El juego de la evolución

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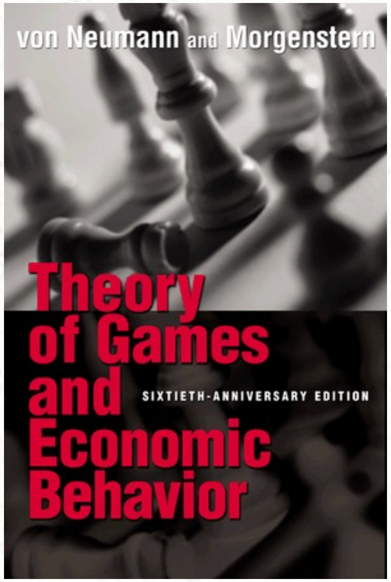
Sumario

Teoría de Juegos

Origen

Von Neumann
(1903-1957)

Morgenstern
(1902-1977)



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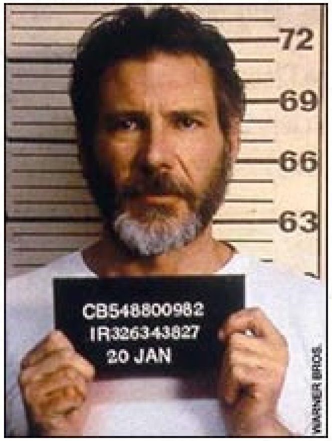
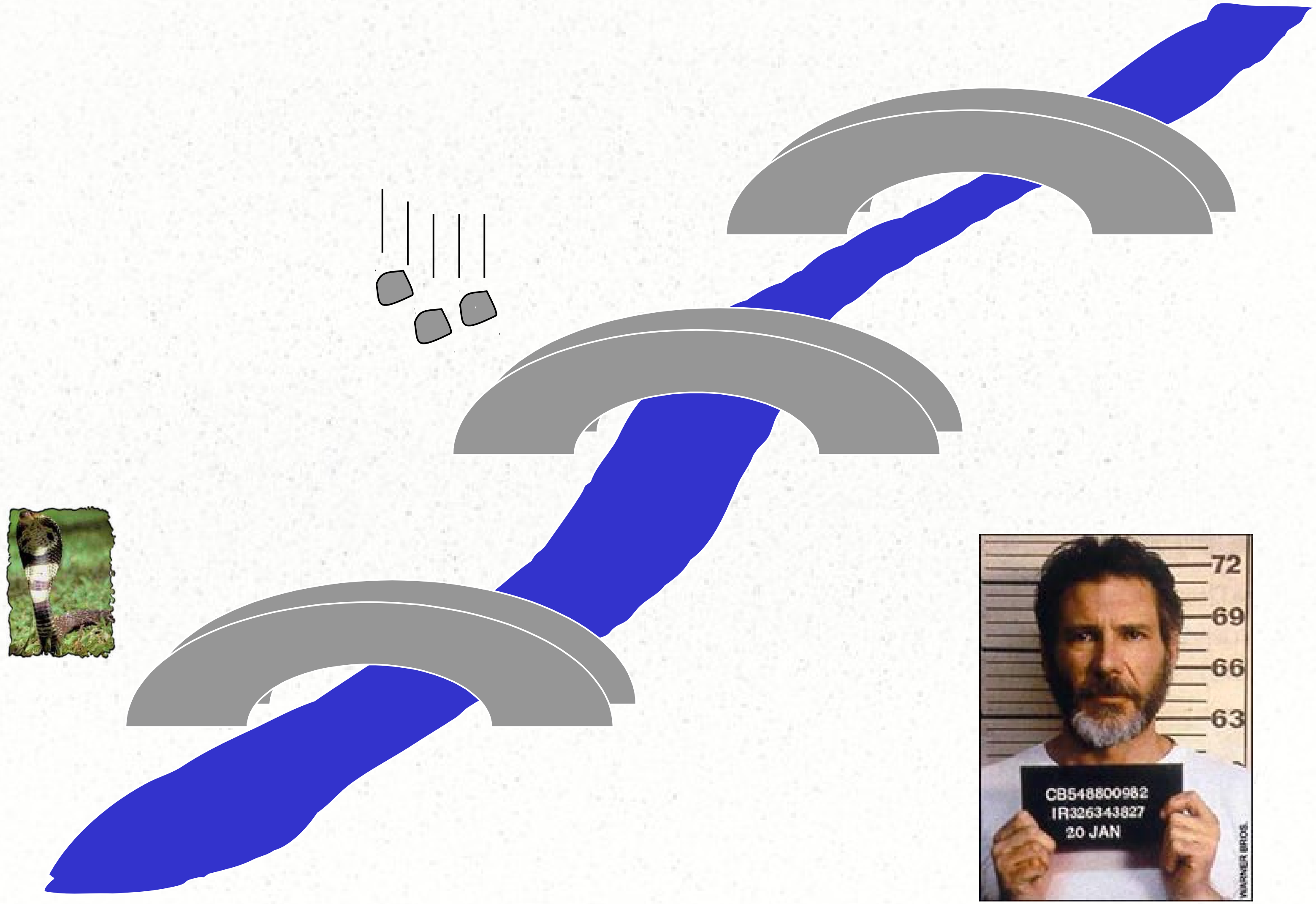
Un problema de decisión

