Chimps, Cheaters, and Bees: The Evolution of Cooperation

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References:

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3. Nash equilibria. (n.d.). Retrieved March 20, 2019, from http://ess.nbb.cornell.edu/nash.html
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Nash Equilibrium and ESS: Definitions

Let A be a symmetric matrix game with payoff matrix R for the row player. A strategy $\overline{\mathbf{d}}$ is an **evolutionarily stable strategy** if the following holds:

1. $\overline{\mathbf{d}}$ is a symmetric Nash equilibrium.
2. For every pure strategy $\overline{\mathbf{p}}$ that is a best response to $\overline{\mathbf{d}}$, we have

$$\overline{d^T}\, R\, \overline{p} > \overline{p^T}\, R\, \overline{p}$$

A pair of strategies $\overline{p}$ and $\overline{q}$ form a **strict Nash equilibrium** if $\overline{p}$ and $\overline{q}$ are best responses to each other and $\forall\ \overline{r_1} \neq \overline{p}$, $\overline{r_2} \neq \overline{q}$ we have,

$$\overline{p}\, R\, \overline{q} > \overline{r_1}\, R\, \overline{q}$$

and

$$\overline{p}\, R\, \overline{q} > \overline{p}\, R\, \overline{r_2}$$

That is, if neither player can unilaterally switch to another strategy without reducing their payoff. [3]

A pair of pure strategies which is a strict Nash equilibrium is always an evolutionarily stable strategy. [1]

Prisoner's Dilemma

A symmetric matrix game, with entries S for sucker, P for punishment, R for reward, and T for temptation (as below) is a prisoner's dilemma if

$$S < P < R < T$$

[1]

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (R, R) & (S, T) \\ (T, S) & (P, P) \end{pmatrix} \end{array}$$

Matrix Game

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}$$

Row Player's Payoff Matrix

Direct Reciprocity: "I help you, you help me"

Define w to be the probability that two individuals will play another round of prisoners dilemma. Then, $\frac{1}{1-w}$ is the average number of rounds. [1] We also define two strategies:

1. **Defectors** will always defect.
2. **Cooperators** will play tit-for-tat.

If two Cooperators meet, they cooperate every time. If two Defectors meet, they defect every time. [1]

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \frac{R}{1-w} & S + \frac{wP}{1-w} \\ T + \frac{wP}{1-w} & \frac{P}{1-w} \end{pmatrix} \end{array}$$

Defecting is ESS

$$\begin{aligned} & w < 1 \\ \implies & w(P-S) < P-S \\ \implies & S(1-w) + wP < P \\ \implies & S + \frac{wP}{1-w} < \frac{P}{1-w} \end{aligned}$$

Cooperation is ESS iff

$$\begin{aligned} & T + \frac{wP}{1-w} < \frac{R}{1-w} \\ \implies & T(1-w) + wP < R \\ \implies & T - R < w(T-P) \\ \implies & \frac{T-R}{T-P} < w \end{aligned}$$

Direct Reciprocity: Example

Chimps exhibit direct reciprocity when they engage in grooming. The **costs** of grooming include $\downarrow$ vigilance, $\downarrow$ resting time, and $\uparrow$ exposure to disease. The **benefits** of grooming include $\uparrow$ hygiene, and $\downarrow$ stress.

Suppose each chimp values these things for their well-being in the same way. For example:

- $\uparrow$ hygiene $\implies$ +6
- $\downarrow$ stress $\implies$ +2
- $\downarrow$ vigilance $\implies$ -1
- $\downarrow$ resting time $\implies$ -1
- $\uparrow$ exposure to disease $\implies$ -1

Then, we can assign values to R, T, S, and P as follows:

- $S = -3$: I groom you, but it is not reciprocated. In this case, the costs of a grooming session are incurred.
- $P = 0$: No grooming takes place, so no benefits or costs incurred.
- $R = 5$: I groom you, and you groom me. Costs and benefits incurred.
- $T = 8$: I get groomed, but do not reciprocate. Benefits of grooming incurred.

Then, $\frac{T-R}{T-P} = \frac{3}{8}$, so if the probability of another round of grooming is greater than 37.5%, cooperation can evolve.

