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The Game Theory of Evolution

Ever since Jon Nash popularized the field of game theory, economists, psychologists, and other professionals have theorized how to apply game theoretical strategies to all facets of life. The utility and applicability of game theory has grown so vast that even evolutionary biologists are discovering how its strategies can help explain seemingly unrelated phenomena like Charles Darwin's Theory of Evolution. The Prisoner's Dilemma and similar game theoretical models have shown scientists that evolution and game theory are intrinsically linked. Behavior like altruism in monkeys and tree growth in populations of trees are now being explained as the strategies organisms employ to win the game known as natural selection.

The first person to practice what we now call evolutionary game theory was R.A. Fisher in 1930. Fisher conceptualized the field by attempting to explain why there were equal numbers of males and females in many mammal populations. He was able to reconcile the sex ratio by postulating that fitness should be measured not by the number of children that an individual in a population has, but rather how many grandchildren they have. If there were more men, women would be more fit and vice versa. Since the fitness of men and women would be unequal if there were more of either sex, the only way to ensure that there are equal numbers of grandchildren would be to have a balanced sex-ratio. Fisher's research became the foundation upon which the entire field of evolutionary game theory was constructed. Later, John Maynard Smith would add another element to evolutionary game theory by introducing the concept of an evolutionarily stable strategy, which was the term for a strategy that ensured the survival of a population. Since published, evolutionary game theorists and biologists have used Smith's work to explain how critical decision-making and behaviors passed along genetically were responsible for the evolution of life to its present state (Alexander 1).

To understand how game theory plays a role in evolution, it is essential to first understand evolution and its mechanics. The theory of evolution, popularized by Charles Darwin in the 1800s, is an explanation for both the origin of life on earth and why life has taken on many different forms since its inception. Fundamentally, evolution relies on the process of natural selection to gradually weed out any species or populations that are not fit to survive and reproduce. Natural selection occurs when a selective pressure appears in a population such that those individuals who exhibit traits that are advantageous to survival will survive and the rest will die out, leaving only the fit individuals. Over an extended period, natural selection can phase out entire species while ensuring that survivors are suitably adapted to their environment.

Another detail that is imperative to understand before applying game theory to evolution is heritable behavior. Certain behaviors are known to be passed from generation to generation. For example, if a species is aggressive, then their children are likely to be aggressive, and science has found that the trait is not just acquired from observation, but also by genetics. The same genetic heritability applies to traits like compassion and extraversion. Since biologists determined that behavior can be genetic, natural selection would apply to behavior in the same way that it applies to any physical trait (Bouchard 148-151).

To understand the game theory of evolution, a firm understanding of evolutionarily stable strategies is necessary. Consider the metaphorical survival Grand Prix. In the race, the cars are akin to evolving organisms, the engines are akin to natural selection, and the fuel in each car is akin to a strategy that the organism exhibits. The cars that would win are the cars that survive by practicing a strategy that best suits natural selection: the fuel that best matches the needs of the car. If the cars all have the same motor, then the car with the most compatible fuel would win the race. The winning car's fuel, or their strategy, can be considered an evolutionarily stable strategy. An evolutionarily stable strategy is one that all the members of a population who do not employ it die out in favor of those who do. However, just because a strategy is considered the evolutionarily stable strategy, it is not always the Nash equilibrium strategy as well. Nash equilibrium strategies are strategies where it is disadvantageous for any player in a game to change their strategy. In evolutionary game theory, there exist strategies that when practiced result in survival, but are not considered the Nash equilibrium. In the Stag Hunt Game, where two hunters are deciding to hunt either stag or hare, the payoff matrix might look like figure 1.0. The higher the number, the greater the fitness payout.

	Hunt Stag	Hunt Hare	
Hunt Stag	4,4	0,3	
Hunt Hare	3,0	3,3	

Figure 1.0

Figure 1.0 shows an example of an evolutionarily stable strategy and a Nash equilibrium strategy. Hunting stag is an evolutionarily stable strategy because no strategy can be employed that would cause the hunting stag strategy to be less fit and it is a Nash equilibrium strategy because no tactic that can be employed that would benefit either player more. However, consider Figure 1.1, which shows an example of a game where the evolutionarily stable strategy is not necessarily a Nash equilibrium strategy (Easley and Kleinberg 219-220).