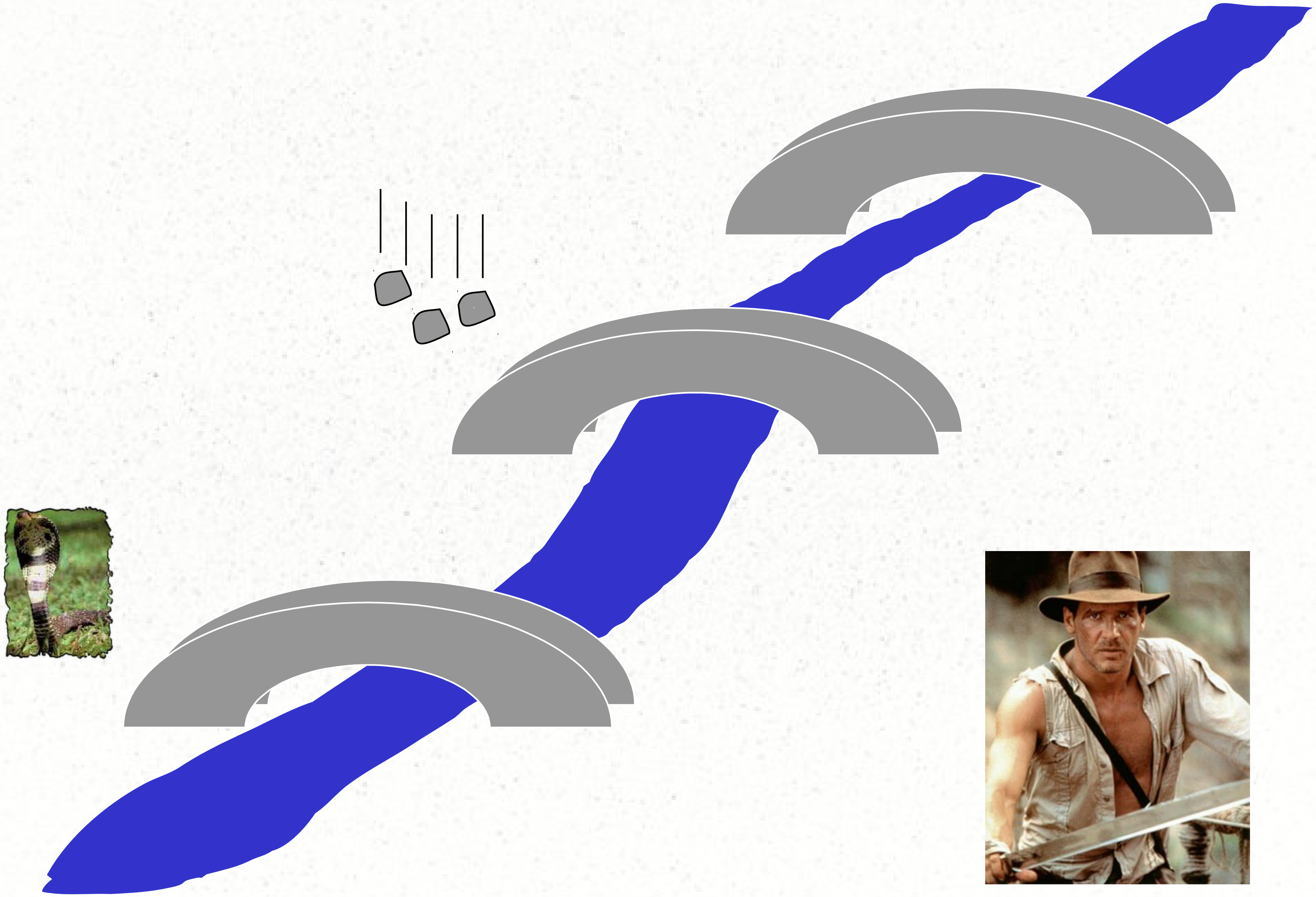
Un problema de decisión



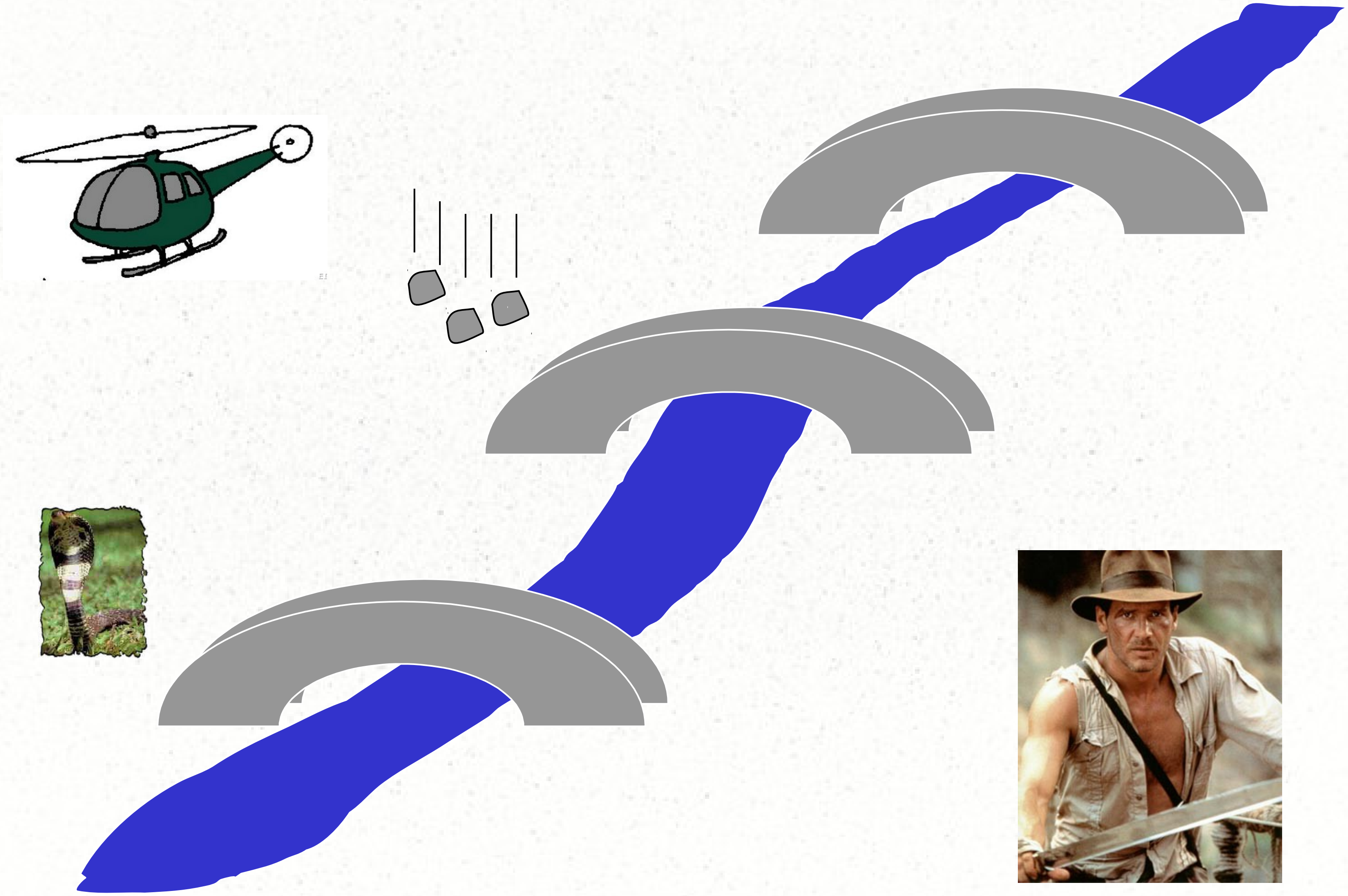
Un problema de decisión



