Social behavior: game theory and inclusive fitness

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Game theory in the wild

Game theory is the study of interactions. When the outcome of something depends on the actions of more than one individual, you have a game. Here are some examples:

Hawk-Dove

Two individuals are involved in a fight over a resource, of value V. Individuals can either fight aggressively (Hawks), or be relatively passive (Doves). If a Hawk is matched with a Dove, the Dove concedes immediately, the Hawk gets the resource, and thus, payoff V, with the Dove getting 0. If a Dove fights a Dove, they peacefully divide the resource equally, each getting $V/2$. If two Hawks are matched, they fight to a draw, and share the resource equally, but pay a cost of fighting, C, so that each gets $V/2 - C$. We can summarize the payoffs in a game matrix[1]:

$$\begin{array}{ccc} & \text{Hawk} & \text{Dove} \\ \text{Hawk} & V/2 - C & V \\ \text{Dove} & 0 & V/2 \end{array} \tag{1}$$

[1] This game is also known as the "Game of Chicken" or "Snowdrift".

Prisoner's Dilemma

Perhaps the most famous of all games in evolutionary game theory.[2]. Consider a version of the Prisoner's Dilemma that's sometimes called a "donation game": there are two individuals matched to play the game, each can simultaneously donate a resource to the other (with the donated resource more valuable to the recipient than the donor. The benefit from receiving the donation (assumed to be symmetric) is b while the cost of donating to self is c, with $b > c$. The game matrix takes the form on the margin:

[2] It is usually introduced with a story about two prisoners being interrogated but I find the story to be not very helpful beyond explaining why the game has this weird name `http://en.wikipedia.org/wiki/Prisoner's_dilemma`

$$\begin{array}{ccc} & \text{Donate} & \text{Don't Donate} \\ \text{Donate} & b - c & -c \\ \text{Don't donate} & b & 0 \end{array} \tag{2}$$

In a single-shot game, no matter what the other player is currently doing, it is best for a focal individual to not donate, because donating is simply a direct cost of $-c$. Accordingly, "Don't Donate" is the only Nash equilibrium in this game.

Public goods game

Suppose an interaction where individuals invest into creating or defending a resource (e.g., a territory, an extra-cellular matrix, a common nest) that all individuals benefit from. Since investments are individually costly, but benefits accrue to everyone, there is a conflict of interest. Suppose the benefit function is given by $B(\sum_j a_j)$ where a_j are the contributions of the jth individual, and the cost to individual i is given by ca_i, with $c > 0$ a constant. The total payoff to individual i is then:

$$w_i = B(\sum_j a_j) - ca_i \tag{3}$$

Evolutionarily stable strategy (ESS)

First we need to define what we mean by "strategy". We are dealing with actors that can not be supposed to have any order of cognitive capacity: we want our theory to apply to plants, bacteria, or even viruses as well as cognitively advanced animals. So obviously, we cannot mean a premeditated aspect to the term "strategy". Instead, a strategy in evolutionary game theory is simply an inherited disposition to behave in certain ways. This is deliberately vague, but "inherited" is the operational word here. The strategy can be a very complicated conditional behavior, such that the behavior that a given individual does might never be seen in its progeny, but the rule (or mechanism) that produces the behavior needs to be inherited for it to count as a strategy in evolutionary game theory terms.

The concept of an evolutionarily stable strategy (ESS) itself was introduced by Maynard Smith and Price (1973): a strategy is an ESS if, when almost all members of a population adopt the strategy, no "mutant" employing an alternative strategy has a higher fitness.[3,4]

[3] Technically, the original definition of ESS allows for mutants that have the same fitness as the resident strategy, provided that the resident has a higher fitness against such "neutral" mutants.

[4] Although Maynard-Smith and Price coined the term of ESS, the idea behind it has a long antecedent, starting with at least Fisher's sex ratio theory Fisher (1958).

