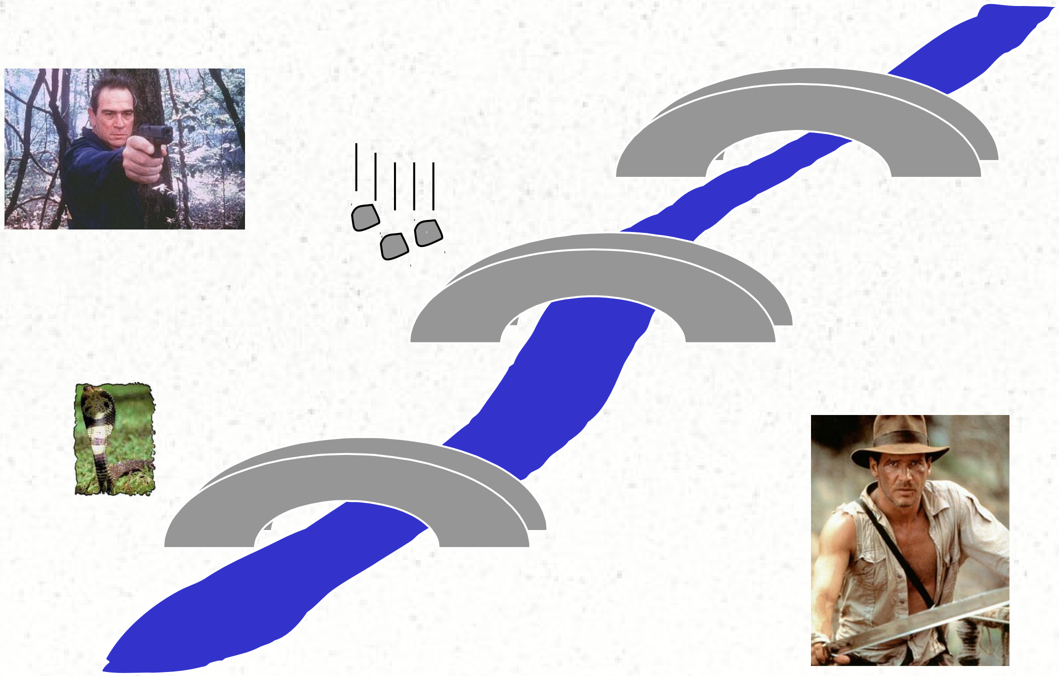
Estrategias mixtas

- Se elige cada estrategia pura con una probabilidad.
- Cada asignación de probabilidades es una **estrategia mixta.**

$p(\text{piedra}) = p(\text{papel}) = p(\text{tijeras}) = 1/3$

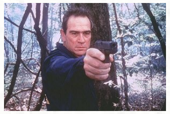
Equilibrio mixto

- Asignación de probabilidades que haga indiferente la elección del contrario.



Equilibrio mixto

B



A

	s	p	c
s	1	0	0
p	0.1	1	0.1
c	0.2	0.2	1

$$u_B(s) = 1.0 \times p_A(s) + 0.1 \times p_A(p) + 0.2 \times p_A(c)$$

$$u_B(p) = 0.0 \times p_A(s) + 1.0 \times p_A(p) + 0.2 \times p_A(c)$$

$$u_B(c) = 0.0 \times p_A(s) + 0.1 \times p_A(p) + 1.0 \times p_A(c)$$

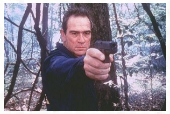
$$u_B(s) = u_B(p) = u_B(c)$$

$$p_A(s) + p_A(p) + p_A(c) = 1$$

$$p_A(s) = 0.30$$
$$p_A(p) = 0.33$$
$$p_A(c) = 0.37$$

Equilibrio mixto

B



A

	s	p	c
s	0	1	1
p	0.9	0	0.9
c	0.8	0.8	0

$$u_A(s) = 0.0 \times p_B(s) + 1.0 \times p_B(p) + 1.0 \times p_B(c)$$

$$u_A(p) = 0.9 \times p_B(s) + 0.0 \times p_B(p) + 0.9 \times p_B(c)$$

$$u_A(c) = 0.8 \times p_B(s) + 0.8 \times p_B(p) + 0.0 \times p_B(c)$$

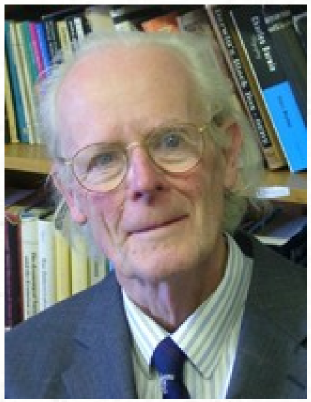
$$u_A(s) = u_A(p) = u_A(c)$$

$$p_B(s) + p_B(p) + p_B(c) = 1$$

$$p_B(s) = 0.40$$
$$p_B(p) = 0.34$$
$$p_B(c) = 0.26$$

La evolución como un juego

“La lógica del conflicto animal”



Maynard Smith
(1920-2004)

Price
(1922-1975)

NATURE VOL. 246 NOVEMBER 2 1973 15

The Logic of Animal Conflict

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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.

In a typical combat between two male animals of the same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes. Consequently, one might expect that natural selection would develop maximally effective weapons and fighting styles for a “total war” strategy of battles between males to the death. But instead, intraspecific conflicts are usually of a “limited war” type, involving inefficient weapons or ritualized tactics that seldom cause serious injury to either contestant. For example, in many snake species the males fight each other by wrestling without using their fangs[1,2]. In mule deer (*Odocoileus hemionus*) the bucks fight furiously but harmlessly by crashing or pushing antlers against antlers, while they refrain from attacking when an opponent turns away, exposing the unprotected side of its body[3]. And in the Arabian oryx (*Oryx leucoryx*) the extremely long, backward pointing horns are so inefficient for combat that in order for two males to fight they are forced to kneel down with their heads between their knees to direct their horns forward[4]. (For additional examples, see Collins[5], Darwin[6], Hingston[6], Huxley *et al.*[7], Lorenz[8] and Wynne-Edwards[9].)

How can one explain such oddities as snakes that wrestle with each other, deer that refuse to strike “foul blows”, and antelope that kneel down to fight?

The accepted explanation for the conventional nature of contests is that if no conventional methods existed, many individuals would be injured, and this would militate against the survival of the species (see, for example, Huxley[7]). The difficulty with this type of explanation is that it appears to assume the operation of “group selection”. Although one cannot rule out group selection as an agent producing adaptations, it is only likely to be effective in rather special circumstances[10–12]. Consequently it seems to us that group selection cannot by itself account for the complex anatomical and behavioural adaptations for limited conflict found in so many species, but there must also be individual selection for these, which means that a “limited war” strategy must be differentially advantageous for individuals.

We consider simple formal models of conflict situations, 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.

A Computer Model

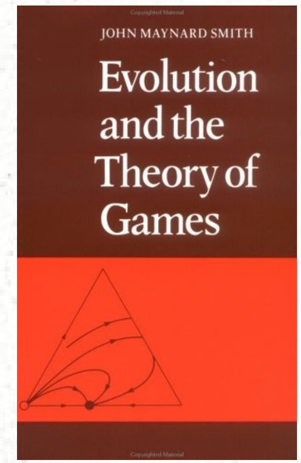
A main reason for using computer simulation was to test whether it is possible even in theory for individual selection to account for “limited war” behaviour.

We consider a species that possesses offensive weapons capable of inflicting serious injuries. We assume that there are two categories of conflict tactics: “conventional” tactics, *C*, which are unlikely to cause serious injury, and “dangerous” tactics, *D*, which are likely to injure the opponent seriously if they are employed for long. (Thus in the snake example, wrestling involves *C* tactics and use of fangs would be *D* tactics. In many species, *C* tactics are limited to threat displays at a distance, without any physical fighting. We consider a conflict between two individuals to consist of a series of alternate “moves”. At each move, a contestant can employ *C* or *D* tactics, or retreat, *R*. If a contestant employs *D* tactics, there is a fixed probability that his opponent will be seriously injured: a contestant who is seriously injured always retreats. If a contestant retreats, the contest is at an end and his opponent is the winner. A possible conflict between contestants *A* and *B* can be represented in this way:

A's move *C C C C C C C C C C C D C C C C C C C D*
B's move *C C C C C C C C C C C D C C C C C C C R*

If a contestant plays *D* on the first move of a contest, or plays *D* in response to *C* by his opponent, this is called a “probe” or a “provocation”. A probe made after the opening move is said to “escalate” a contest from *C* to *D* level. A contestant who plays *D* in reply to a probe is said to “retaliate”. In the example shown above, *A* probes on his twelfth and twentieth moves; *B* retaliates after the first probe, but retreats after the second, leaving *A* the winner. At the end of a contest there are “pay-offs” to each contestant. The pay-offs are taken as measures of the contribution the contest has made to the reproductive success of the individual. They take account of three factors: the advantages of winning as compared with losing, the disadvantage of being seriously injured, and the disadvantage of wasting time and energy in the contest.

Nature, 1973



1982

Teoría de Juegos evolutiva

	TJ clásica	TJ evolutiva
jugadores	racionales	irracionales
estrategias	elegibles	heredadas (fenotipos)
interacción	todos a la vez	muestreo aleatorio de una población
resultados	utilidad	capacidad reproductiva *(fitness)*

Halcones y palomas

R = recurso (comida)
D = daño recibido en conflicto

D > R

individuo 2

individuo 1

	halcón	**paloma**
halcón	(R-D)/2	R
paloma	0	R/2

Halcones y palomas

R = recurso (comida)
D = daño recibido en conflicto

D > R

individuo 2

individuo 1

	halcón	**paloma**
halcón	(R-D)/2	R
paloma	0	R/2

Halcones y palomas

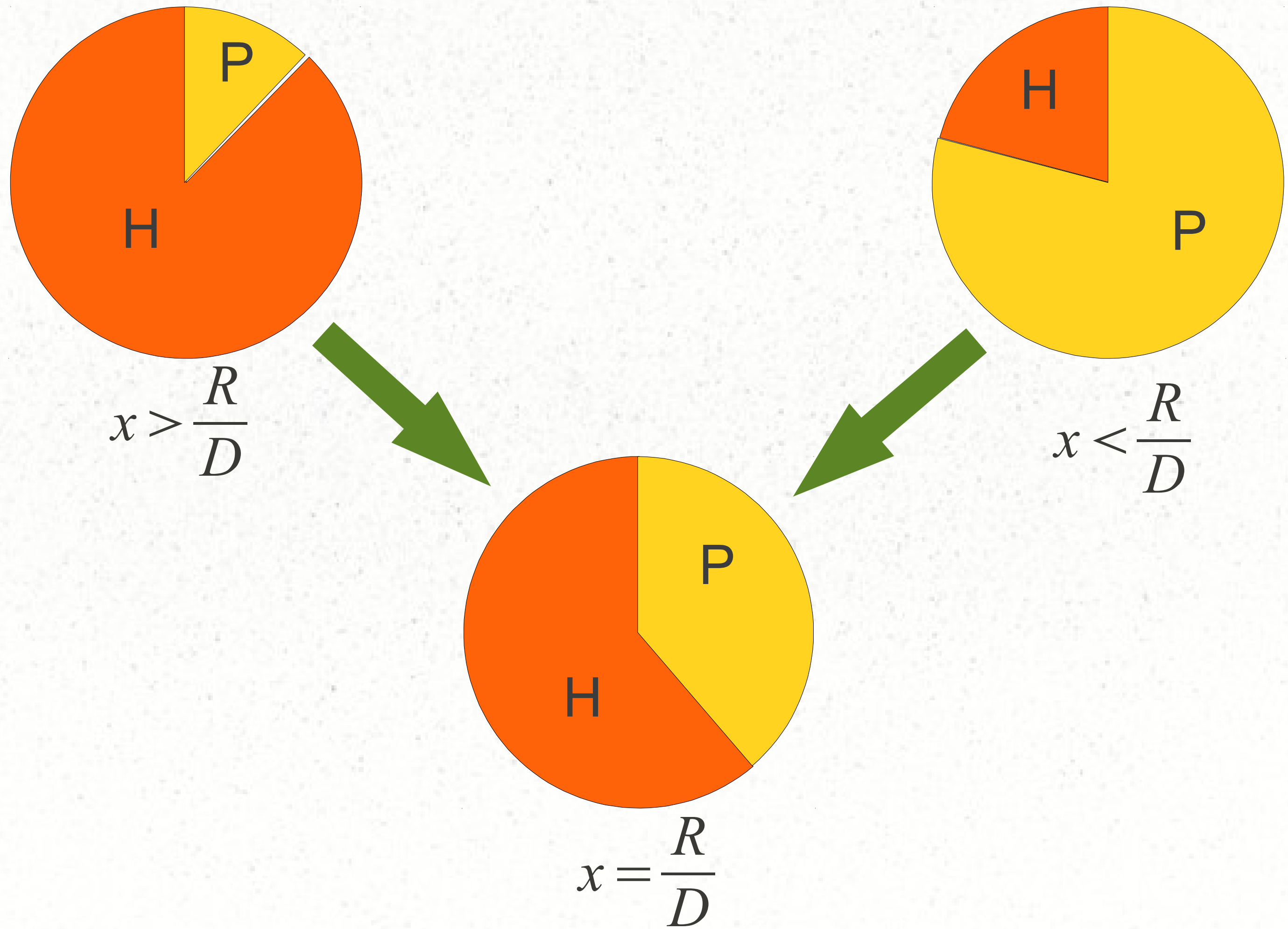
x = fracción de halcones

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

$$f_{\text{P}}(x)=\frac{R}{2}(1-x)$$

$$f_{\text{H}}(x)-f_{\text{P}}(x)=\frac{R-Dx}{2} \quad \begin{cases} f_{\text{H}}(x)>f_{\text{P}}(x) & \text{si} \quad x<\dfrac{R}{D} \\ \\ f_{\text{H}}(x)<f_{\text{P}}(x) & \text{si} \quad x>\dfrac{R}{D} \end{cases}$$