	Hunt Stag	Hunt Hare
Hunt Stag	4,4	0,4
Hunt Hare	4,0	3,3
Hunt Hare	4,0	3,3

Figure 1.1

In Figure 1.1, hunting stag is still a Nash equilibrium strategy; if both hunters think that the other hunter is going to hunt stag, no strategy will result in both players benefitting more than hunting stag. However, in this situation, hunting stag is not evolutionarily stable because there exists another strategy (hunting hare) that not practicing would be disadvantageous. Since all those in a population might survive with the same fitness even if they did not hunt stag, there is no evolutionarily stable strategy (Easley and Kleinberg 219-220).

While there are many examples of game theory in evolution, the prisoner's dilemma game theoretical scenario tends to appear often. The prisoner's dilemma entails two prisoners who are given the option to either confess to a crime or remain silent. If both of them remain silent, they will serve a reduced sentence. However, it one of them confesses, and one of them remains silent, the one that confesses will be set free while the silent prisoner serves a lengthy sentence. Lastly, if both of the prisoners confess, they will both face a standard sentence.

The prisoner's dilemma is widespread in the evolution of trees. Trees would benefit from being the same low height because they would not have to expend resources trying to grow taller to get more sunlight. However, if one of the trees grows taller than the rest of the other trees, that tree would have a sunlight advantage at the expense of the other trees. That said, if both of the trees grew taller to outgrow the other trees, both trees would end up expending resources for equal sunlight. From an evolutionary game theoretical perspective, the evolutionarily stable strategy is to grow taller. Growing taller is advantageous because if every tree stayed at the same height, but one mutant tree grew higher than the rest of the trees, there would be a selective pressure on the rest of the trees to grow taller to compete for the same resources. Trees not only practice the prisoner's dilemma with height, but also with root systems. If allowed to grow unimpeded, the trees will grow long roots down through the soil in an attempt to outgrow each other. However, if one were to place a divider between to plants growing in the same pot, then the roots would not grow very far and the tree would be healthier. If the trees do not need to compete, then they do not need to expend resources trying to outgrow the other trees for the same resources. The prisoner's dilemma applies to the roots as well because if there were no divider, the trees could both grow short roots, one could grow long roots, or they could both grow long roots with different fitness payoffs.

It must be noted, though, that in the previous example, a tree cannot arbitrarily "decide" to grow taller than other trees. It is not a conscious decision for the trees and instead relies on the tree's genetics, which is why evolution can occur. This is a relevant point when discussing the game theory of evolution because traditional game theory relies on the players having intentions and being able to identify the other players' intentions. In evolutionary game theory, there is no concept of intention, as none of the organisms studied are capable of conscious thought and rational decision-making except humans.

A similar yet somewhat different example of the prisoner's dilemma occurring in nature is the hypothetical case of squirrel altruism. Suppose that there is a population of monkeys and the monkeys live in an area with a natural predator. The monkeys have two behaviors that they can exhibit when an individual monkey encounters a predator. The monkey can warn the rest of the population of squirrels, perhaps imperiling itself, or the monkey can hide to ensure selfpreservation, putting the rest of the monkeys in danger. Objectively, it would seem like being selfish would be the best strategy for each monkey, as not warning the rest of the monkeys ensures its survival. However, the evolutionarily stable strategy for the monkeys is to cooperate. Despite endangering itself, if the monkey who spots a predator warns the rest of the group, there is a higher chance that more monkeys survive in the long run. Since evolution is about the survivability of a population, the strategy that can ensure the survival of the species would be the evolutionarily stable strategy (Khan Academy).

Two examples of a prisoner's dilemma occurring in nature have so far been mentioned, but each yields a different result. The tree scenario explains why trees will attempt to outgrow each other by exhibiting the "defect" strategy, while the monkey example explains the presence of altruistic behavior by exhibiting the "cooperate" strategy. The tree example differs from the monkey example because the trees do not necessarily have to do anything besides growing to fit in with their environment. To survive, with or without an advantage, trees simply have to grow. For the monkeys, it is more complex; to ensure survival, the monkeys cannot just "defect" because over time the monkeys would die out. The critical difference between the monkeys and the trees is that for the monkeys, there is a significantly higher cost to choose the "defect" strategy due to their environment, which makes their evolutionarily stable strategies different.

