Applications of Game Theory to Biology

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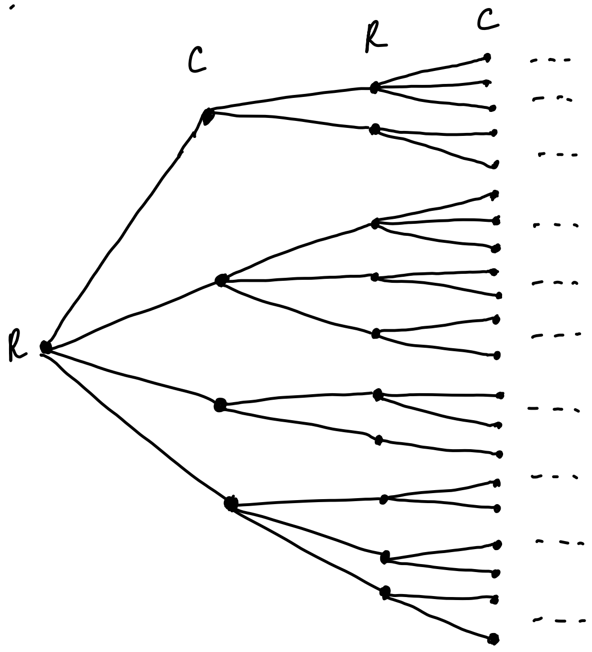
References Game Theory and Strategy by Philip D. Straffin

The Selfish Gene by Richard Dawkins

What is a game?

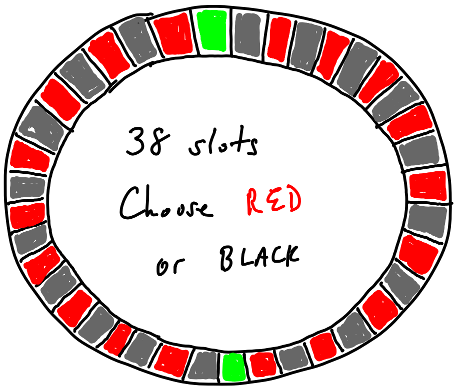
Example 1 Chess

Player R
vs. Player C



- Game Tree
- Finite because of various ways of resolving stalemate situations
- Playing chess is equivalent to two players navigating the game tree

Example 2 Roulette



You pick RED.

You bet $1.

If you're wrong, you lose $1

If you're right, you win $1

(as determined by house odds of 1 to 1)

NOTE: Prob (RED) = $\frac{18}{38}$

Prob (Not RED) = $\frac{20}{38}$

$$\text{Expected value} = \frac{18}{38} \cdot (\$1) + \frac{20}{38}(-\$1) \approx -0.53 \text{ cents}$$

The games we will study have some of the characteristics of our example games

- Two players
- Well-defined payoffs and strategies known to both players
- Strategies are played simultaneously

Example 3 "Rose" vs. "Colin"

Colin

		A	B	C	D	E	F
	A	4	−4	3	2	−3	3
Rose	B	−1	−1	−2	0	0	4
	C	−1	2	1	−1	2	−3

- Payoffs are to Rose
- Colin's payoffs are opposite of Rose's
- "Zero-sum" game

- Rose A, Colin C

  ⇒ Rose gets +3,
  Colin gets −3

Example 4

	A	B
A	1	−2
B	0	−1

Example 5

	A	B
A	1	2
B	3	0

Example 4

$$\begin{tikzcd} & & \text{Colin} & \\ & & A & B \\ \text{Rose} & A & 1 \arrow[r] & -2 \arrow[d] \\ & B & 0 \arrow[u] \arrow[r] & -1 \end{tikzcd}$$

Analysis Colin should always play B

Therefore Rose should also play B

"Pure strategy equilibrium" at (Rose B, Colin B)

Colin B dominates Colin A

Example 5

Colin

Rose

$$\begin{tikzcd} & A & B \\ A & 1 \arrow[d] & 2 \arrow[l] \\ B & 3 \arrow[r] & 0 \arrow[u] \end{tikzcd}$$

Analysis If Colin always plays A, Rose knows to play B $\Rightarrow$ Colin loses 3.