Estrategia Evolutivamente Estable



Ecuación del replicador

$$\frac{dx_i}{dt} = x_i\left[f_i(\boldsymbol{x}) - \overline{f}(\boldsymbol{x})\right]$$

- Equilibrios de Nash mixtos = Puntos fijos de la ecuación del replicador
- Puntos fijos atractores = Estrategias Evolutivamente Estables

Ejemplos

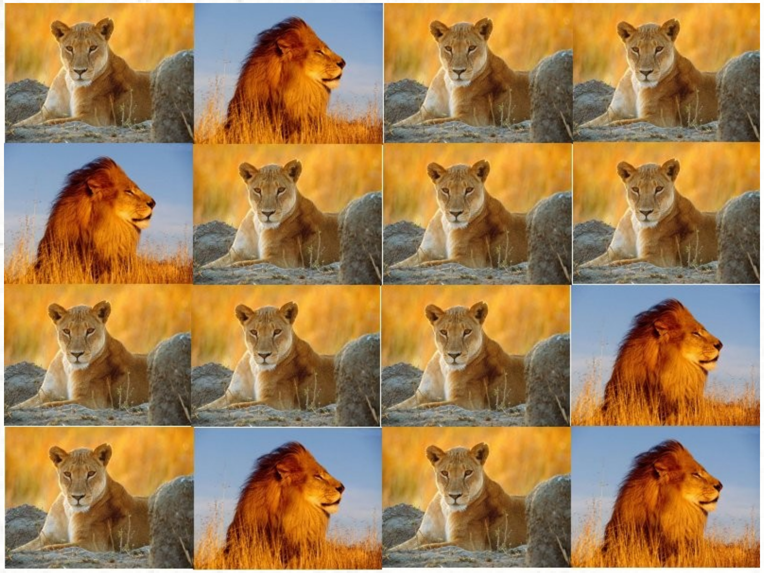
Demostraciones de fuerza

¿Por qué hay tantos machos como hembras?

¿Por qué hay tantos machos como hembras?

¿Por qué hay tantos machos como hembras?

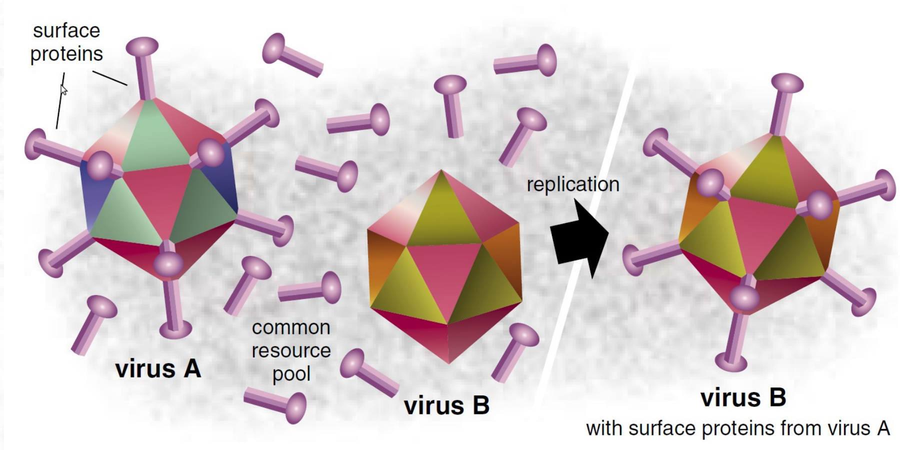
si hay más machos, ten hijas...

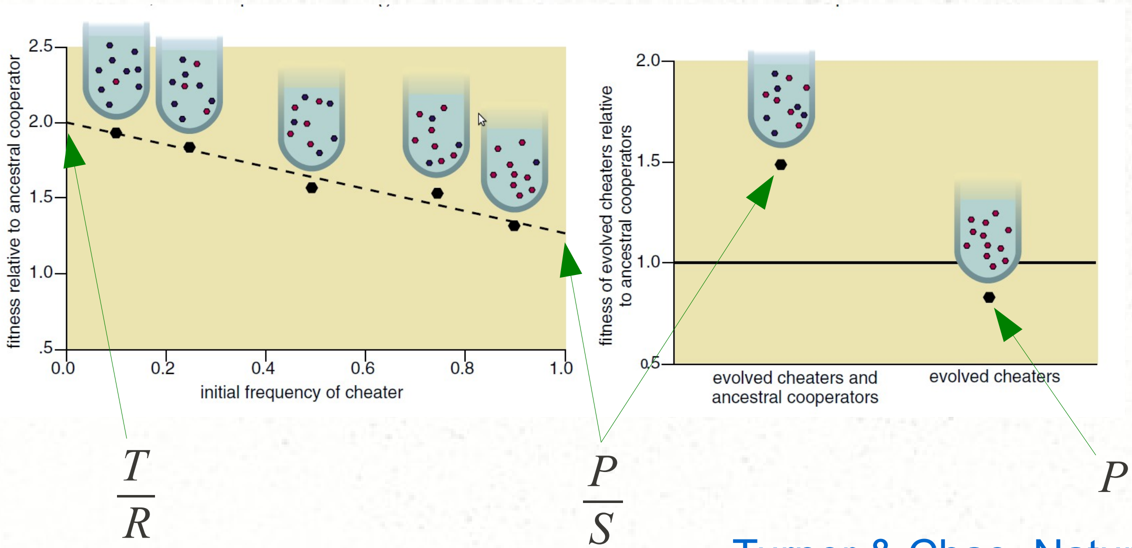


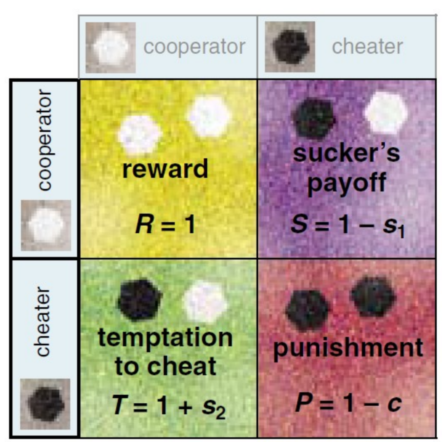
si hay más hembras, ten hijos...

...y tendrás más nietos

Parásitos de parásitos



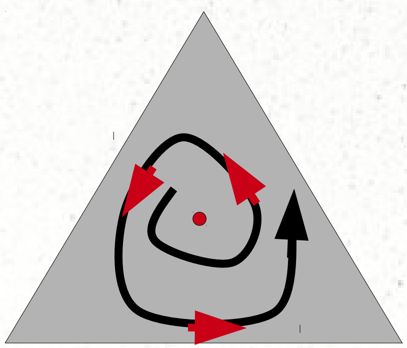




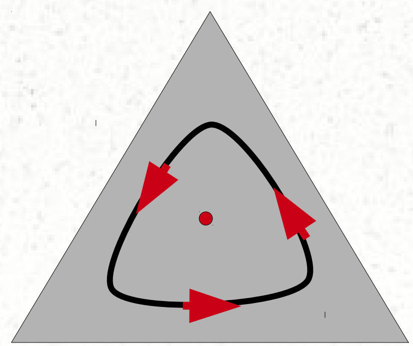
Turner & Chao, Nature **398**, 441-443 (1999)

Piedra-papel-tijeras

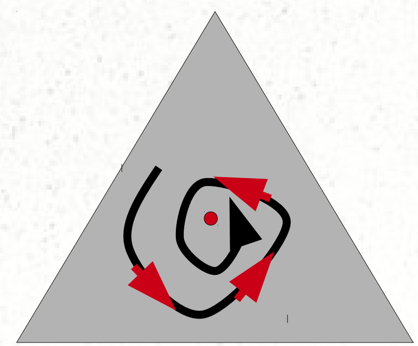
$$
W = \begin{array}{cc} & \begin{array}{ccc} \text{Pi} & \text{Pa} & \text{Ti} \end{array} \\ & \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix} \begin{array}{c} \text{Pi} \\ \text{Pa} \\ \text{Ti} \end{array} \end{array}
$$