Indirect Reciprocity: "I help you, someone will help me"

Define q to be the probability of knowing the reputation of another individual. We also define two strategies:

1. **Defectors** will always defect.
2. **Cooperators** will cooperate unless they know their opponent's reputation as a defector.

Note that a cooperator will cooperate with a defector with probability $1 - q$. [1]

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & (1-q)S + qP \\ (1-q)T + qP & P \end{pmatrix} \end{array}$$

Defecting is ESS

$$q < 1 \text{ and } S < P$$
$$\implies (1-q)S < (1-q)P$$
$$\implies (1-q)S + qP < P$$

Cooperation is ESS iff

$$R > (1-q)T + qP$$
$$\implies R - T > -qT + qP$$
$$\implies R - T > q(P - T)$$
$$\implies q > \frac{T-R}{T-P}$$

Indirect Reciprocity: Example

When homework is assigned, each student in MATH 304 can choose to keep their assignment to themselves (defect) or to share their solutions with another student (cooperate).

Suppose each student values these things in the same way. For example:

- $\uparrow$ my mark $\implies$ $+5$
- $\uparrow$ class average because $\uparrow$ your mark $\implies$ -2

Then, we can assign values to R, T, S, and P as follows:

- $S = -2$: If I share my solution with you, but you don't share your solution with me, then your mark $\uparrow$, so the class average $\uparrow$, but my mark does not change.
- $P = 0$: When neither student shares their solution, there is no gain or loss.
- $R = 3$: If we both share our solutions, then both of our marks $\uparrow$, but so does the class average.
- $T = 5$: If you share your solution with me, but I don't share my solution with you, then your mark does not change, and my mark $\uparrow$, so I'm not too worried about the class average $\uparrow$.

Then $\frac{T-R}{T-P} = \frac{2}{5}$, so if the probability of knowing the reputation of another student is greater than 40%, cooperation can evolve.

Kin Selection: "% of caring"

Define r to be the average relatedness between interacting individuals. [1]

$$\begin{array}{ccc} & C & D \\ \begin{array}{c} C \\ D \end{array} & \multicolumn{2}{c}{\begin{pmatrix} R & \frac{S+rT}{1+r} \\ \frac{T+rS}{1+r} & P \end{pmatrix}} \end{array}$$

Defecting is ESS iff

$$\frac{S+rT}{1+r} < P$$
$$\implies S + rT < (1+r)P$$
$$\implies r(T-P) < P - S$$
$$\implies r < \frac{P-S}{T-P}$$

Define $r_d = \frac{P-S}{T-P}$ to be the maximum value of r so that defection is ESS.

Cooperation is ESS iff

$$R > \frac{T+rS}{1+r}$$
$$\implies R(1+r) > T + rS$$
$$\implies r(R-S) > T - R$$
$$\implies r > \frac{T-R}{R-S}$$

Define $r_c = \frac{T-R}{R-S}$ to be the minimum value of r so that cooperation is ESS.

Kin Selection: "% of caring"

The evolutionary outcome depends on the relative ranking of r, r_c, and r_d. [1] There are several cases:

1. $r_d > r_c \Leftrightarrow R + P > T + S$
    - $r_d > r_c > r \implies$ Defectors dominate.
    - $r_d > r > r_c \implies$ Both cooperators and defectors are ESS.
    - $r > r_d > r_c \implies$ Cooperators dominate.

2. $r_c > r_d \Leftrightarrow R + P < T + S$
    - $r_c > r_d > r \implies$ Defectors dominate.
    - $r_c > r > r_d \implies$ Neither cooperators or defectors are ESS.
    - $r > r_c > r_d \implies$ Cooperators dominate.

3. $r_c = r_d \Leftrightarrow R + P = T + S$
   $\Leftrightarrow P - S = T - R \Leftrightarrow R - S = T - P$

This final case is called "Equal gains from switching" and gives rise to Hamilton's Rule. Define $cost = P - S = T - R$ and $benefit = R - S = T - P$. Then, cooperators and defectors are ESS when $r > \frac{cost}{benefit}$.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix} \end{array}$$

Example: Kin selection occurs in nature with eusocial insects such as bees, and with cooperative breeding practices of lionesses.