While the monkeys are an excellent example of a population or species exhibiting the "cooperate" strategy, scientists have found that the "defect" strategy is much more common. Researchers at the University of California-Berkeley developed a spatial model that graphically displays the results of setting payoffs at different levels in a game theoretical scenario (Nowak and May). For example, if the payoff matrix in Figure 1.2, the output will look like Figure 1.3. Again, the higher the number of the payoff, the more fit the strategy is.

	Cooperate	Defect
Cooperate	1.1, 1.1	0.1, 2.8
Defect	2.8, 0.1	0,0

Figure 1.2



Figure 1.3 Payoff Model (from McKenzie, 2009)

Figure 1.3 shows that in just six generations with the payoffs above, the white "cooperate" strategy will be completely dominated in favor of the black "defect" strategy. However, the elimination speed of the "cooperate" strategy is completely determined by how advantageous it is to defect. For example, if in Figure 1.2 the payoff value for defecting was 2.0 instead of 2.8, the "cooperate" strategy would die out much slower since it would be less advantageous (yet still advantageous) to "defect." The spatial model also showed that the payoff values have a large effect on whether or not the "defect" result would be the outcome of an evolutionary prisoner's dilemma. If the payoff value were 1.2 instead of 2.8 for the defector, the spatial model (Figure 1.4)



Figure 1.4 Payoff Model (from McKenzie, 2009)

Would result in a graphic oscillation where the defectors and cooperators co-exist. Since the payoff for defecting is only marginally higher than cooperating, neither strategy would have a distinct survival advantage, and a population could survive by employing



both strategies. Additionally, if the payoff value for defecting was set to 1.61 instead of 1.1 and the payoff value for cooperating was set to 1.01 instead of 1.1, the spatial model would result in a chaotic graphic display where the "defect" and "cooperate" regions would be in flux. In this scenario, there is no evolutionarily stable strategy, and the two strategies commonly dominate each other. The concept of changing the payouts to change the way the strategies interact is critical to identifying the difference between the tree example and the monkey example. In the monkey example, there is lower payoff value for defecting since it would accrue a higher cost to the population over time, whereas there is an extremely high payoff value for defecting in the tree example because it results in a significant survival advantage. Therefore, if the spatial model is applied to the monkey and tree examples, the monkey scenario would look like Figure 1.4 while the tree example would look like Figure 1.3.

Despite the advances that evolutionary game theorists have made in the last few decades, some in the field question the accuracy of the practice. The dissenters' main criticism is that "fitness" cannot be quantified as simply as scientists do. Fitness, in their opinion, is a general amalgam of factors, not a simple reduction of how an organism might perform in one situation. Additionally, since traditional game theory relies on the players being rational actors, evolutionary game theory is problematic because almost all of the players are not rational. Any non-sentient organism does not feature the decision-making skills necessary for traditional game theory to apply. For critics, irrationality renders the foundation of evolutionary game theory bogus. Moreover, many in the field question whether or not game theory even provides any useful information. First, critics claim that many of the results that scientists arrive upon are not the result of solid evolutionary science, but rather are a manifestation of the researcher's personal biases. When scientists are looking for a relationship, some claim, they are more likely to find one where none exists. Lastly, detractors contend that evolutionary game theory is a poor way to investigate social phenomena. Evolutionary game theory yields conclusions that are too broad to inform our understanding of behavior. Some say that the only utility of evolutionary game theory is to identify if evolutionary behaviors remain today, which can be done by merely observing said behavior (Alexander 5).

Until recently, the evolution of behavior was thought to be independent of strategy. However, by investigating the prisoner's dilemma model, scientists have found a direct relationship between the survival of behaviors and their game theoretical survival payoffs. The overwhelming consensus of evolutionary game theorists is that behaviors that contribute to the fitness of an organism will survive until a selective pressure forces the behavior to be disadvantageous. SMK

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