$|W|<0$
$(a_1 a_2 a_3 > b_1 b_2 b_3)$



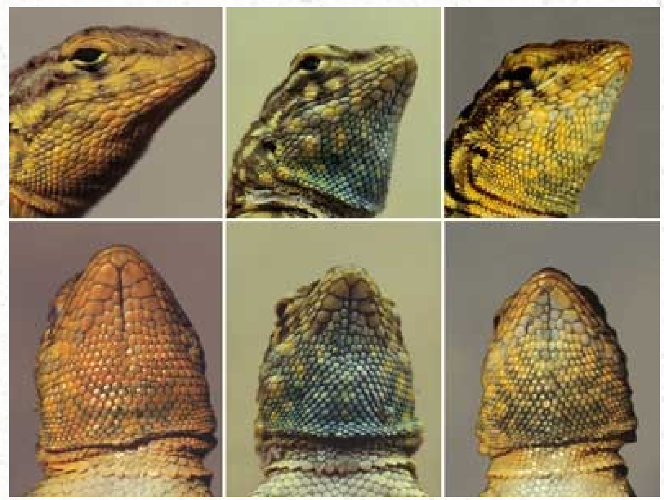
$|W|=0$
$(a_1 a_2 a_3 = b_1 b_2 b_3)$



$|W|>0$
$(a_1 a_2 a_3 < b_1 b_2 b_3)$

Piedra-papel-tijeras

Uta stansburiana

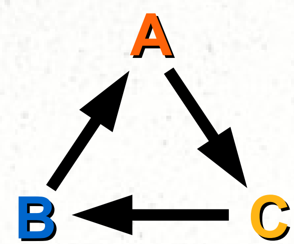


A B C

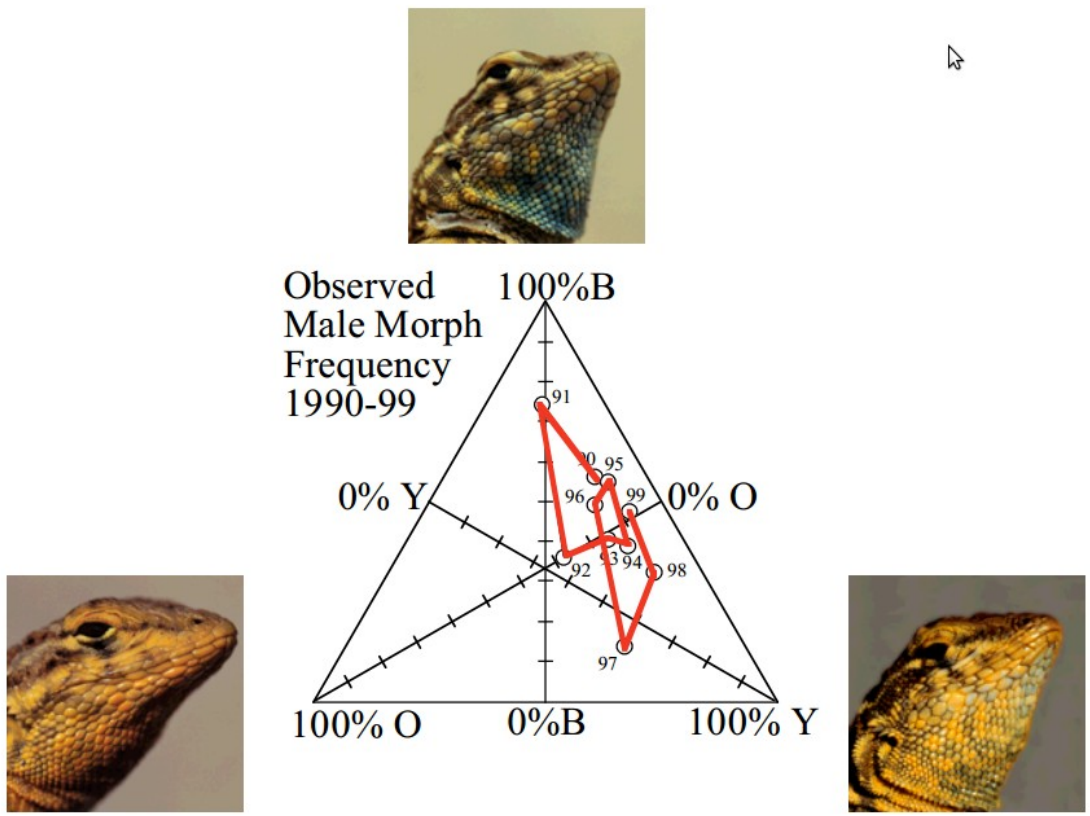
A monógamo y celoso

B polígamo y descuidado

C oportunista



Piedra-papel-tijeras



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

La evolución de la cooperación

Un problema fundamental

Special Section

How Did Cooperative Behavior Evolve

When Charles Darwin was working out his grand theory on the origin of species, he was perplexed by the fact that animals from ants to people form social groups in which most individuals work for the common good. This seemed to run counter to his proposal that individual fitness was key to surviving over the long term.

By the time he wrote *The Descent of Man*, however, he had come up with a few explanations. He suggested that natural selection could encourage altruistic behavior among kin so as to improve the reproductive potential of the "family." He also introduced the idea of reciprocity: that unrelated but familiar individuals would help each other out if both were altruistic. A century of work with dozens of social species has borne out his ideas to some degree, but the details of how and why cooperation evolved remain to be worked out. The answers could help explain human behaviors that seem to make little sense from a strict evolutionary perspective, such as risking one's life to save a drowning stranger.

Animals help each other out in many ways. In social species from honeybees to naked mole rats, kinship fosters cooperation: Females forgo reproduction and instead help the dominant female with her young. And common agendas help unrelated individuals work together. Male chimpanzees, for example, gang up against predators, protecting each other at a potential cost to themselves.

Generosity is pervasive among humans. Indeed, some anthropologists argue that the evolution of the tendency to trust one's relatives and neighbors helped humans become Earth's dominant vertebrate: The ability to work together provided our early ancestors more food, better protection, and better childcare, which in turn improved reproductive success.

However, the degree of cooperation varies. "Cheaters" can gain a leg up on the rest of humankind, at least in the short term. But cooperation prevails among many species, suggesting that this behavior is a better survival strategy, over the long run, despite all the strife among ethnic, political, religious, even family groups now rampant within our species.

Evolutionary biologists and animal behavior researchers are searching out the genetic basis and molecular drivers of cooperative behaviors, as well as the physiological, environmental, and behavioral impetus for sociality. Neuroscientists studying mammals from voles to hyenas are discovering key correlations between brain chemicals and social strategies.

Others with a more mathematical bent are applying evolutionary game theory, a modeling approach developed for economics, to quantify cooperation and predict behavioral outcomes under different circumstances. Game theory has helped reveal a seemingly innate desire for fairness: Game players will spend time and energy to punish unfair actions, even though there's nothing to be gained by these actions for themselves. Similar studies have shown that even when two people meet just once, they tend to be fair to each other. Those actions are hard to explain, as they don't seem to follow the basic tenet that cooperation is really based on self-interest.

The models developed through these games are still imperfect. They do not adequately consider, for example, the effect of emotions on cooperation. Nonetheless, with game theory's increasing sophistication, researchers hope to gain a clearer sense of the rules that govern complex societies.

Together, these efforts are helping social scientists and others build on Darwin's observations about cooperation. As Darwin predicted, reciprocity is a powerful fitness tactic. But it is not a pervasive one.

Modern researchers have discovered that a good memory is a prerequisite: It seems reciprocity is practiced only by organisms that can keep track of those who are helpful and those who are not. Humans have a great memory for faces and thus can maintain lifelong good—or hard—feelings toward people they don't see for years. Most other species exhibit reciprocity only over very short time scales, if at all.

Limited to his personal observations, Darwin was able to come up with only general rationales for cooperative behavior. Now, with new insights from game theory and other promising experimental approaches, biologists are refining Darwin's ideas and, bit by bit, hope that one day they will understand just what it takes to bring out our cooperative spirit.

—Elizabeth Pennisi

Why do we dream?
Freud thought dreaming provides an outlet for our unconscious desires. Now, neuroscientists suspect that brain activity during REM sleep—when dreams occur—is crucial for learning. Is the experience of dreaming just a side effect?

JUPITER IMAGES

Why are there critical periods for language learning?
Monitoring brain activity in young children—including infants—may shed light on why children pick up languages with ease while adults often struggle to learn train station basics in a foreign tongue.

Do pheromones influence human behavior?
Many animals use airborne chemicals to communicate, particularly when mating. Controversial studies have hinted that humans too use pheromones. Identifying them will be key to assessing their sway on our social lives.

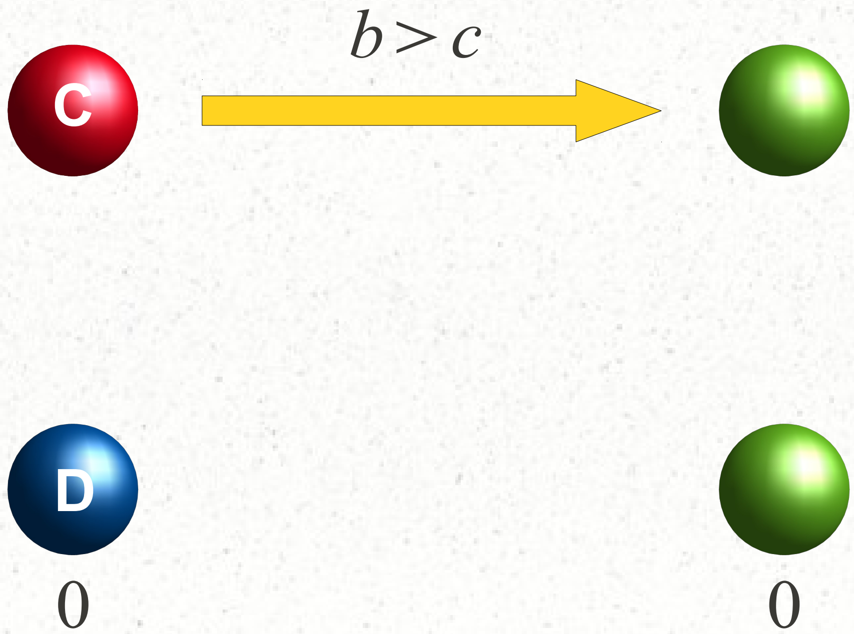
CORBIS

continued >>

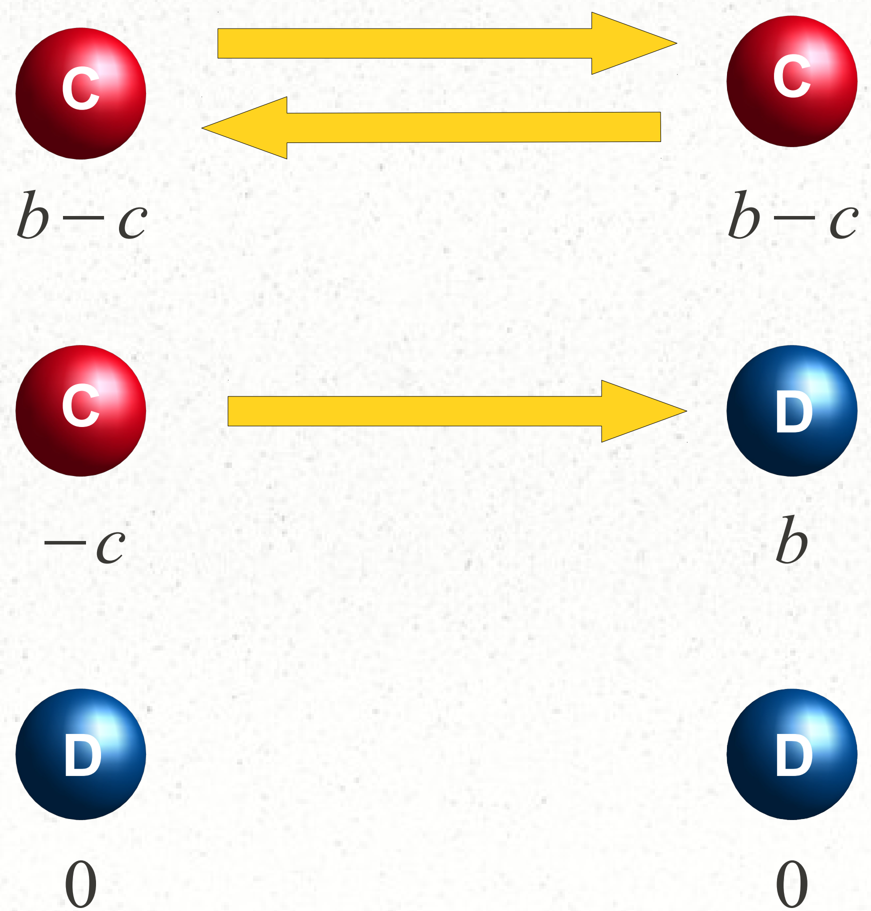
How do general anesthetics work?
Scientists are chipping away at the drugs' effects on individual neurons, but understanding how they render us unconscious will be a tougher nut to crack.