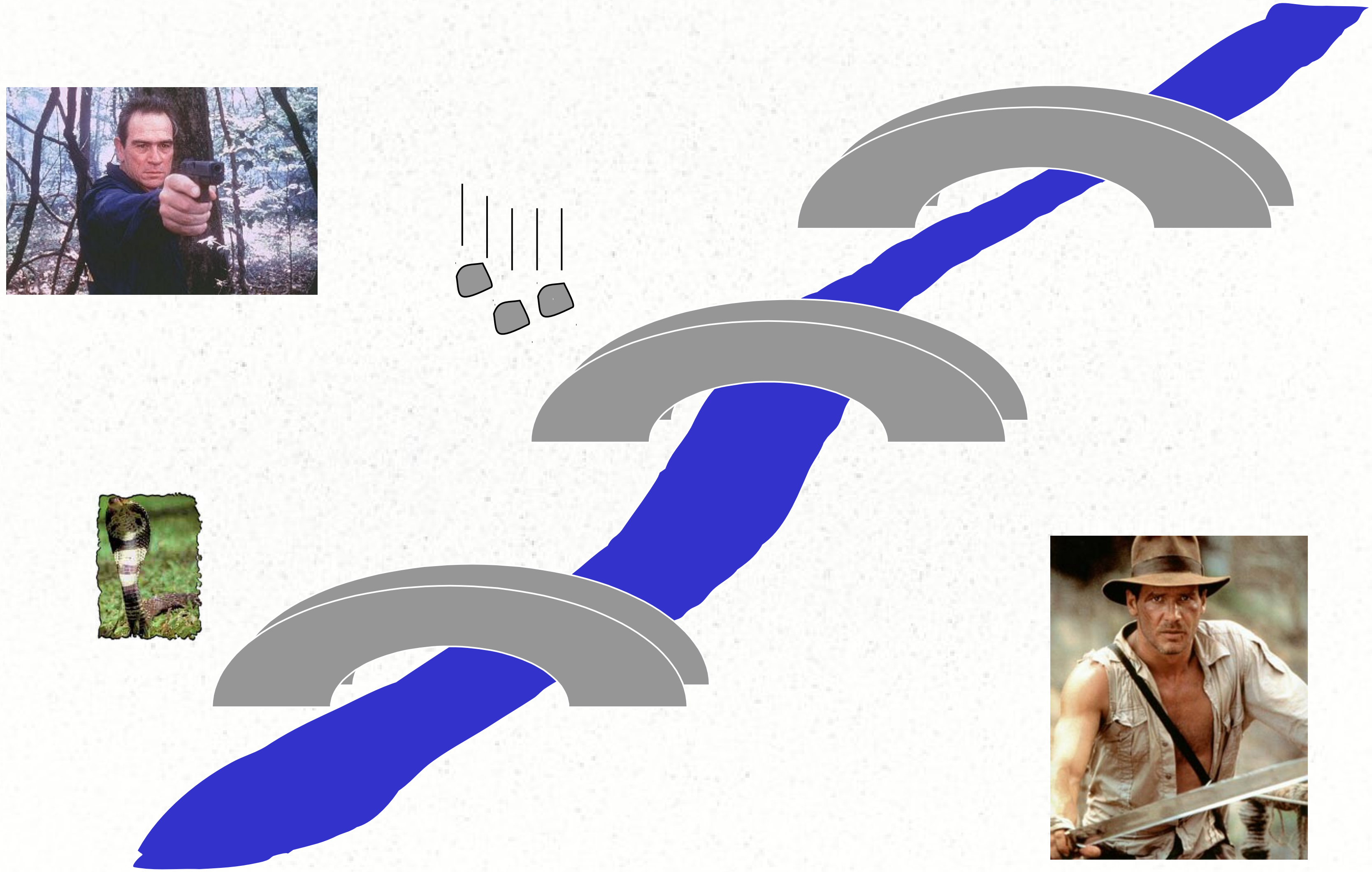
Un problema de decisión



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:

