Social behavior: evolutionary game theory

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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 following form:

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

[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`

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 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)

Strategies versus actions

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 (and indeed, can have) 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, or take some actions. 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. But there is an important distinction between the actions (what we actually observe organisms do) and the strategies (what is inherited) that produce them.

The simplest type of strategy one can think of is one that prescribes a fixed action: i.e., we might consider a strategy that always plays "Don't Donate" and another that always plays "Donate" in the prisoner's dilemma. This is called a "pure strategy" in classical game theory. Alternatively, one can think of strategies that prescribe a *probability* of playing Donate or Don't Donate. Such strategies are called "mixed strategies" in classical game theory. Note that when you allow mixed strategies in a discrete action game (such as Hawk-Dove and Prisoner's Dilemma examples above), you have effectively introduced a new strategy space, where you are now dealing with some probability π of playing one or the other strategy. Each value of π is now itself a pure strategy, rather like the as in the continuous public goods game. Of course, if there are more than two strategies, π would be a vector (adding up to 1) specifying the probabilities for taking each action.

Furthermore, one can clearly also define mixed strategies over continuous action sets.

Evolutionarily stable strategy

The concept of an evolutionarily stable strategy (ESS) itself was introduced by Maynard Smith and Price (1973): Roughly, 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]

[3] 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.

Hawk-Dove game with pure strategies Suppose we only allow pure strategies (in other words, the propensity to do either behavior is genetically encoded). Further, assume 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.

This shows that an ESS is not guaranteed to exist. What happens when the ESS fails to exist? For that, we'd have to define the dynamics for the change in strategy dynamics. As it turns out, we can borrow the dynamics we have for haploid population genetics, since we are essentially dealing with the same situation. Our strategies can be thought of as two alleles. We do have to be cognizant of a slight issue, which is that in population genetics, fitness is a non-negative quantity (negative offspring doesn't make sense), but our payoffs as defined above can be negative or positive. A way out of this is to assume that each individual has a baseline fitness w_0, and the payoffs here really represent addition (or subtraction as the case might be) to this baseline. In other words, we define the fitness of strategy X, f_X as

$$f_X = w_0 + w_X \ , \tag{7}$$

where w_X is the payoff from the game. If we chose w_0 big enough so that even the lowest payoff outcome yields positive fitness, we can write for the change in p as:

An alternative and more widely used approach is to normalize $w_0 = 1$, and multiply the payoff with a scaling number, i.e., define $f_X = 1+sw_X$, where s is called the strength of selection.

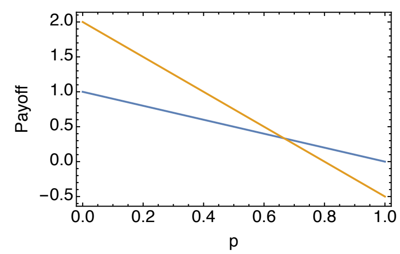
$$\Delta p = \frac{f_H - f_D}{\bar{f}} p(1-p) = \frac{w_H - w_D}{w_0 + pw_H + (1-p)w_D} p(1-p) \ . \tag{8}$$

Now you can see why we don't much care about the actual value of w_0: it changes the numerical value of Δp, but not its sign (since it cancels in the difference in the numerator).

as long as it's big enough so that the denominator is positive for all p

We do often care about the relative magnitude of w_0 and the payoffs, or equivalently, the strength of selection, for other reasons.

Note that both w_H and w_D are linear decreasing functions of p, but from the above we know they intersect at some $0 < p^* < 1$ (see Figure in the margin). In other words, there is a p^* where $\Delta p = 0$, meaning that we have an internal, or polymorphic equilibrium.



Plot of w_D (blue) and w_H (orange) as a function of p, with $V = 2$ and $C = 1.5$. The intersection point corresponds to the polymorphic equilibrium.