Published by AAAS

El problema



El problema



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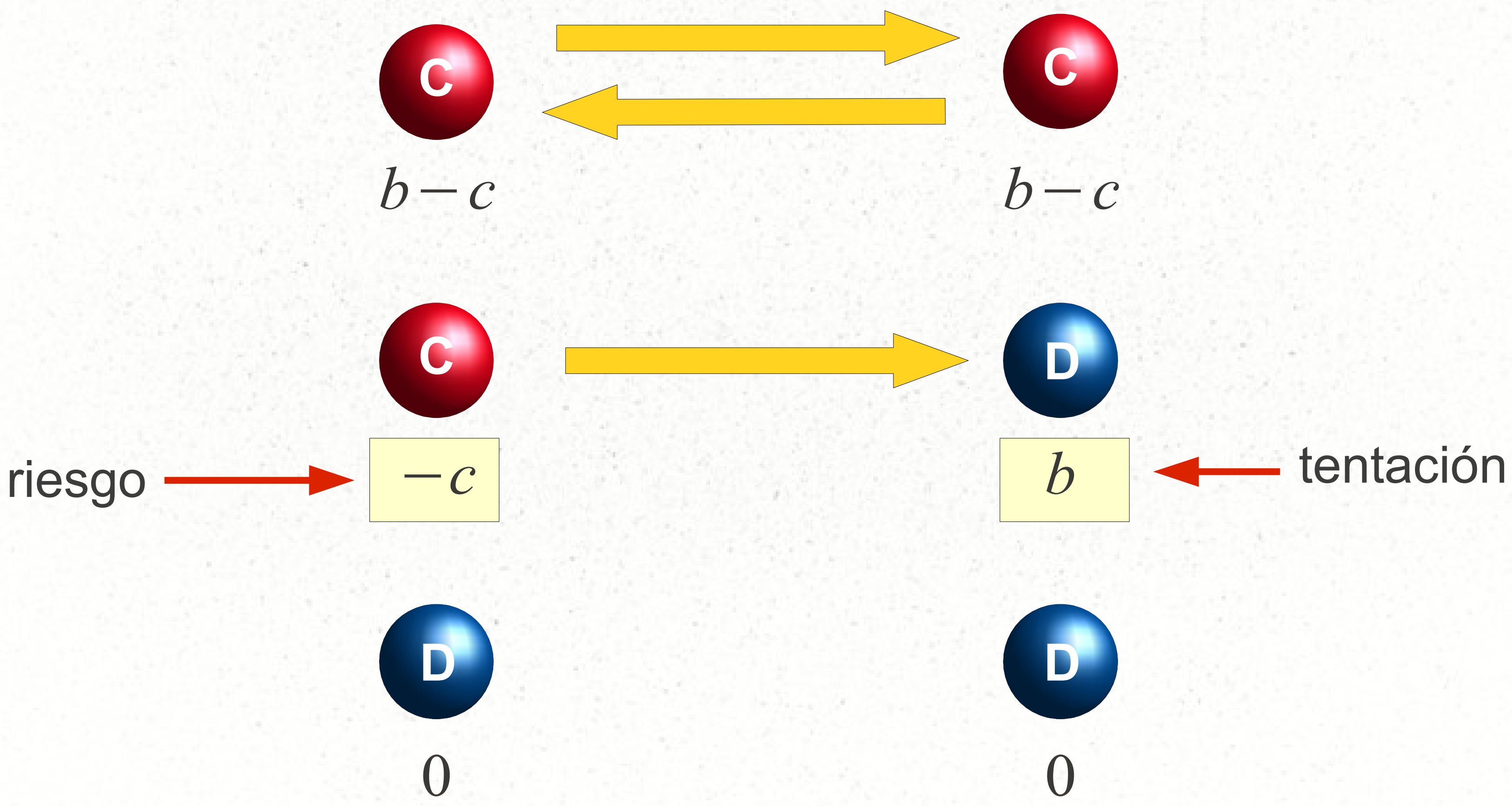
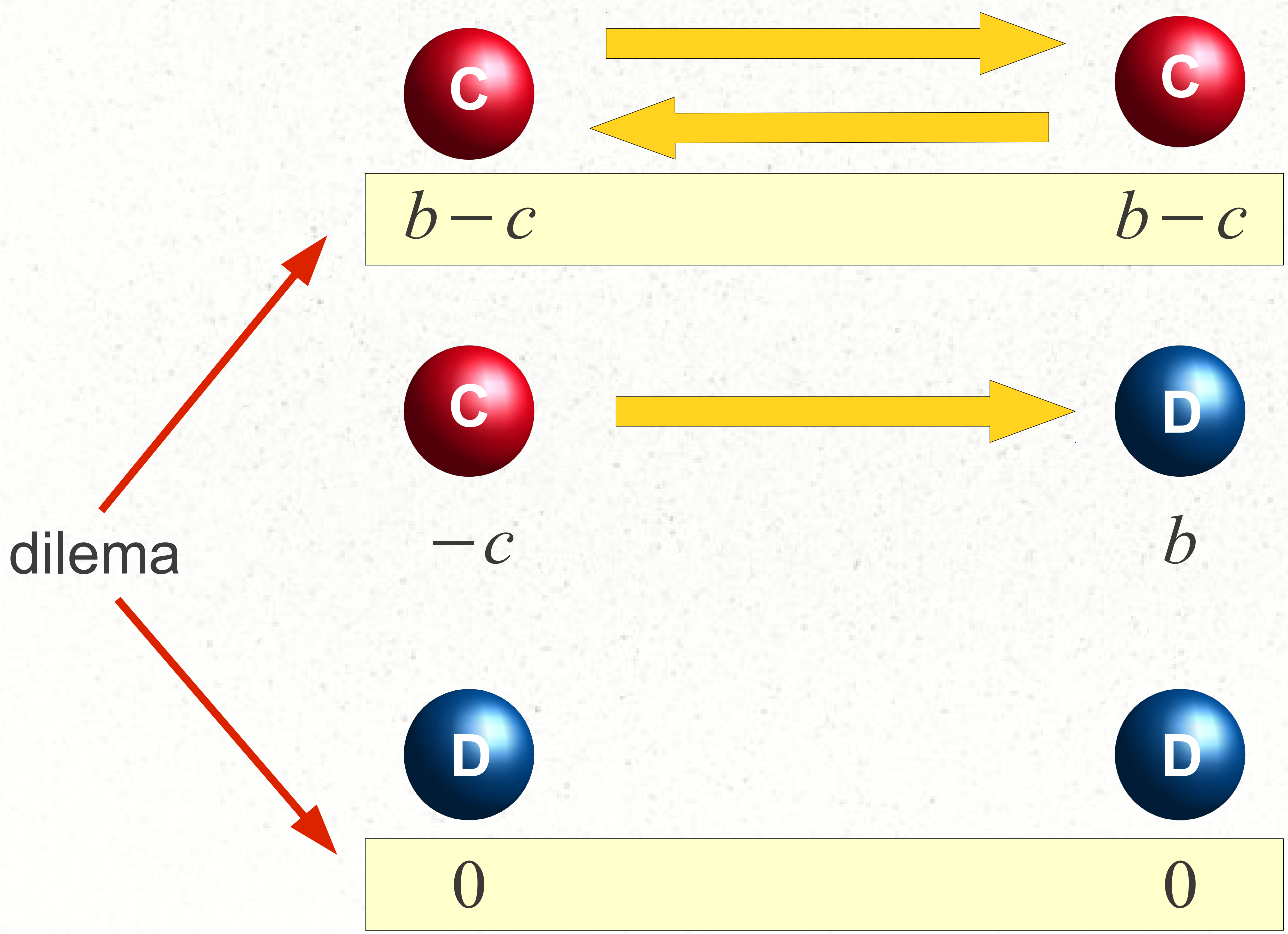


El problema

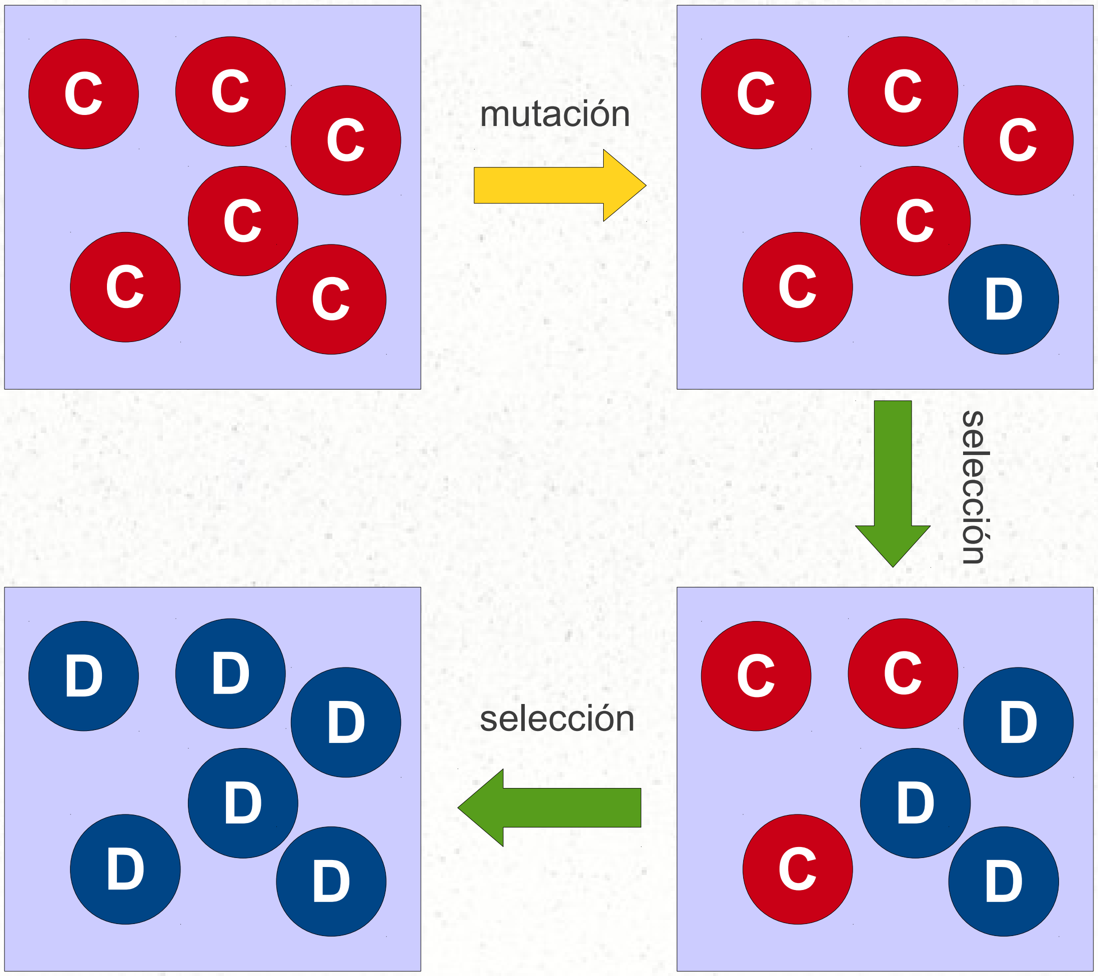


El problema

Aquél que está dispuesto a sacrificar su vida […] a menudo no deja descendientes que hereden su noble naturaleza. […] Por lo tanto, es sumamente improbable que el número de hombres dotados de tales virtudes […] aumente por obra de la selección natural, es decir, por la supervivencia de los más aptos.

Charles Darwin, *El Origen del Hombre,* 1871

El problema



C
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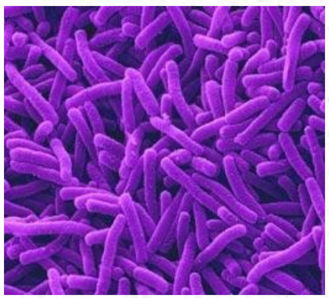
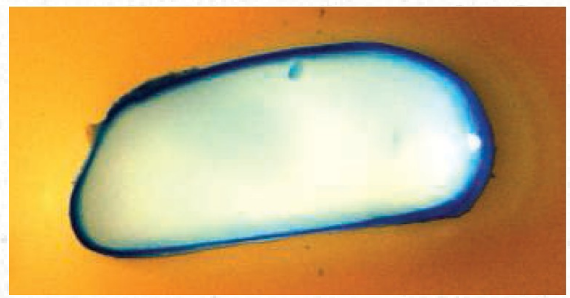
¿Por qué es un problema?