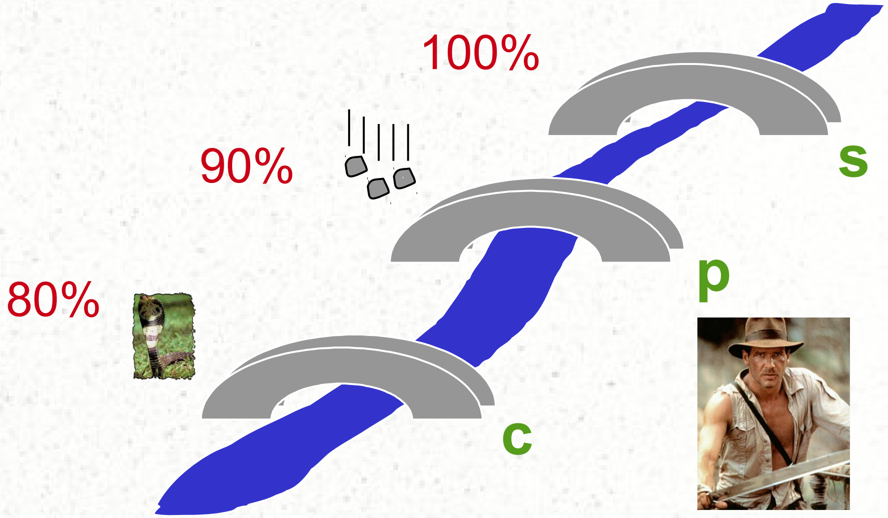
  vivir ($u = 1$) / morir ($u = 0$)

- Estrategias:

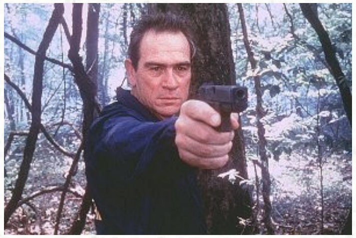
  seguro / **p**iedras / **c**obras

- Utilidad:

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

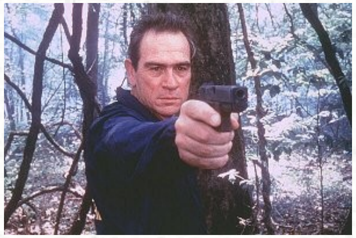


Forma estratégica



	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

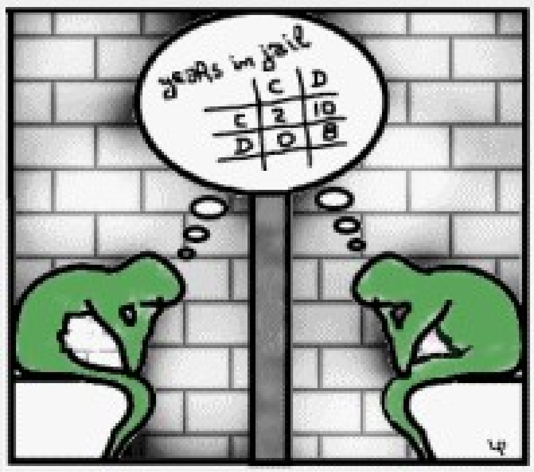
Principio de racionalidad

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

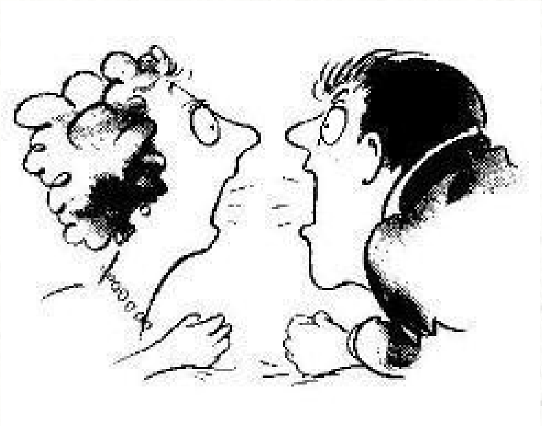
jugador 2

jugador 1

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

Juegos clásicos

la batalla de los sexos

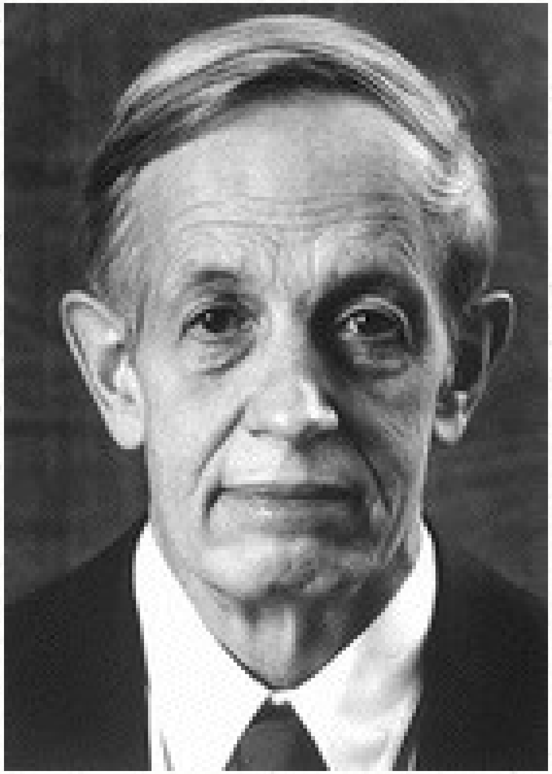


ÉL

ELLA

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

Equilibrio de Nash



Nash (1928-)