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

Hawk-Dove game with mixed strategies Now let's return to the Hawk Dove game but now allow mixed strategies. Now, we can have a pure evolutionary strategy π that denotes the probability that an individual plays Hawk. Let us consider a population fixed for strategy π and consider the payoff of an alternative strategy, π' against this one. The expected fitness of a π-strategist against itself, is given by:

regardless of whether we have pure or mixed strategies

$$w(\pi, \pi) = \pi^2 \left(\frac{V}{2} - C \right) + \pi(1-\pi)V + (1-\pi)^2 \frac{V}{2} \ ,$$

whereas the payoff of π' playing against π is:

$$w(\pi', \pi) = \pi'\pi \left(\frac{V}{2} - C \right) + \pi'(1-\pi)V + (1-\pi')(1-\pi) \frac{V}{2} \ . \tag{9}$$

Now, we want $w(\pi, \pi) \geq w(\pi', \pi)$ for all π', which means:

$$w(\pi, \pi) - w(\pi', \pi) \geq 0 \ . \tag{10}$$

We can write the difference as:

$$\pi \left(\frac{V}{2} - C \right) (\pi - \pi') + (1-\pi)V(\pi - \pi') - (1-\pi)\frac{V}{2}(\pi - \pi') \geq 0 \tag{11}$$

$$\Rightarrow \qquad (\pi - \pi') \left(\frac{V}{2} - \pi C \right) \geq 0 \tag{12}$$

Now in this last expression, if $V/2 - \pi C$ is non-zero, then for either $\pi' > \pi$, or $\pi' < \pi$, the inequality will be violated. That means the only possible way the inequality is satisfied is when $V/2 - \pi C = 0$, when it becomes an equality. So

$\pi = V/2C$ is the only candidate ESS, and we have to look at the second ESS condition to see if it actually is an ESS. The latter is $w(\pi, \pi') - w(\pi', \pi) > 0$, and it evaluates to:

$$(\pi' - \pi)\left(\frac{V}{2} - \pi' C\right) < 0\,, \tag{13}$$

which holds for all $\pi' \neq \pi$, since for $\pi' < \pi$ the first term is negative while the second one is positive, and for $\pi' > \pi$, the opposite. Thus, the second order condition is satisfied, and $\pi = V/2C$ is a mixed-strategy ESS. Note that the value of the mixed-strategy ESS is the same as the stable polymorphic frequency of Hawks in the pure strategy case. This is not a coincidence.

It is a consequence of the fact that the payoffs are linear in both the mixed strategy and pure strategy frequency.

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:

$$\left.\frac{\partial w_i}{\partial a_i}\right|_{a_i = a_r = 0} = 0 \tag{14}$$

$$= B'(na_r) - c = 0\,, \tag{15}$$

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 $B(na)$);

$$\frac{\partial \sum_i w_i}{\partial a} = 0 \tag{16}$$

$$= n^2 B'(na) - nc = 0 \tag{17}$$

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:

$$\begin{array}{ccc} & \text{Cooperate} & \text{Defect} \\ \text{Cooperate} & R & S \\ \text{Defect} & T & P \end{array}\quad, \tag{18}$$

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 $T > R > P > S$.[4] Now assume that this game is played repeatedly between the same pair of individuals, with a probability continuation δ after each repetition.[5] 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:

$$x + \delta x + \delta^2 x + \delta^3 x + \cdots = x\underbrace{\left(1 + \delta + \delta^2 + \delta^3 + \cdots\right)}_{\tau}\,. \tag{19}$$

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

$$\begin{array}{ccc} & \text{Always C} & \text{Always D} \\ \text{Always C} & \frac{1}{1-\delta}r & \frac{1}{1-\delta}s \\ \text{Always D} & \frac{1}{1-\delta}t & \frac{1}{1-\delta}p \end{array}\quad, \tag{20}$$

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:

$$\begin{array}{cccc} & \text{Always C} & \text{Always D} & \text{TFT} \\ \text{Always C} & \frac{1}{1-\delta}r & \frac{1}{1-\delta}s & \frac{1}{1-\delta}r \\ \text{Always D} & \frac{1}{1-\delta}t & \frac{1}{1-\delta}p & t+\frac{\delta}{1-\delta}p \\ \text{TFT} & \frac{1}{1-\delta}r & s+\frac{\delta}{1-\delta}p & \frac{1}{1-\delta}r \end{array}\quad, \tag{21}$$

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

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

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:

$$\begin{aligned} \frac{1}{1-\delta}r &> t + \frac{\delta}{1-\delta}p \\ \delta &> \frac{t-r}{t-p}\,. \end{aligned} \tag{22}$$

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:

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

Since $s < t$, TFT cannot invade All-D when the latter is established in the population. Thus All-D is still an ESS. In other words, the shadow of the future can make cooperation tough reciprocity stable once it is established, but may not be enough to actually build it up is defection is established.

References

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