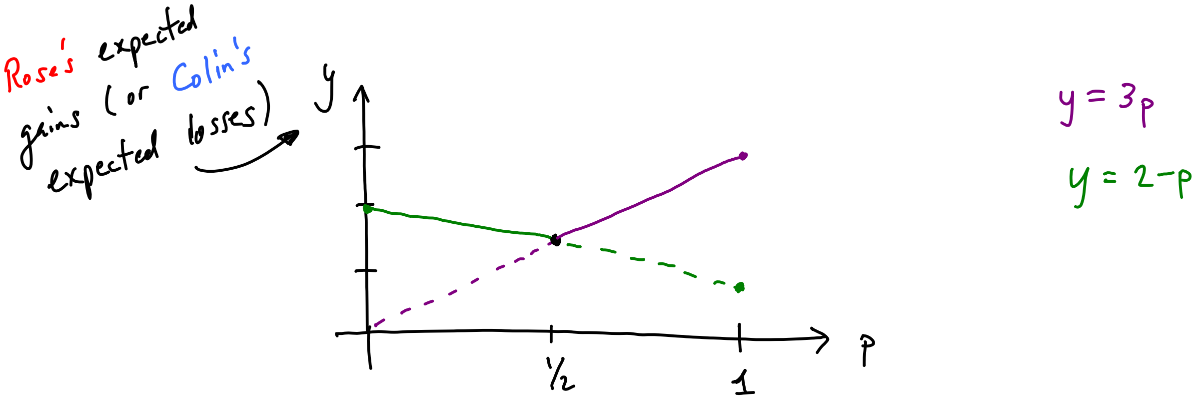
If Colin always plays B, Rose knows to play A $\Rightarrow$ Colin loses 2.

Can Colin do better by being unpredictable ?

$$\begin{array}{c|cc} & \boxed{p} & \boxed{1-p} \\ & A & B \\ \hline A & 1 & 2 \\ B & 3 & 0 \end{array}$$

$\Rightarrow$ Rose A gets her $p \cdot 1 + (1-p) \cdot 2 = 2-p$

$\Rightarrow$ Rose B gets her $3p$



Colin's optimal strategy is at the intersection point :

Play A with probability ½, B with probability ½.

Either way Colin loses $2 - \frac{1}{2} = 3 \cdot \frac{1}{2} = \frac{3}{2}$ per play, on average.

Rose's optimal strategy:

$$\begin{array}{cc|cc} & & A & B \\ \hline \textcircled{q} & A & 1 & 2 \\ \textcircled{1-q} & B & 3 & 0 \\ & & \Downarrow & \Downarrow \\ & & q+(1-q)\cdot 3 & 2q \\ & & = 3-2q & \end{array}$$

$$2q = 3-2q$$

$$\Leftrightarrow \quad 4q = 3$$

$$\Leftrightarrow \quad q = 3/4, \quad 1-q = 1/4$$

Rose plays $3/4$ A, $1/4$ B.

Her expected payoff is $2\cdot\frac{3}{4} = 3 - 2\cdot\frac{1}{4} = \frac{3}{2}$

Rose gains $\frac{3}{2}$ per play.

Rose $\frac{3}{4}A, \frac{1}{4}B$ and Colin $\frac{1}{2}A, \frac{1}{2}B$ are a

"Mixed Strategy Equilibrium"

von Neumann's Minimax Theorem (1928)

In an $m \times n$ zero-sum game there is at least one pure or mixed equilibrium of optimal strategies for Rose and Colin. For any two such equilibria, the expected payoffs are the same.