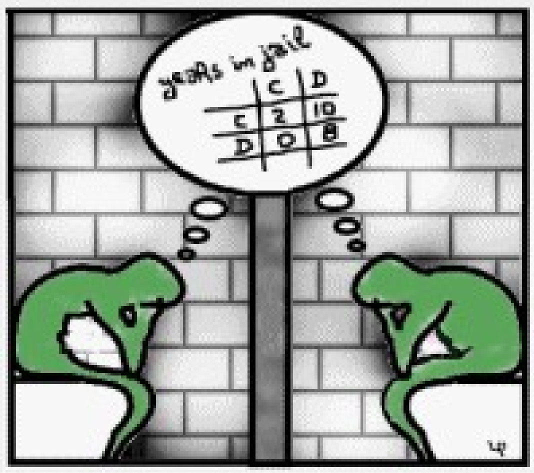
tesis de máster: 1949 - premio Nobel de Economía: 1994

Equilibrio de Nash

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

Equilibrio único

dilema del prisionero



prisionero 1 \ prisionero 2	coop.	traic.
coop.	3	0
traic.	4	1

Sin equilibrio

piedra, papel, tijeras

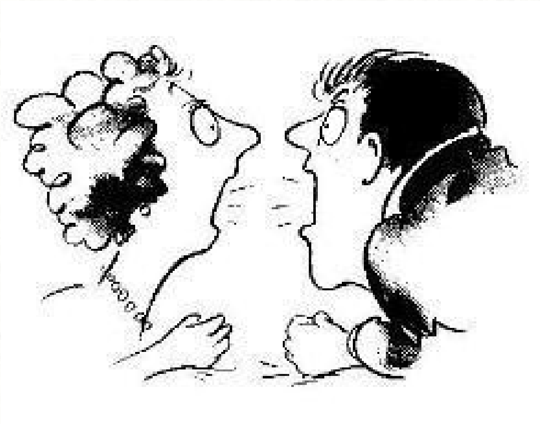
jugador 2

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

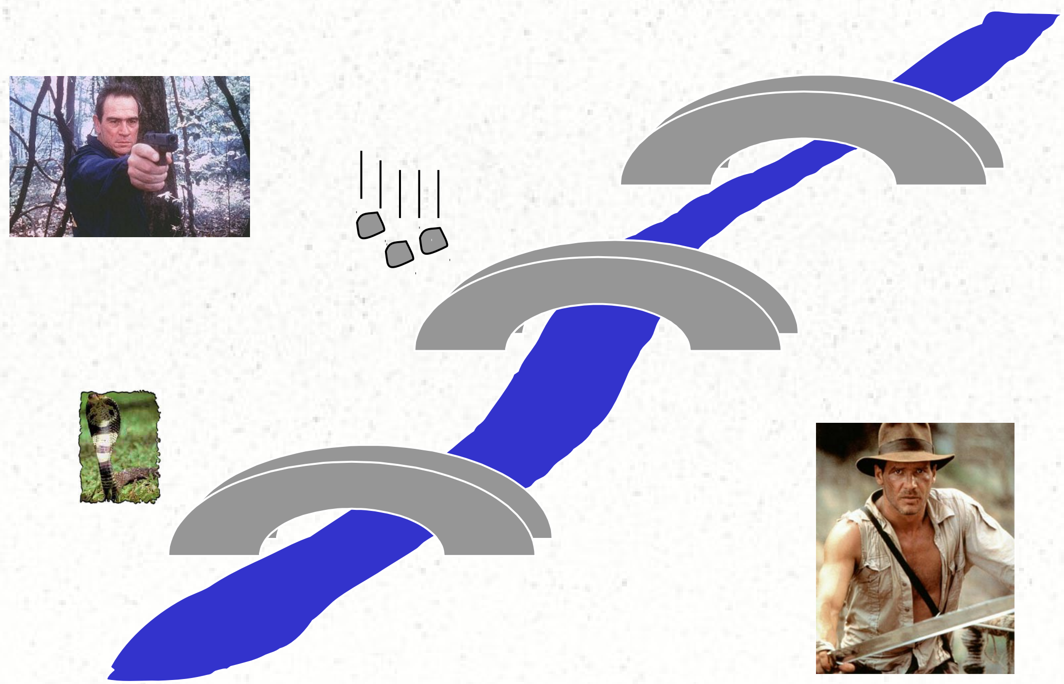
Estrategias mixtas

- 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

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

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

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

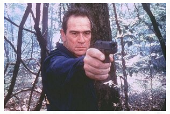
$$u_B(s) = u_B(p) = u_B(c)$$

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

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

Equilibrio mixto

B



A

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

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

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

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

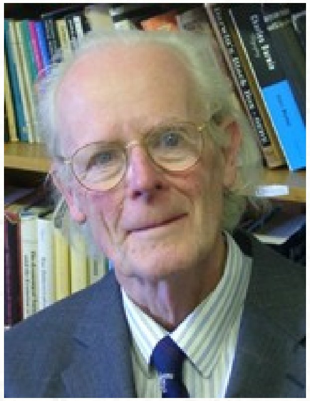
$$u_A(s) = u_A(p) = u_A(c)$$

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

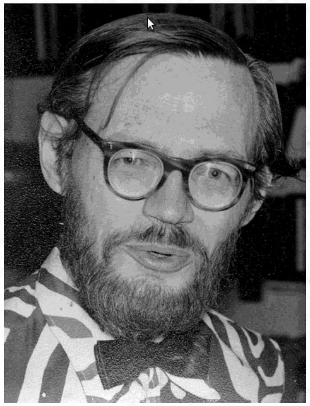
$$p_B(s) = 0.40$$
$$p_B(p) = 0.34$$
$$p_B(c) = 0.26$$

La evolución como un juego

“La lógica del conflicto animal”



Maynard Smith
(1920-2004)



Price
(1922-1975)

NATURE VOL. 246 NOVEMBER 2 1973

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[4], 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

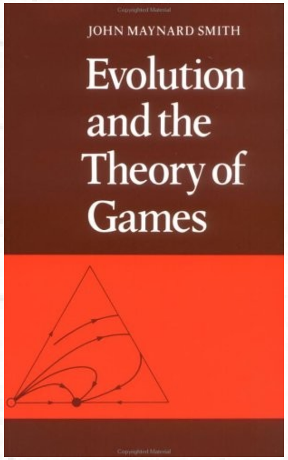
A main reason for using computer simulation was to test whether it is possible even in theory for individual selection to account for “limited war” behaviour.