"quorum sensing"



células de levadura en etanol

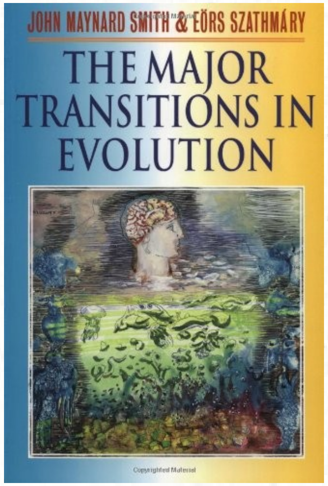
hormigas

papiones

cazadores-recolectores

socorrismo

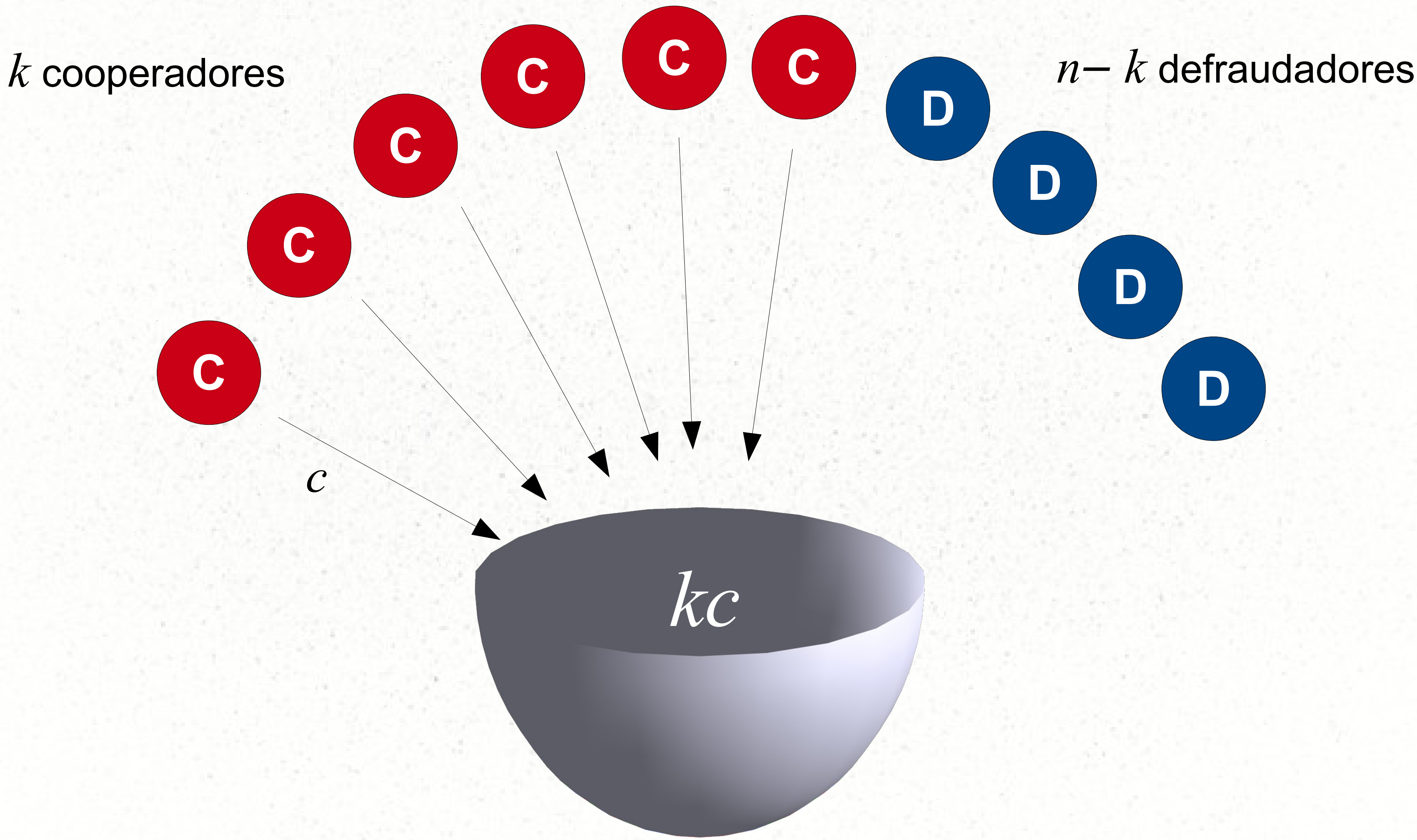
¿Por qué es tan importante?



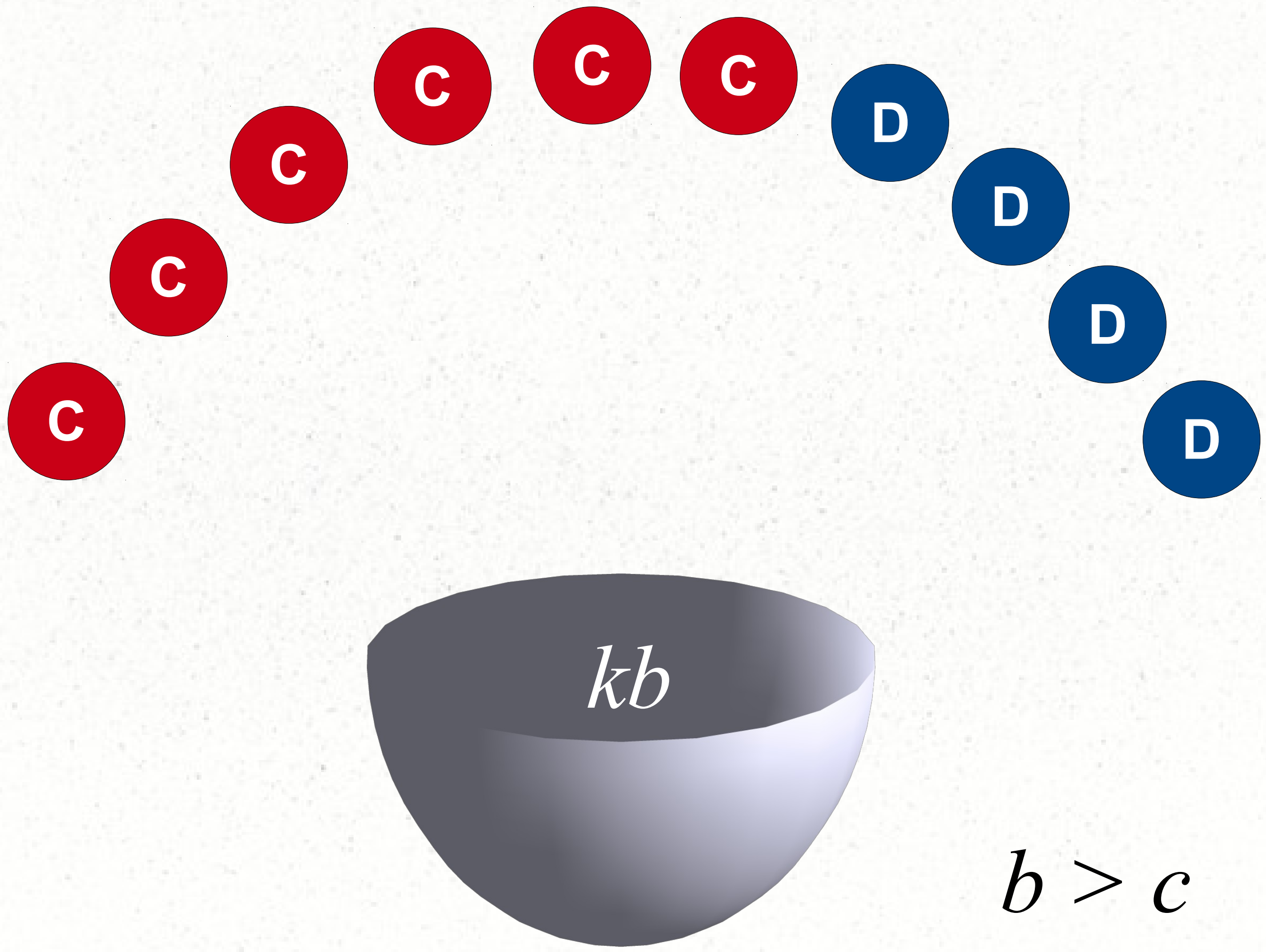
1995

moléculas replicadoras	⟶	poblaciones compartimentalizadas de moléculas
replicadores individuales	⟶	cromosomas
mundo ARN	⟶	ADN y proteínas *(código genético)*
procariotas	⟶	eucariotas
clones asexuales	⟶	poblaciones sexuales
organismos unicelulares	⟶	organismos pluricelulares *(diferenciación celular)*
individuos	⟶	colonias sociales *(castas no reproductivas)*
sociedades de primates	⟶	sociedades humanas *(lenguaje)*

Juego de bienes públicos

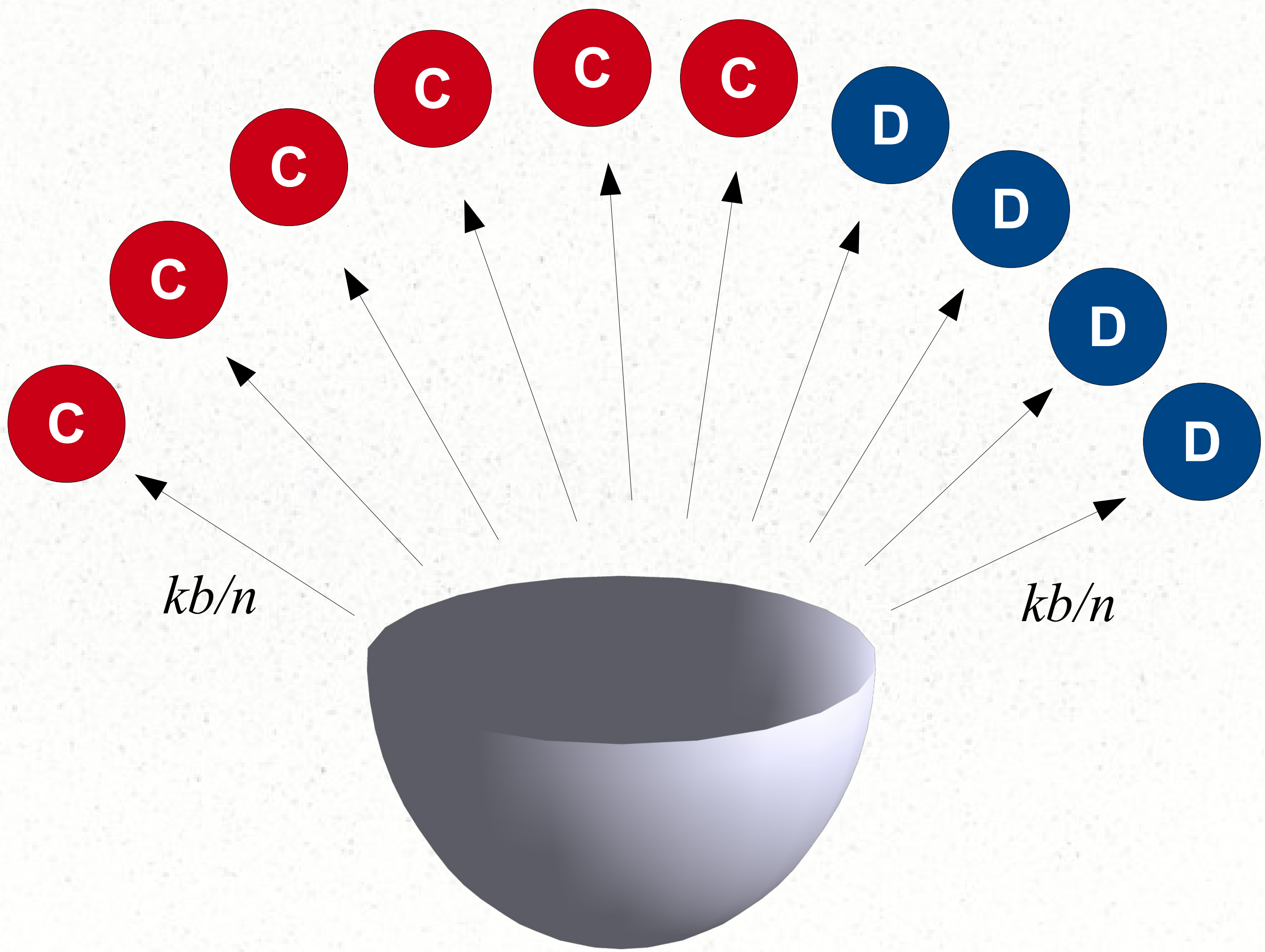


Juego de bienes públicos



$b > c$

Juego de bienes públicos



Juego de bienes públicos

$$G_C(k) = k\frac{b}{n} - c, \qquad k = 1, \ldots, n$$

$$G_D(k) = k\frac{b}{n}, \qquad k = 0, \ldots, n-1$$

$n = 2 \quad \rightarrow$ dilema del prisionero

Juego de bienes públicos

	propia	ajena
G_C	$\frac{b}{n} - c$	$(k-1)\frac{b}{n}$
G_D	0	$k\frac{b}{n}$

$\frac{b}{n} - c < 0 \quad \rightarrow$ altruismo “fuerte”

$\frac{b}{n} - c > 0 \quad \rightarrow$ altruismo “débil”