In mathematical terms, let S denote the strategy that is resident in a population (i.e., is at frequency very close to 1), and S' the alternative "mutant" strategy that we introduce at low (almost zero) frequency into this population, and let $w_x(x, y)$ be the fitness of an x-strategists when the population is almost entirely composed of y-strategists. Then the condition for a strategy S to be an ESS is:

$$\begin{gathered} w_{S'}(S', S) \leq w_S(S, S) \quad \text{and} \\ \text{if} \quad w_{S'}(S', S) = w_S(S, S), \quad \text{then} \quad w_S(S, S') > w_{S'}(S', S') \end{gathered} \tag{4}$$

Let's apply the ESS condition to the examples above, supposing the strategies are the actual behaviors (in other words, the propensity to do either behavior is genetically encoded).

Hawk-Dove game Suppose that the frequency of the Hawks in the population is p, and individuals encounter each other randomly in a large, well-mixed population. With probability p then, a Hawk individual encounters another Hawk individual, and gets payoff $V/2 - C$, and with probability $1 - p$ it encounters a Dove individual and gets V. So the expected payoff to a Hawk player is:

$$w_H = p(V/2) - C + (1-p)V = V - p(C + V/2) \tag{5}$$

Likewise, the expected payoff to a Dove is:

$$w_D = p \times 0 + (1-p)V/2 = (1-p)V/2 \tag{6}$$

Assume that $2C > V$: for $p \approx 1$, we have $w_H \approx V/2 - C < 0 \approx w_D$, so Hawks cannot be an ESS. But if $p \approx 0$, we have $w_H = V > V/2 \approx w_D$. Which means that there is no (pure strategy) ESS in the H-D game.

In the case of the **Prisoner's Dilemma**, it is obvious what the sole ESS is: not donate.

Public goods game We know have a different type of game, with continuous strategies. The task now is to find a local maximum of the payoff function in a_i, assuming that everyone else is investing a_r (where r stands for "resident") into the public good. If the payoff of individual i is maximized at $a_i = a_r$, we have ourselves an ESS. We can use the techniques for the optimization from the optimal foraging lecture, using the first partial derivative of payoff as the first order ESS condition:

$$\left.\frac{\partial w_i}{\partial a_i}\right|_{a_i = a_r = 0} = 0 \tag{7}$$

$$= B'(na_r) - c = 0\,, \tag{8}$$

where n is the number of individuals in the group. It is important to first take the derivative of w_i and *then* substitute $a_i = a_r$, because the individual optimization needs to happen *while keeping everyone else constant*. To see what this ESS condition entails, consider the "socially optimal" investment level, where the total payoff $\sum_i w_i$ is maximized assuming that everyone invests at the same level a (i.e., the benefit is given by $B(na)$);

$$\frac{\partial \sum_i w_i}{\partial a} = 0 \tag{9}$$

$$= n^2 B'(na) - nc = 0 \tag{10}$$

If B is a concave function (i.e., diminishing returns to investment, or $B'' < 0$, that means the socially optimal investment is higher than the individually optimal investment. Hence the "tragedy of commons" (Hardin, 1968).

Repeated or iterated games

Now, all of the analysis above applies to a rather peculiar situation where individuals play the game, but they only play it once in their lives. That's not a very social situation. Most social interactions consists of repeated interactions, each of which have some small effect on the total outcome. And there the space of strategic possibilities explodes. Consider the general prisoner's dilemma matrix:

$$\begin{array}{lcc} & \text{Cooperate} & \text{Defect} \\ \text{Cooperate} & R & S \\ \text{Defect} & T & P \end{array} , \qquad (11)$$

where R stands for reward (of mutual cooperation), T for temptation (for defecting), S is the sucker's payoff, and P is punishment (for mutual defection), and $T > R > P > S$.[5] Now assume that this game is played repeatedly between the same pair of individuals, with a probability continuation δ after each repetition.[6] Now the strategies in this game can be much more complicated than simple defect or cooperate; in particular, they can depend on the history of the game, the number of rounds played at the moment, etc. First, consider the payoffs to players that always defect or cooperate regardless of the history of the interaction. Since the behaviors are unconditional, whatever the first roux payoffs are, all rounds will yield the same payoffs; labeling that payoff by x, the expected payoff from the game is:

[5] So, in the donation game, $R = b - c$, $S = -c$, $T = b$, $P = 0$.