Non-zero-sum games

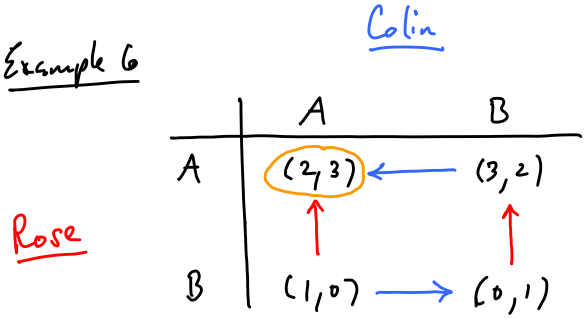
Example 6

	A	B
A	(2,3)	(3,2)
B	(1,0)	(0,1)

Example 7

	A	B
A	(2,4)	(1,0)
B	(3,1)	(0,4)

Example 6



	A	B
A	(2,3)	(3,2)
B	(1,0)	(0,1)

Pure strategy equilibrium

Rose A , Colin A

Example 7

$$\begin{tikzcd}
 & & \text{Colin} & & \\
 & & p & 1-p & \\
 & & A & B & \\
\text{Rose} & q \quad A & (2,4) \arrow[d] & (1,0) \arrow[l] \arrow[r, Rightarrow] & 2p+(1-p)=p+1 \\
 & 1-q \quad B & (3,1) \arrow[r] \arrow[d, Rightarrow] & (0,5) \arrow[u] \arrow[r, Rightarrow] \arrow[d, Rightarrow] & p+5(1-p)=-4p+5 \\
 & & 2q+3(1-q) & q & \\
 & & -q+3 & &
\end{tikzcd}$$

$$p+1=-4p+5$$
$$5p=4$$
$$p=4/5, \quad 1-p=1/5$$

$$q=-q+3$$
$$2q=3$$
$$q=2/3, \quad 1-q=1/3$$

Mixed strategy equilibrium Rose $\frac{2}{3}A, \frac{1}{3}B$, Colin $\frac{4}{5}A, \frac{1}{5}B$.

Example 8

What's a good name for this one?

	A	B
A	(0, 0)	(-2, 1)
B	(1, -2)	(-100, -100)

"Chicken"

A = swerve

B = don't swerve

Nash's Equilibrium Theorem (1950)

Every two-player non-zero-sum game has an equilibrium in pure or mixed strategies.

Example 9 Hawks vs. Doves

	Hawk	Dove
Hawk	(-25, -25)	(50, 0)
Dove	(0, 50)	(15, 15)

Hawk vs. Hawk

Winner ⇒ +50 fitness points

Loser ⇒ -100

$\text{Avg} = \frac{50-100}{2} = -25$

Hawk vs. Dove

Winner ⇒ 50

Loser ⇒ 0

Dove vs. Dove

Winner ⇒ $50 - 10 = 40$

for wasting time

Loser ⇒ $0 - 10 = -10$

$\text{Avg} = \frac{-10+40}{2} = 15$

Rose is our focal player

Colin is a randomly chosen competitor, possibly Hawk or Dove

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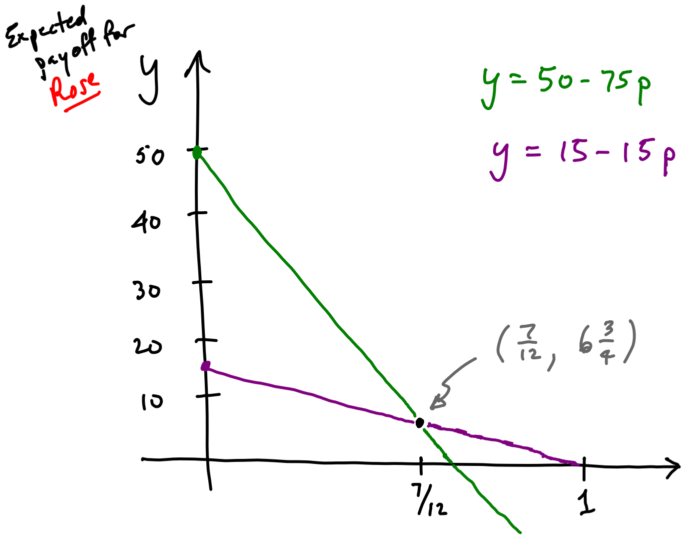
	p	1-p
	H	D
H	-25	50
D	0	15