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 (columns) / **individuo 1** (rows)

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

Halcones y palomas

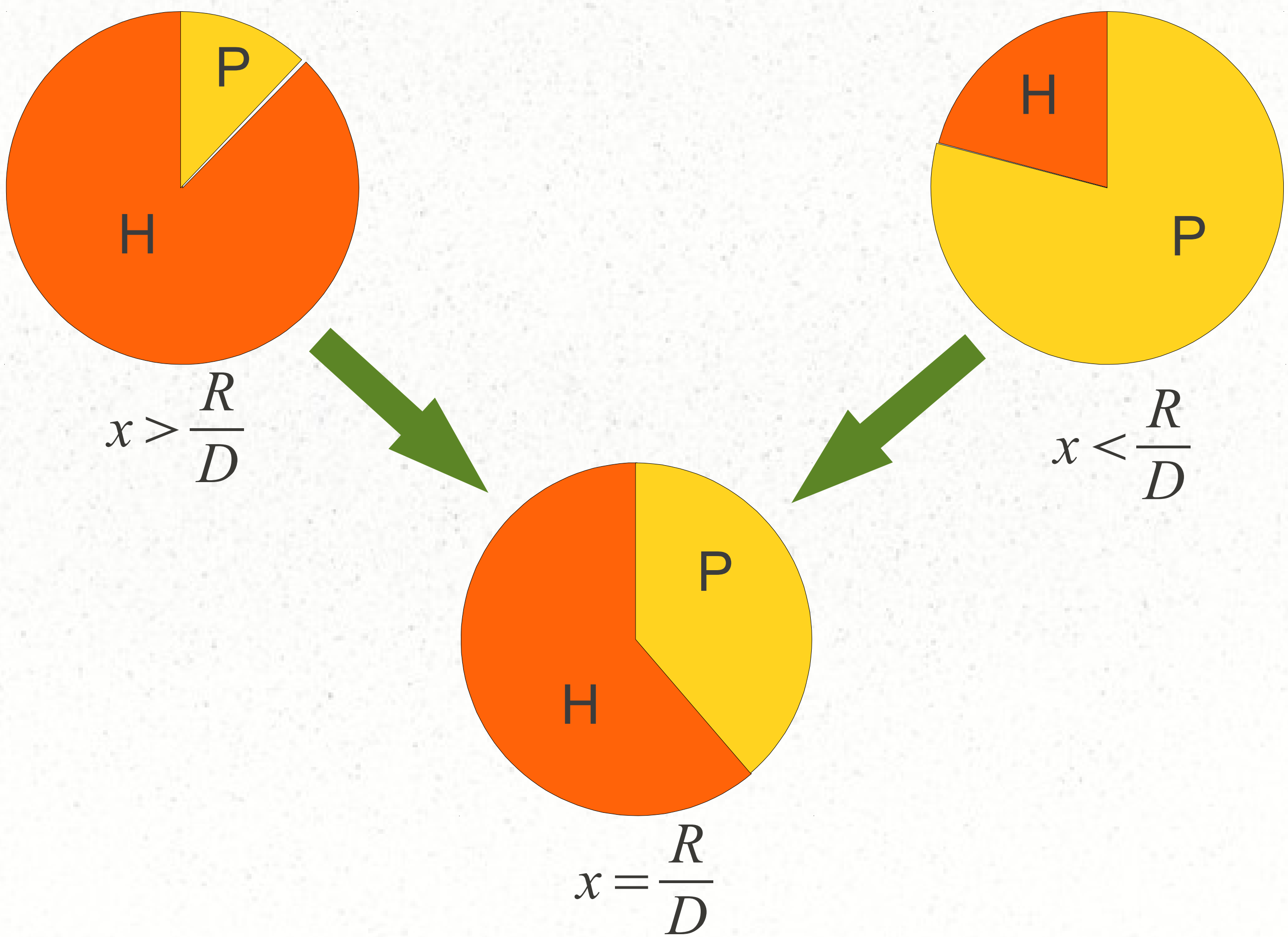
x = fracción de halcones

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

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

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

Estrategia Evolutivamente Estable



Ecuación del replicador

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

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

Ejemplos

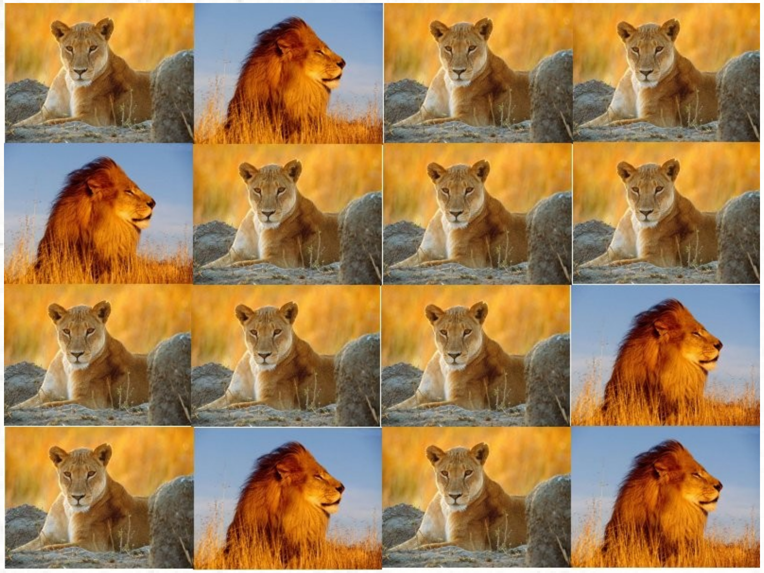
Demostraciones de fuerza

¿Por qué hay tantos machos como hembras?