Una solución: segregación

	propia	ajena
G_C	$\frac{b}{n} - c$	$e_C \frac{b}{n}$
G_D	0	$e_D \frac{b}{n}$

e_C $\rightarrow$ # medio de cooperadores en torno a un cooperador

e_D $\rightarrow$ # medio de cooperadores en torno a un defraudador

Una solución: segregación

	propia	ajena
G_C	$\frac{b}{n}-c$	$e_C\frac{b}{n}$
G_D	0	$e_D\frac{b}{n}$

la cooperación prospera si

$$(e_C+1)\frac{b}{n}-c>e_D\frac{b}{n} \quad \Leftrightarrow \quad \boxed{e_C-e_D>\frac{c\,n}{b}-1}$$

Caso 1: población mezclada

$$e_C - e_D > \frac{c\,n}{b} - 1$$

- Población mezclada con fracción de cooperadores x

$$e_C = e_D = x(n-1)$$

la cooperación prospera sii $\frac{b}{n} > c$ (altruismo débil)

Caso 2: segregación total

$$e_C - e_D > \frac{c\,n}{b} - 1$$

- Los cooperadores solo interactúan con cooperadores
- Los defraudadores solo interactúan con defraudadores

$$e_C = n - 1 \qquad e_D = 0$$

la cooperación prospera sii $b > c$

Caso 3: cooperadores aislados

$$e_C - e_D > \frac{c\,n}{b} - 1$$

- Cada grupo solo contiene 1 cooperador

$$e_C = 0 \qquad e_D = 1$$

la cooperación no prospera

Regla de Hamilton

$$r\,b > c\,, \qquad r = \frac{e_C - e_D + 1}{n}$$

- Hamilton (1964) llamó a r “parentesco”
- Segregación extrema: $r = 1$
- Cooperadores aislados: $r = 0$

Cambio de pregunta

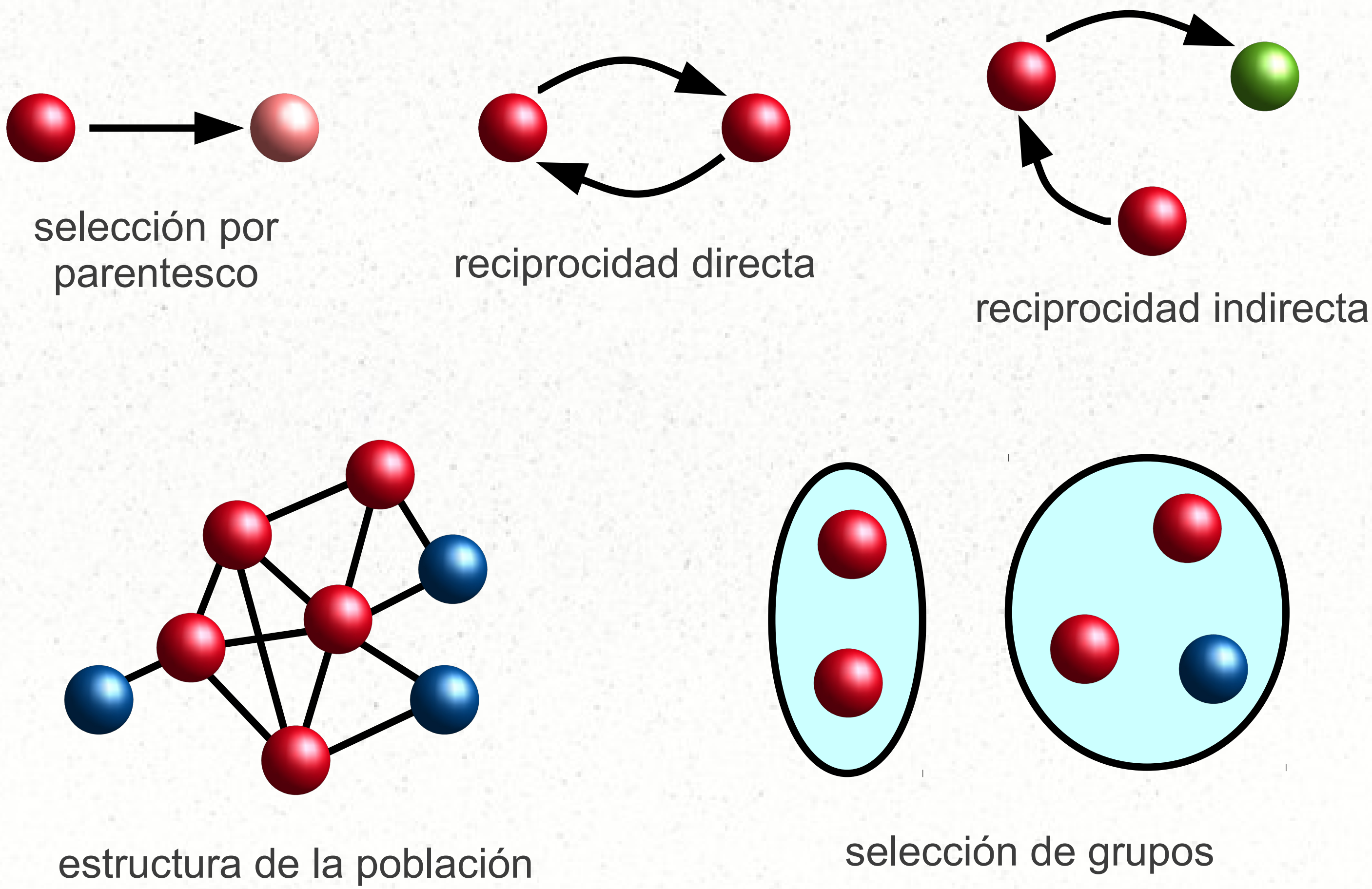
¿por qué emerge la cooperación?

↕

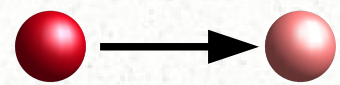
¿cómo se segregan los cooperadores?

Mecanismos de segregación

Nowak, Science (2006) 314, 1560–1563



Selección por parentesco



«¿Que si daría mi vida por un hermano? No, pero sí por dos hermanos o por ocho primos»

John B. S. Haldane

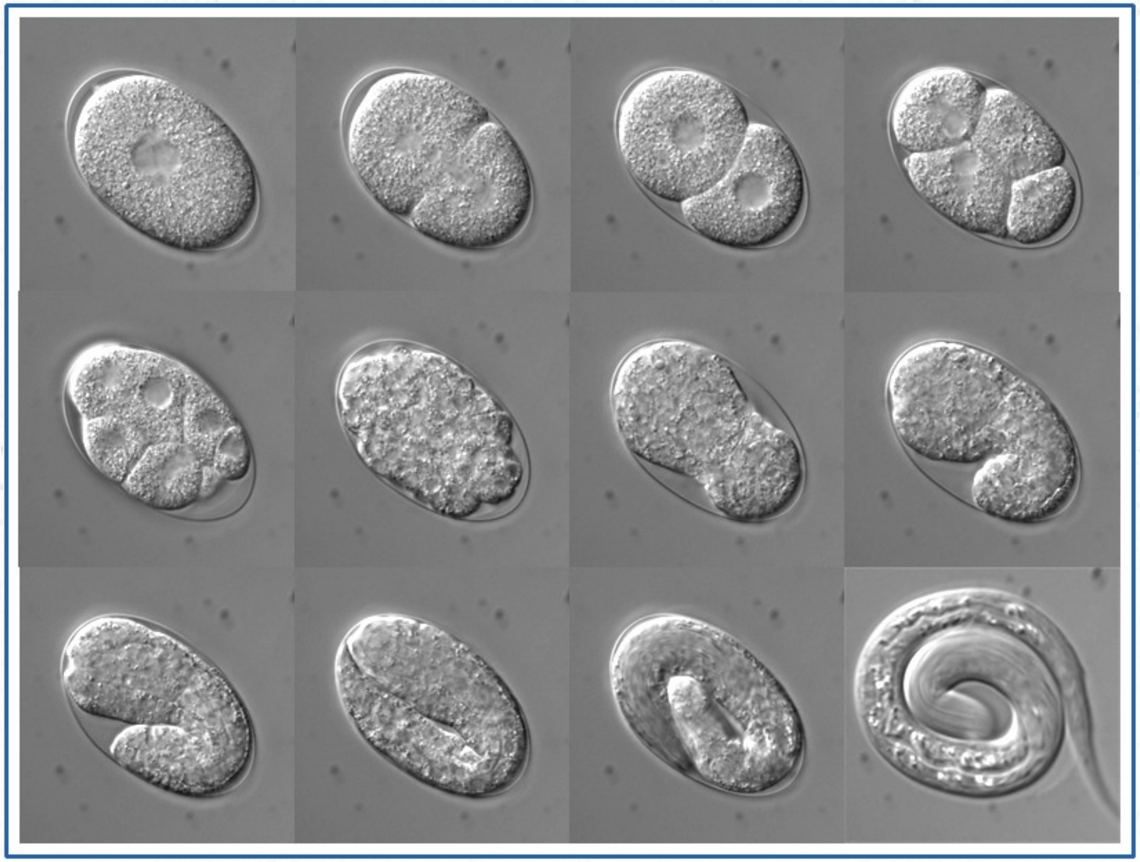
Hamilton's rule:

$$\boxed{r\,b > c}$$

parentesco $\begin{cases} \text{hermanos: } r = 1/2 \\ \text{primos: } r = 1/8 \end{cases}$

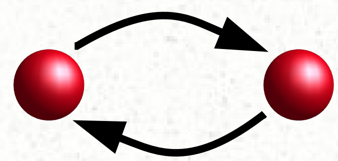
Insectos sociales

Organismos pluricelulares



Caenorhabditis elegans

Reciprocidad directa



dilema del prisionero iterado: se repite el juego con probabilidad w

vengativo → C C C … C C D D … D ...
contrincante → C C C … C D X X … X ...
(n)

$$G(D_n)=\frac{1-w^n}{1-w}(b-c)+b\,w^n$$

$$G(D_\infty)=\frac{1}{1-w}(b-c)$$

$$G(D_\infty)-G(D_n)=w^n\frac{wb-c}{1-w}$$

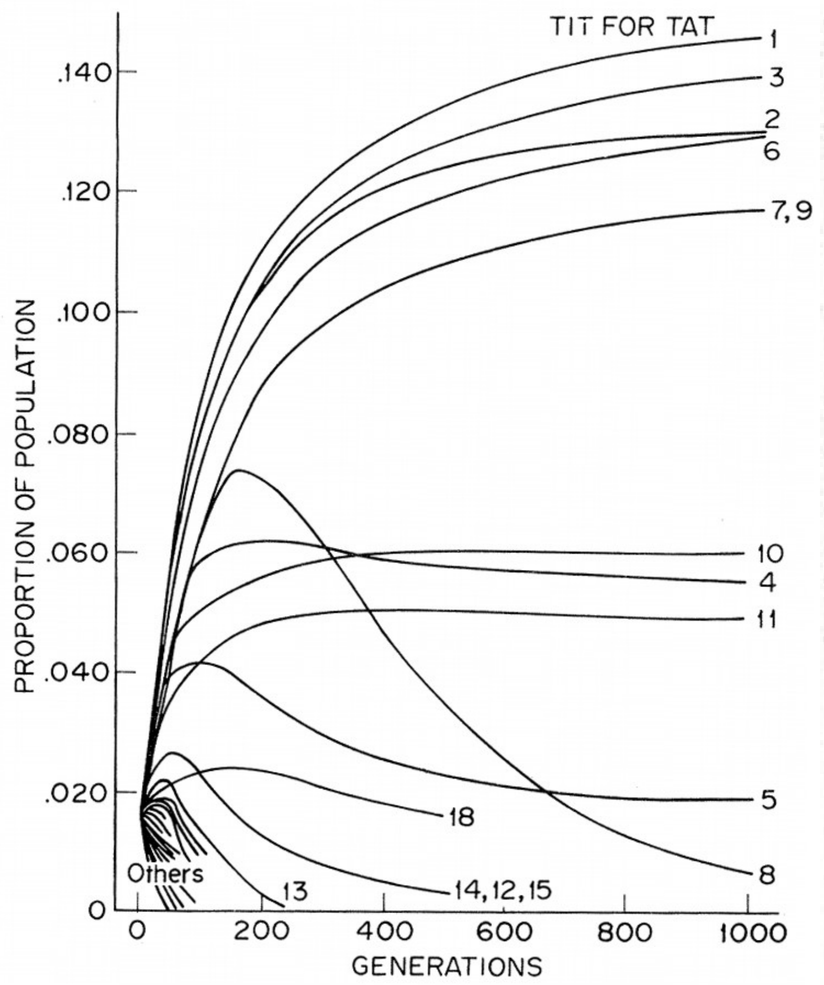
$$\boxed{w\,b>c}$$

Los torneos de Axelrod

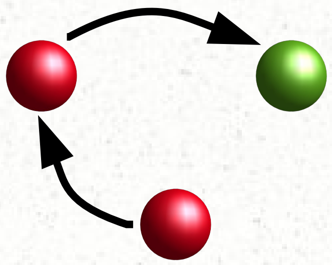
Axelrod (1984) *The evolution of cooperation* (Basic Books)

