Evolutionary Game Theory

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1 The Evolutionarily Stable Strategy (ESS)

An evolutionarily stable strategy (ESS) is a strategy that, if adopted by nearly all members of a population, can not be invaded by a rare mutant strategy. Consider a game in which D is an ESS. If a rare mutant H with very low frequency ($p \ll 1$) were to enter the population, would it invade? We can write the fitness of the two strategies as follows:

$$W(D) = C + (1-p)\mathbb{E}(D, D,) + p\mathbb{E}(D, H)$$

$$W(H) = C + (1-p)\mathbb{E}(H, D) + p\mathbb{E}(H, H)$$

where C is the fitness of an individual before the encounter. If D is an ESS, this means that $W(D) > W(H)$ Solving the inequality $W(D) > W(H)$, we get:

$$\frac{\mathbb{E}(D, D) - \mathbb{E}(H, D)}{\mathbb{E}(H, H) - \mathbb{E}(D, H)} > \frac{p}{1-p}$$

We assumed that $p \ll 1$ so the fraction on the right-hand side of the inequality is essentially equal to zero. Thus for the left-hand side to be greater than zero means that the numerator on the right-hand side must be positive. This yields the condition:

$$\mathbb{E}(D, D) > \mathbb{E}(H, D).$$

This is the Nash Equilibrium solution. However, an ESS can arise even when this condition is not met. If $\mathbb{E}(D, D) = \mathbb{E}(H, D)$ and $\mathbb{E}(D, H) > \mathbb{E}(H, D)$, then D is still an ESS. That is, while H mutants are not at a disadvantage when playing D's, D nonetheless shares an advantage in the population because it does better against H than H does against itself.

The Hawk-Dove game was originally developed by Maynard Smith and Price to describe animal conflict. Animals playing the Dove strategy (i.e., "Doves") avoid conflict. When faced

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with competition over a resource, two doves will split the benefit of the resource v. In contrast, Hawks always escalate conflicts and fight over resources. When a Hawk plays a dove, it always takes the full value of the resource, however, when a Hawk plays another Hawk, there is a 50% chance either will win. These fights between Hawks are costly, incurring a cost c on Hawks during each encounter. Figure 1 presents the payoff matrix for the Hawk-Dove game. Each cell of the matrix contains to entries. The first is the payoff to the row player. The second is the payoff to the column player. Frequently, payoff matrices will simply list the payoff to the row player, since if the game is symmetric, the payoffs to the row players and column players will be identical when facing the same type of opponent.

		Player 2	
		H	D
Player 1	H	$(v-c)/2, (v-c)/2$	$v, 0$
	D	$0, v$	$v/2, v/2$

Figure 1: Maynard Smith and Price's Hawk-Dove game. Row player's payoffs given first in each cell.

2 Evolutionary Game Theory

Evolutionary game theory (EGT) focuses on evolutionary dynamics that are *frequency dependent*. The fitness payoff for a particular phenotype depends on the population composition.

Classical game theory focuses largely on the properties of the equilibria of games. One of the central defining features of EGT is the focus on the *dynamics* of strategies and their composition in a population rather than on the properties of equilibria.

The approach is to study replicator equations. The attractors of these dynamical equations are the evolutionary stable strategies (ESSs) – or the Nash Equilibria of the game.

Consider the Prisoner's Dilemma game. This game is defined by two strategies: Cooperate and Defect. The prisoner's dilemma game is defined such that the payoff to a defector playing against a cooperator is greatest; the payoff of mutual cooperation is next greatest; the payoff for mutual defection is next greatest; and the payoff to cooperating when the opponent defects is least. These features can be economically summarized in a payoff matrix that lists the payoff to the row strategy when playing the column strategy (figure 2). We can name the payoffs in game 2 $T > R > P > S$, where T is the temptation, R is the reward for mutual cooperation, P is the punishment for mutual defection, and S is the sucker's payoff. It is conventional to also assume that $R > (T + P)/2$. Without this, then alternating rounds between cooperation and defection leads to a greater payoff than pure cooperation.

		Player 2	
		C	D
Player 1	C	R	S
	D	T	P

Figure 2: Prisoner's Dilemma. $T > R > P > S$ and $R > (T + P)/2$.

We assume a large population (effectively infinite) so that we can reasonably model the proportions of the two strategies, x_c and x_d. If the population were sufficiently small, we would need to worry about things like the random extinction of strategies at low frequency (this is the so-called "finite" population model). Let w_c and w_d be the fitnesses of cooperators and defectors respectively. Further, let $\Delta w(s_1, s_2)$ denote the change in fitness for an s_1 individual against an s_2 opponent. Fitness is a function of the proportions of strategies d and c:

$$\begin{aligned} w_c &= W_{c,0} + x_c \Delta w(C,C) + x_d \Delta w(C,D) \\ w_d &= W_{d,0} + x_c \Delta w(D,C) + x_d \Delta w(D,D) \\ \bar{w} &= x_c w_c + x_d w_d \end{aligned} \tag{1}$$

where $W_{i,0}$ is the initial fitness of strategy i and $\bar{w}$ is mean fitness. The change in frequencies from one generation to the next will be a function of the current proportions and the relative fitnesses. For example, the proportion of strategy c in the next generation will be $x'_c = x_c w_c / \bar{w}$, the proportion of strategy d will be $x'_d = x_d w_d / \bar{w}$. The change from one generation to the next for the c strategy will be:

$$\Delta x_c = x'_c - x_c = \frac{x_c(w_c - \bar{w})}{\bar{w}}$$

For small change, and where reproduction is continuous, we can approximate this equation with the differential equation,

$$\dot{x}_c = \frac{x_c(w_c - \bar{w})}{\bar{w}}.$$

Since by definition of the Prisoner's Dilemma $(w_c - \bar{w})/\bar{w} < 0$, it is clear that the c strategy will decay exponentially at a rate equal to $(w_c - \bar{w})/\bar{w}$.