¿Por qué hay tantos machos como hembras?

¿Por qué hay tantos machos como hembras?

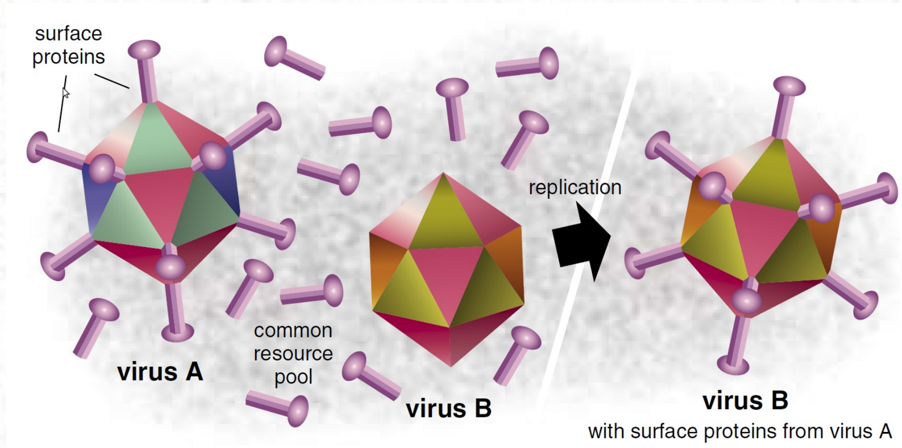
si hay más machos, ten hijas...

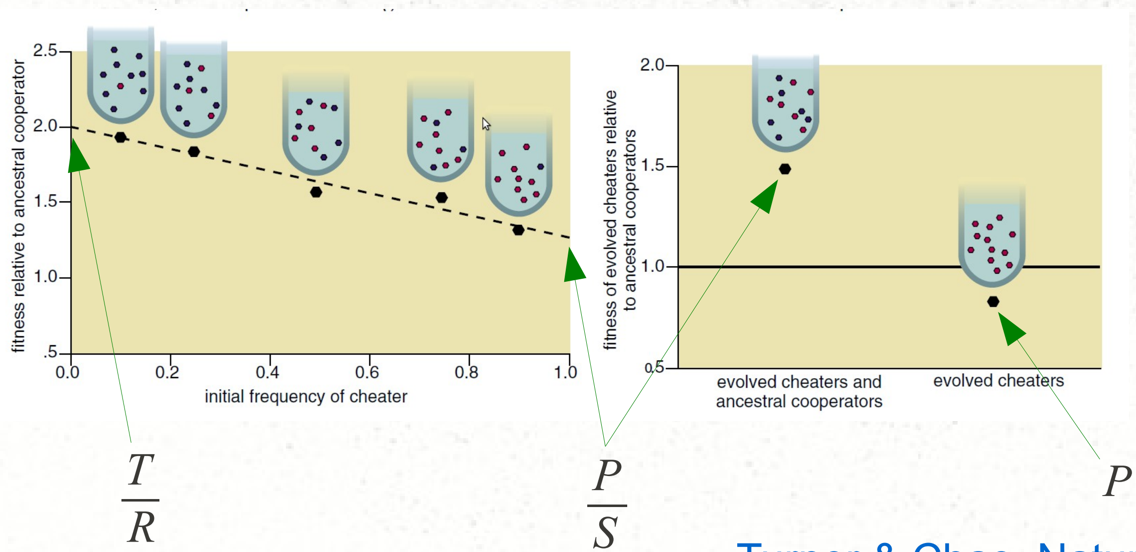


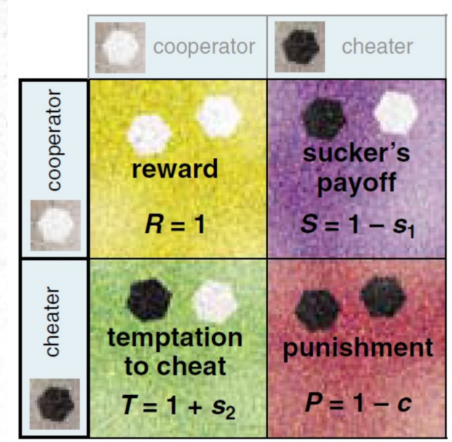
si hay más hembras, ten hijos...

...y tendrás más nietos

Parásitos de parásitos



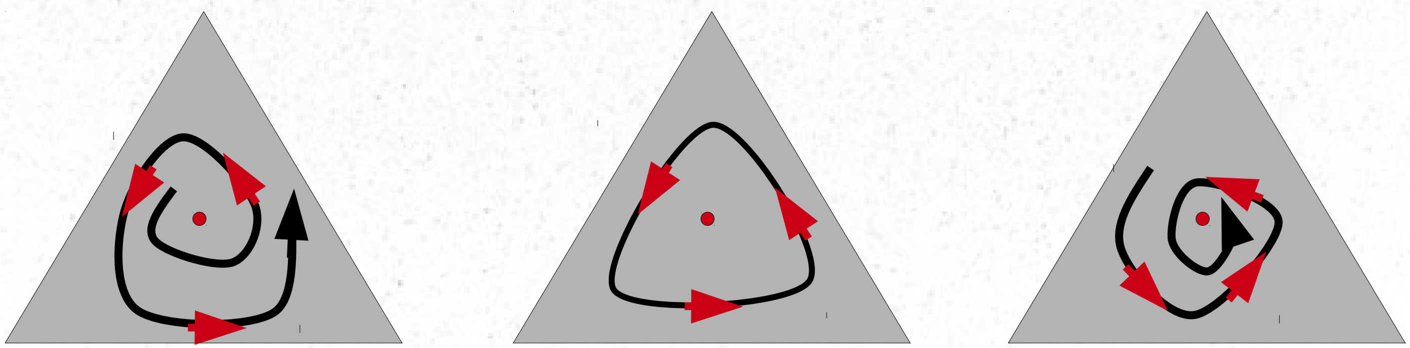




Turner & Chao, Nature **398**, 441-443 (1999)