⇒ $-25p + 50(1-p) = 50 - 75p$

⇒ $15(1-p) = 15 - 15p$



- Hawk is favored if $p < \frac{7}{12}$
- Dove is favored if $p > \frac{7}{12}$
- So, a population of $\frac{7}{12}$ Hawk, $\frac{5}{12}$ Dove is stable

It is stable in the sense that if we perturb the equilibrium slightly, then the tendency is to self-correct and move back toward the equilibrium.

Example 10

(Payoffs are to Rose)

	Hawk	Dove	Bully	Retaliator
Hawk	-25	50	50	-25
Dove	0	15	0	15
Bully	0	50	25	0
Retaliator	-25	15	50	15

In this game, a population of Retaliators is stable.

(Also, a population of Retaliators and Doves is stable if no more than 30% Doves.)

In game-theoretic analyses of more generic conflict scenarios than the one presented here, retaliator proves to be a fairly robust – stable – strategy.

In a population of Retaliators, what would we see?

Posturing, symbolic conflict, signalling

Example 11 Gender distribution

$$\begin{array}{c|cc} & \overset{p}{M} & \overset{1-p}{F} \\ \hline M & 0 & 1 \\ F & 1 & 0 \end{array} \quad \left.\begin{array}{l} \Rightarrow \quad 1-p \\ \\ \Rightarrow \quad p \end{array}\right\} \quad \begin{array}{r} p = 1-p \\ 2p = 1 \\ p = \frac{1}{2} \end{array}$$

$$\boxed{\text{In a two-gendered species, the strategy } \tfrac{1}{2}M, \tfrac{1}{2}F \text{ is stable for the gender distribution game.}}$$

But what about ...

- The returning-soldier effect?
- High male-female birth ratios in China and India?
- 13-gendered slime molds?
- Hermaphroditic flatworms?

Example 12 A mating game (see Dawkins *The Selfish Gene*, Ch 9)

Payoffs

Mating, with offspring ⇒ + 15 for each player
Total cost of rearing offspring ⇒ − 20 for the pair
Cost of courtship ⇒ − 3 for each player

Strategies

Males: Faithful = go through courtship, help raise offspring
Philandering = won't court, then deserts

Females: Coy = insist on courtship
Fast = willing to mate with anyone

The game

	Faithful	Philandering
Coy	(2, 2)	(0, 0)
Fast	(5, 5)	(−5, 15)

Equalizing payoffs for females

	p	$1-p$
	Faithful	Philandering
Coy	2	0
Fast	5	−5

Coy $\Rightarrow 2p$

Fast $\Rightarrow 5p - 5(1-p) = -5 + 10p$

$$2p = -5 + 10p$$
$$8p = 5$$
$$p = \frac{5}{8}, \quad 1-p = \frac{3}{8}$$

Equalizing payoffs for males

		Faithful	Philandering
q	Coy	2	0
$1-q$	Fast	5	15

Faithful $\Downarrow$ $2q + 5(1-q) = 5 - 3q$

Philandering $\Downarrow$ $15(1-q) = 15 - 15q$

$$15 - 15q = 5 - 3q$$
$$10 = 12q$$
$$q = \frac{5}{6}, \quad 1-q = \frac{1}{6}$$

Mixed strategy equilibrium at Female $\frac{5}{6}$ Coy, $\frac{1}{6}$ Fast,

Male $\frac{5}{8}$ Faithful, $\frac{3}{8}$ Philandering

But... is it stable?

(Both sexes would do better in a population of faithful males and fast females.)