- 13 (primer torneo) y 62 (segundo torneo) estrategias, más RANDOM, jugaban 200 iteraciones del DP iterado
- Ganador absoluto: Tit-for-tat (TFT; “ojo por ojo”), de Rapoport:
    - Empieza cooperando
    - Hace lo que el oponente le hizo en la ronda anterior
- Las mejores estrategias son:
    - **Amables**: empiezan cooperando
    - **Susceptibles**: se vengan tras una decepción
    - **Compasivas**: ayudan a restaurar la cooperación
    - **Simples**: su comportamiento es fácil de entender

Los torneos de Axelrod



Reciprocidad indirecta



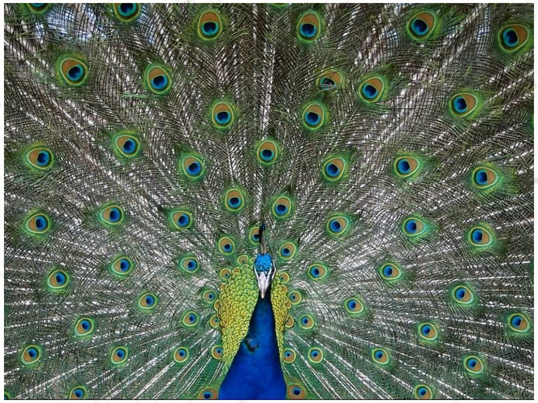
- Segregación conseguida a través de “señales”
- Problema: señales falsas

serpiente de coral oriental
(venenosa)

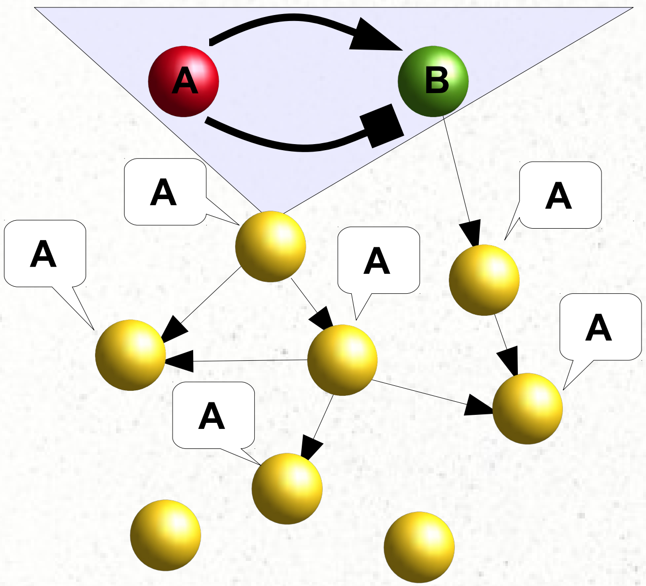
falsa serpiente de coral
(no venenosa)

Señales costosas

principio del “hándicap” (Zahavi)



Reputación



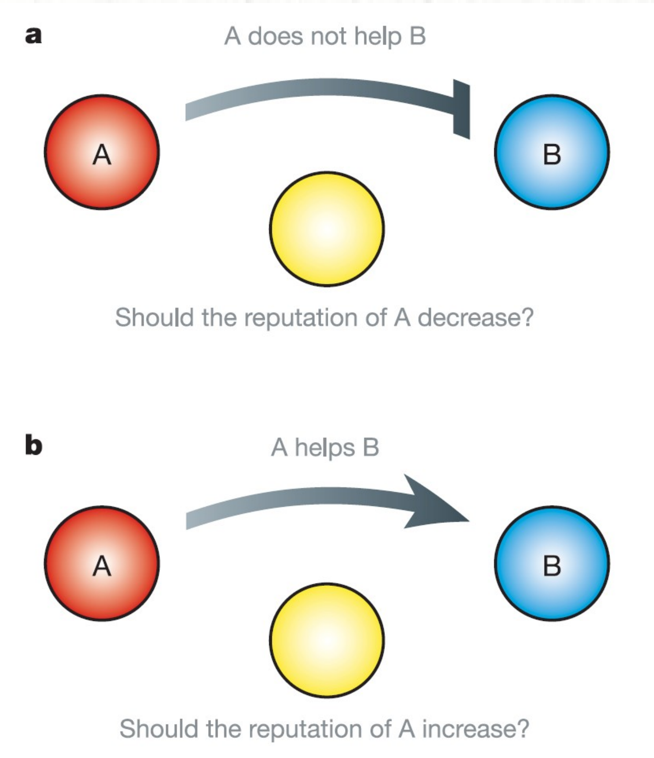
$q \rightarrow$ probabilidad de conocer la reputación del oponente

	C	D
C	$b-c$	$-c(1-q)$
D	$b(1-q)$	0

$$b-c>b(1-q) \quad \Rightarrow \quad \boxed{q\,b>c}$$

Aparición de códigos morales

Brandt & Sigmund (2004) J. Theor. Biol. **231**, 475-486



$A = \{\mathrm{C}, \mathrm{D}\}$ acciones

$R = \{\mathrm{B}, \mathrm{M}\}$ reputaciones

$S = \{R^2 \to A\}$ estrategias

$M = \{A \times R^2 \to R\}$ códigos morales

$|S| = 2^4 = 16 \qquad |M| = 2^8 = 256$

$|S \times M| = 2^{12} = 4096$

Aparición de códigos morales

código moral

reputación del que da y del que recibe

acción del que da

	BB	BM	MB	MM
C	**B**	**B**	**B**	**B**
D	**M**	**M**	**M**	**M**
C	**B**	**B**	**B**	**B**
D	**M**	**B**	**M**	**M**
C	**B**	**M**	**B**	**M**
D	**M**	**B**	**M**	**M**
C	**B**	**M**	**B**	**M**
D	**M**	**M**	**M**	**M**

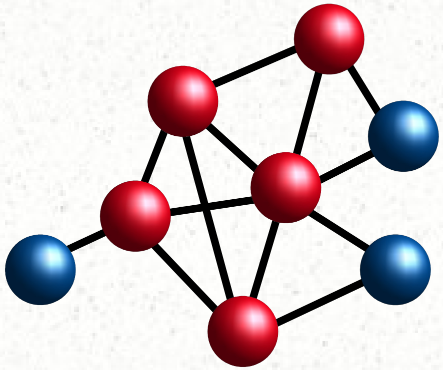
Aparición de códigos morales

las 8 imbatibles

	BB	BM	MB	MM	
C	**B**	*	**B**	*	juicio moral
D	**M**	**B**	**M**	*	
	C	**D**	**C**	*	acción

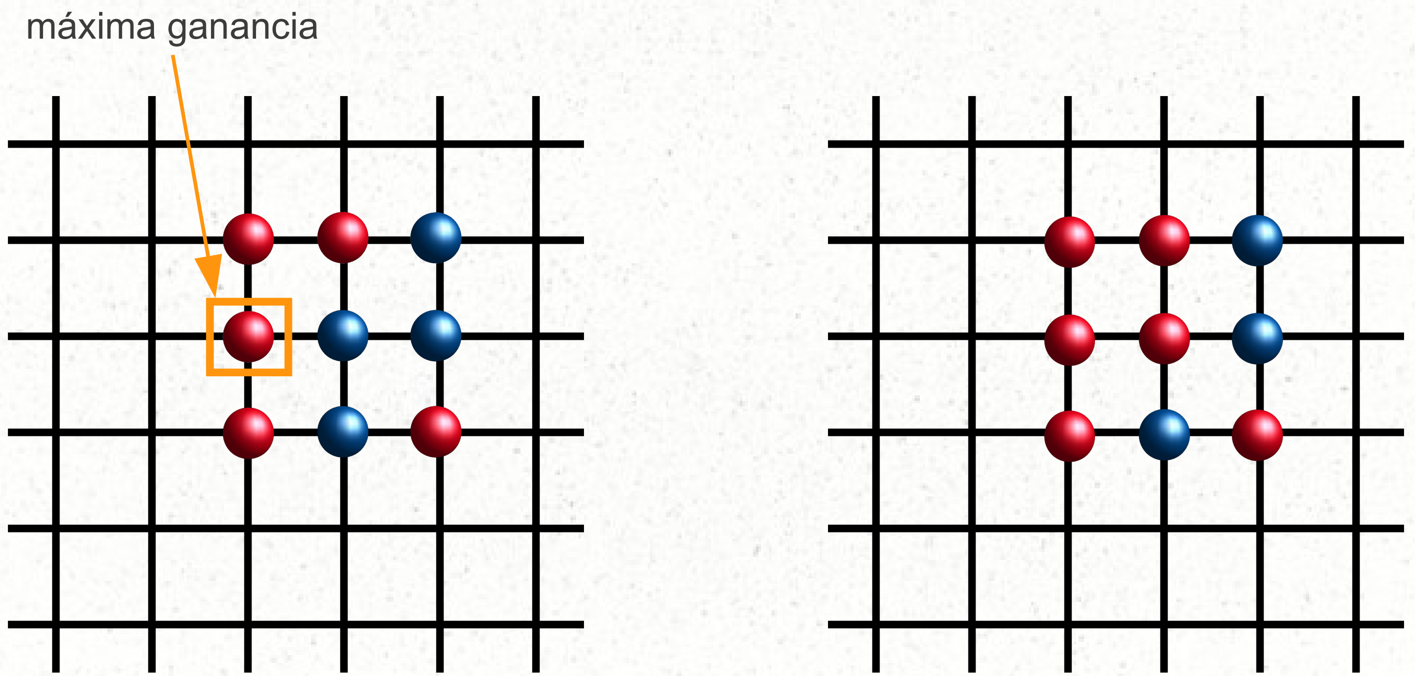
Estructura de la población

Nowak & May (1992) Nature **359**, 826-829



- Segregación por interactuar solo con los vecinos de una red de contactos
- La estructura puede ser espacial o una red social
- Funciona si la dinámica agrupa los cooperadores