Piedra-papel-tijeras

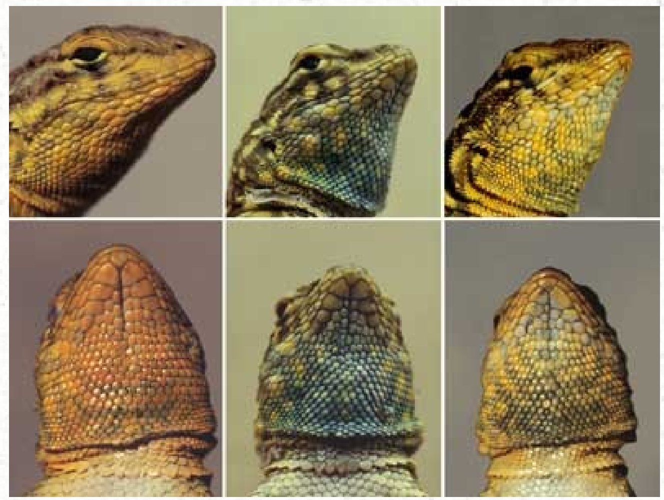
$$W = \begin{array}{c} \\ \\ \\ \end{array} \begin{array}{c} \text{Pi} \quad\quad \text{Pa} \quad\quad \text{Ti} \\ \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix} \end{array} \begin{array}{l} \text{Pi} \\ \text{Pa} \\ \text{Ti} \end{array}$$



$\lvert W \rvert < 0$	$\lvert W \rvert = 0$	$\lvert W \rvert > 0$
$(a_1 a_2 a_3 > b_1 b_2 b_3)$	$(a_1 a_2 a_3 = b_1 b_2 b_3)$	$(a_1 a_2 a_3 < b_1 b_2 b_3)$

Piedra-papel-tijeras

Uta stansburiana

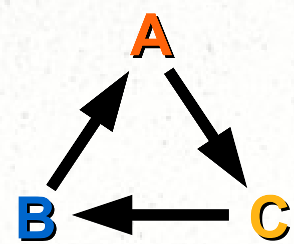


A **B** **C**

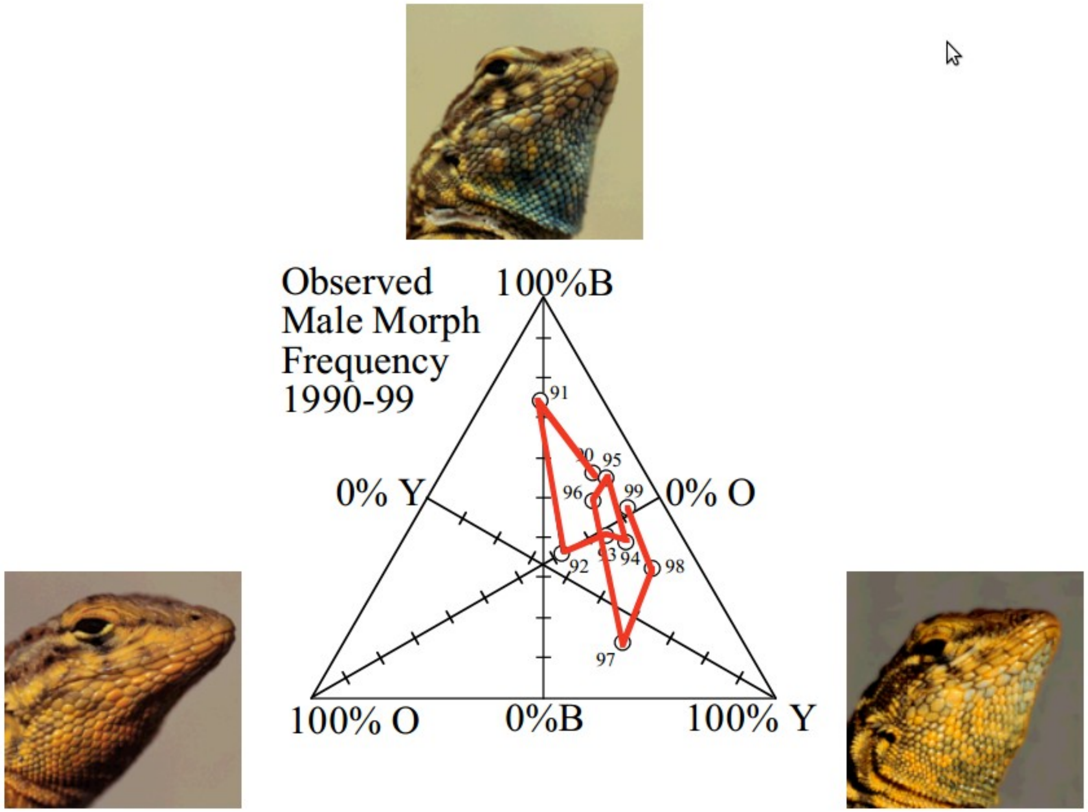
A monógamo y celoso

B polígamo y descuidado

C oportunista



Piedra-papel-tijeras



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

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