The general replicator dynamic equation for n strategies is

$$\dot{x}_i = x_i \left[w_i(\mathbf{x}) - \bar{w} \right] \tag{2}$$

where $\dot{x}_i$ is the time derivative of the proportion playing the ith strategy, $w_i(x)$ is the fitness of strategy i when played against the current state vector $\mathbf{x} = (x_1, x_2, \ldots, x_n)$. This fitness of strategy i comes from the payoff matrix $\mathbf{W} = [w_{ij}]$. Fitness for the i strategy is $w_i(\mathbf{x}) = \sum_j x_i w_{i,j}$. Note that this is just the expected fitness for strategy i: multiply the frequency of strategy i times the fitnesses of i against itself and all other strategies in the population. This sum is its expected fitness.

The system of differential equations in 2 is generally much easier to analyze than the corresponding system of difference equations. For continuously breeding, age-structured populations, the assumption of continuous change is not that bad as long as the change per unit time is not too great.

Assuming that the population size is very large means that we don't have to worry about stochastic variation in strategies due to drift.

2.1 An Example: Hawk-Dove-Retaliator

Hawk-Dove-Retaliator is another game described by Maynard Smith and Price. Like Hawk-Dove, Hawks always fight and Doves always concede to a fight. The game introduces a third strategy, Retaliator, which escalate only if its adversary escalates. That is, Retaliator normally plays Dove but plays Hawk against other Hawks. The payoff to Retaliator is thus equal to that of a Hawk when playing a Hawk and a Dove when playing Doves or itself. These payoffs are summarized in figure 3.

		Player 2		
		H	D	R
	H	$(v-c)/2$	v	$(v-c)/2$
Player 1	D	0	$v/2$	$v/2$
	R	$(v-c)/2$	$v/2$	$v/2$

Figure 3: Maynard Smith and Price's Hawk-Dove-Retaliator game. Row player's payoffs given first in each cell. v is the payoff for victory in a conflict. c is the cost of fighting (e.g., wounding).

The trajectories of the dynamics of this game are plotted in the three-sided simplex of figure 4. In this plot, each vertex of the triangle represents the pure strategy. A point in the interior represents a mixture of strategies. The sum of the distances from each vertex is always one.

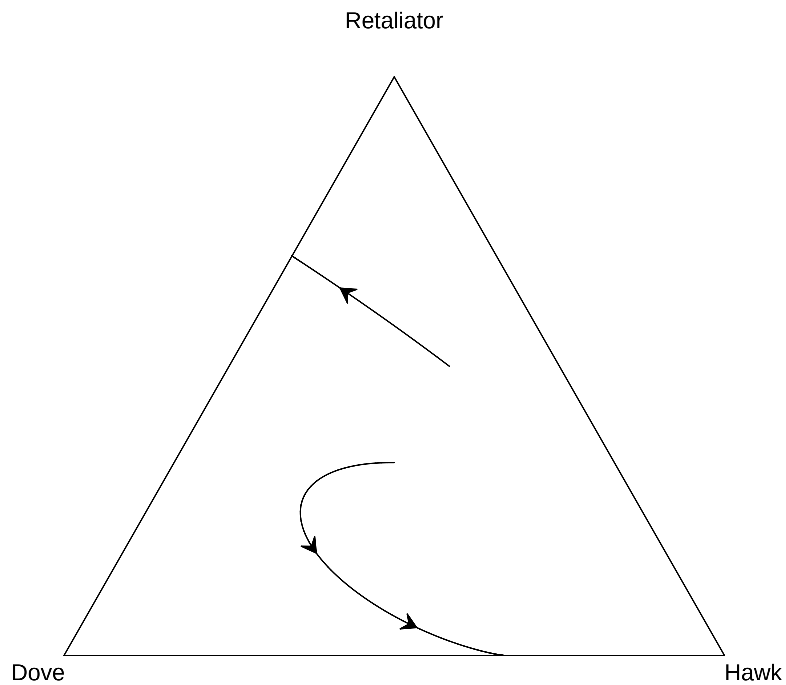

Figure 4: Evolutionary trajectories for the Hawk-Dove-Retaliator game with different starting values. The initial values are $x_0^{(1)} = (1/3, 1/3, 1/3)$ and $x_0^{(2)} = (1/3, 1/2, 1/6)$. Initial values $x_0^{(1)}$ leads to a mixed equilibrium that is 2/3 Doves and 1/3 Hawks, while $x_0^{(2)}$ leads to a mixed equilibrium that is 69% Retaliator and 31% Dove.