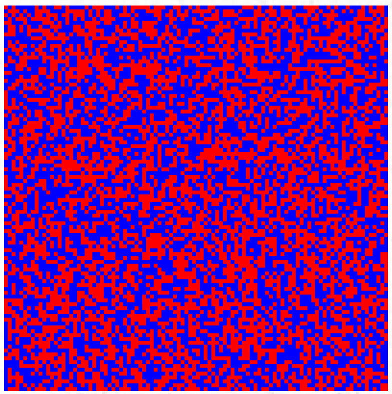
Estructura de la población



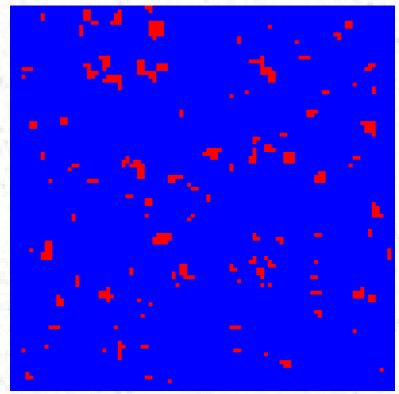
imitación incondicional

Estructura de la población

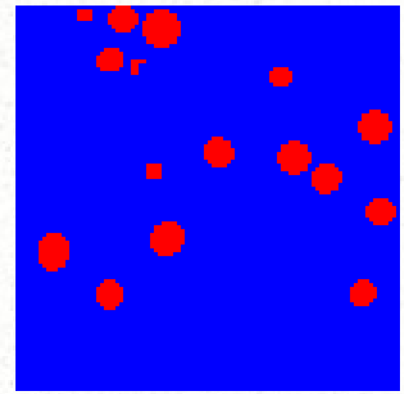
$b = 1.2 \quad c = 0.2$



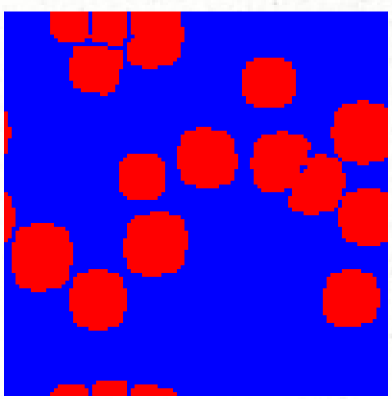
t = 0



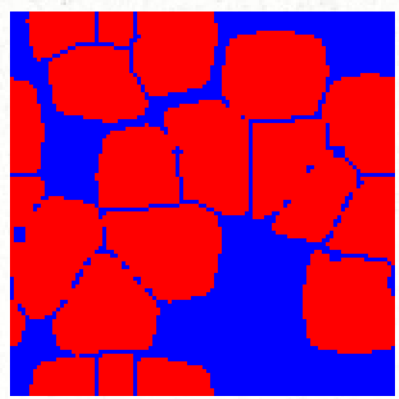
t = 1



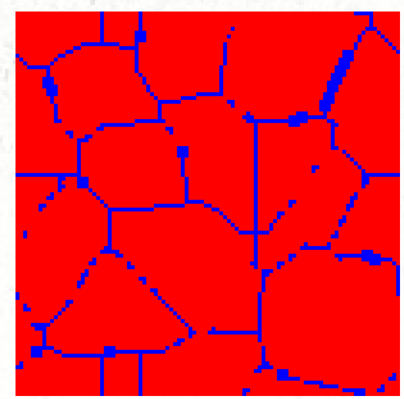
t = 4



t = 9

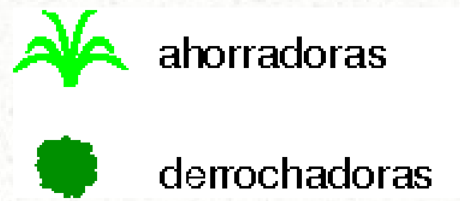


t = 18



t = 35

Competición entre plantas



$$F = k\,\phi$$

fitness

eficiencia

flujo de agua

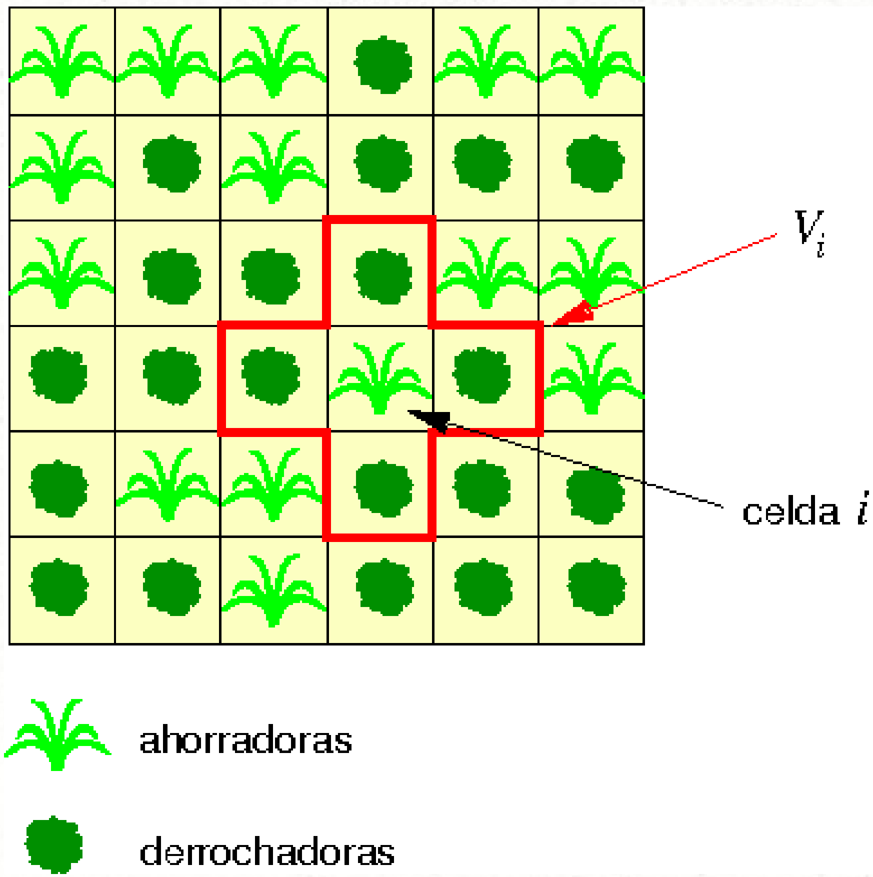
$$\phi_a = \alpha\,\phi_d \quad (\alpha < 1)$$

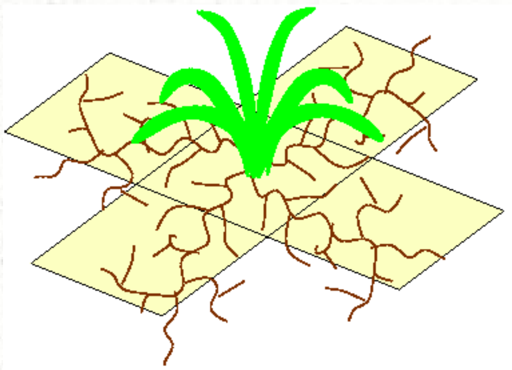
$$k_d = \kappa\,k_a \quad (\kappa < 1)$$

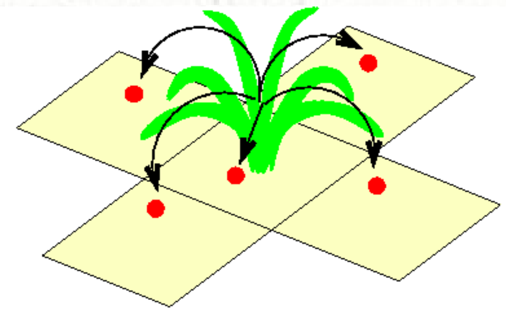
$$f_a = \frac{\alpha}{\alpha x + 1 - x} \qquad f_d = \frac{\kappa}{\alpha x + 1 - x}$$

$0 < \alpha < \kappa < 1 \quad \rightarrow \quad$ tragedia de los comunes

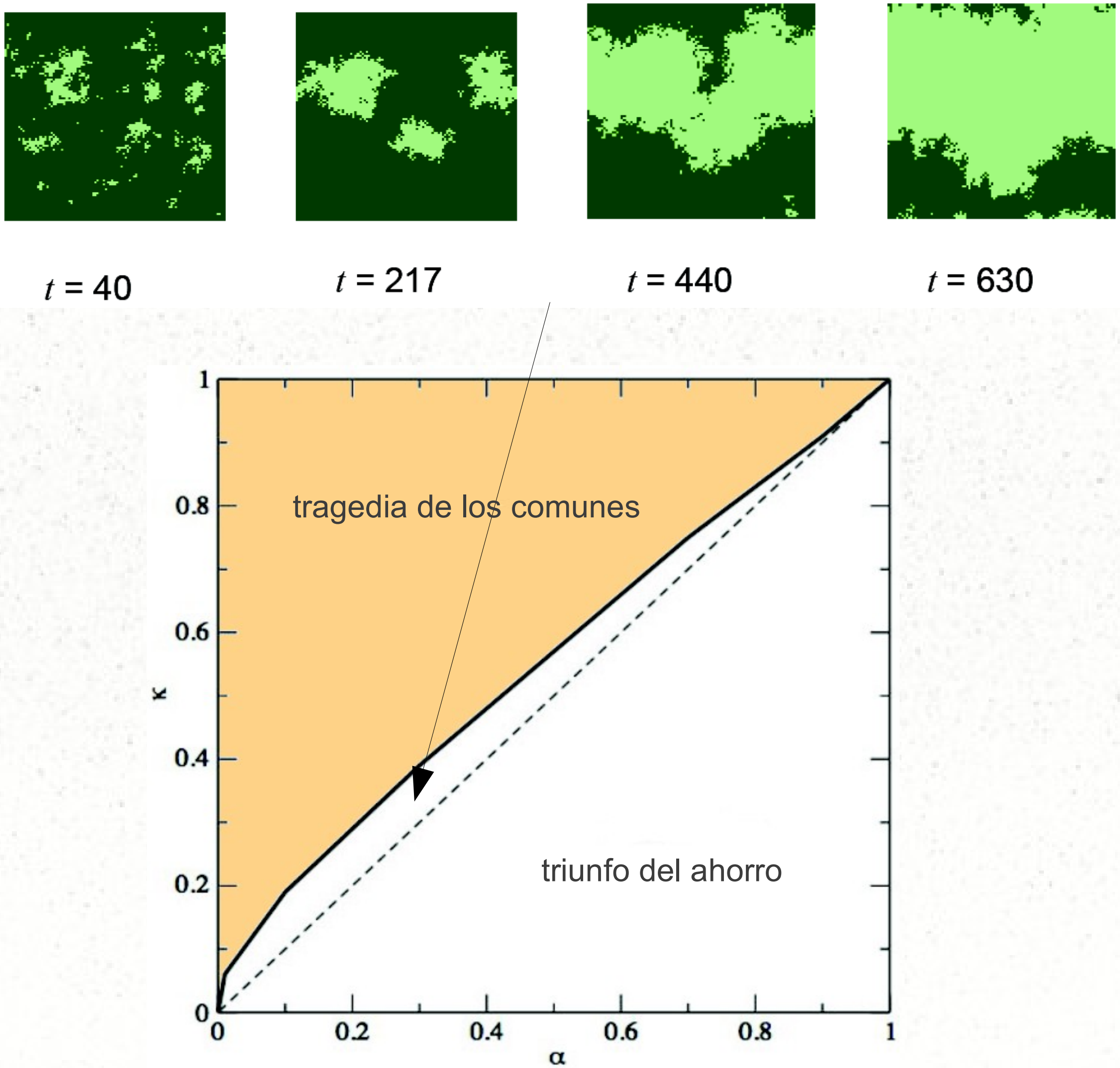
Competición entre plantas



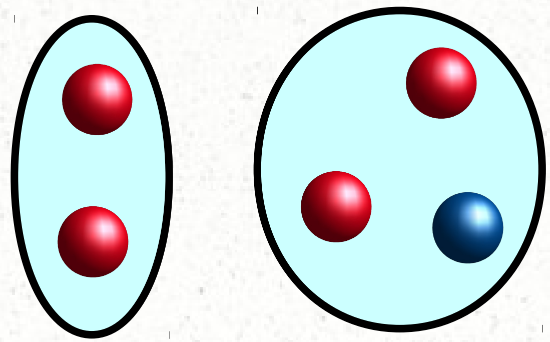




Competición entre plantas



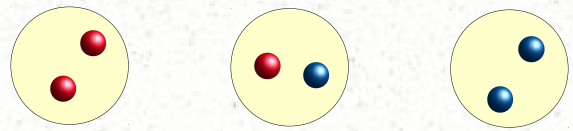
Selección de grupos

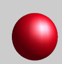
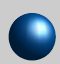
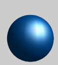


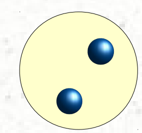
- Primer paso hacia una jerarquía de selección a diferentes niveles
- Los individuos son quienes se reproducen
- La selección actúa sobre los grupos

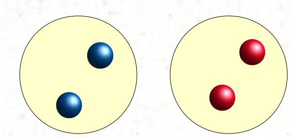
Selección de grupos

grupos de dos individuos



		
	$b-c$	$-c$
	$b/2$	0

$$\frac{1}{2}b < c \longrightarrow$$ 

$$\frac{1}{2}b > c \longrightarrow$$ 

Conclusiones

- La Teoría de Juegos formaliza las interacciones estratégicas
- La TJ clásica resuelve enfrentamientos entre individuos racionales
- La TJ evolutiva adapta la TJ a poblaciones de individuos con distintos fenotipos
- La evolución por selección natural se presenta como un juego estratégico entre especies
- La Biología está llena de ejemplos susceptibles de ser descritos mediante juegos
- La aparición de comportamientos cooperativos es una de las áreas más activas de investigación en TJ evolutiva


Gracias por
vuestra atención