[6] So, on average, the game will be played $1/\delta$ times, but could go on for much longer

$$x + \delta x + \delta^2 x + \delta^3 x + \cdots = x \underbrace{\left(1 + \delta + \delta^2 + \delta^3 + \cdots\right)}_{\tau} . \qquad (12)$$

To evaluate the term in the parentheses, which we have denoted by τ, divide it by δ:

$$\frac{\tau}{\delta} = \frac{1}{\delta} + 1 + \delta + \delta^2 + \cdots = \frac{1}{\delta} + \tau$$

The last step is because the series is infinite, so no end to the summation. The rest is simple algebra to find:

$$\tau = \frac{1}{1-\delta}$$

With this, we can write the new payoff matrix for unconditional cooperators and defectors as

$$\begin{array}{lcc} & \text{Always C} & \text{Always D} \\ \text{Always C} & \frac{1}{1-\delta}r & \frac{1}{1-\delta}s \\ \text{Always D} & \frac{1}{1-\delta}t & \frac{1}{1-\delta}p \end{array} , \qquad (13)$$

which is not very exciting, since it's simply the old matrix multiplied with a positive constant. But now suppose we add a third strategy, the so-called "Tit-for-Tat", which starts out cooperating, but then simply copies the action of the opponent in the last round. So, against an unconditional cooperator, a TFT player will always cooperate (so its payoff is $\frac{1}{1-\delta}r$), and against an unconditional defector, TFT will cooperate in the first round and defect ever after (so its payoff is $s+\frac{\delta}{1-\delta}p$. Against itself, TFT also cooperates forever. So the new game matrix is:

$$\begin{array}{cccc} & \text{Always C} & \text{Always D} & \text{TFT} \\ \text{Always C} & \frac{1}{1-\delta}r & \frac{1}{1-\delta}s & \frac{1}{1-\delta}r \\ \text{Always D} & \frac{1}{1-\delta}t & \frac{1}{1-\delta}p & t+\frac{\delta}{1-\delta}p \\ \text{TFT} & \frac{1}{1-\delta}r & s+\frac{\delta}{1-\delta}p & \frac{1}{1-\delta}r \end{array}, \tag{14}$$

Can TFT be an ESS in this game? The relevant condition is that TFT's payoff against itself is greater than everyone else's payoff against TFT. For All-D, this means:

$$\begin{aligned} \frac{1}{1-\delta}r &> t+\frac{\delta}{1-\delta}p \\ \delta &> \frac{t-r}{t-p}\,. \end{aligned} \tag{15}$$

In other words, if the game is repeated long enough, TFT is stable against All-D.

But we know All-D is an ESS in the two-strategy version of the game. Can TFT invade? The relevant condition is that the payoff of TFT against All-D is greater than All-D's against itself, so:

$$s+\frac{\delta}{1-\delta}p > t+\frac{\delta}{1-\delta}p$$

So, $s > t$, and TFT cannot invade All-D when the latter is established in the population.

Hamilton's rule

In the above, we assumed that interactions are between individuals randomly selected from a well-mixed population. In other words, if the frequency of a strategy in the population is p, a focal individual's partner is of that strategy with probability p as well, regardless of the focal individual's own strategy. This is unrealistic for most real populations, where demographic and spatial processes structure the population such that individuals are more likely to interact with their relatives who are liable to carry the same behavioral strategies as the focal individual. In other words, the strategies of social partners become conditional on the strategy of the focal individual.

Let us consider the simple, single shot donation game above. Now, assume that each individual has probability r with interacting with someone of their own strategy, and $(1-r)$ of interacting with someone at random. Now the expected payoff to Donate and Don't Donate are:

$$w_C = r(b-c) + (1-r)(p(b-c) - (1-p)c) \tag{16}$$

$$w_D = r \times 0 + (1-r)(pb + (1-p) \times 0) \tag{17}$$

Now, if we write down the condition $w_C > w_D$, we find the condition for the cooperators to increase to be:

$$rb - c > 0 \ . \tag{18}$$

In other words, we have just derived Hamilton's rule for a two-person interaction (Hamilton, 1964).

References

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