EVOLUTION OF COOPERATION IN THE LIGHT OF INFORMATION THEORY

By

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ABSTRACT

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Cooperation is ubiquitous in different biological levels and is necessary for evolution to shape the life and create new forms of organization. Genes cooperate in controlling cells; cells efficiently collaborate together to produce cohesive multi-cellular organisms; members of insect colonies and animal clans cooperate in protecting the colony and providing food. Cooperation means that members of a group bear a cost, c, for another individuals to earn a benefit, b. While cooperators of the group help others by paying a cost, defectors receive the benefits of this altruistic behavior without providing any service in return to the group. To address this dilemma, here we use a game theoretic approach to model and study evolutionary dynamics that can lead to unselfish behavior. Evolutionary game theory is an approach to study frequency-dependent systems. In evolutionary games the fitness of individuals depends on the relative abundance of the various types in the population. We explore different strategies and different games such as iterated games between players with conditional strategies, multi player games, and iterated games between fully stochastic strategies in noisy environments to find the necessity conditions that lead to cooperation. Interestingly, we see that in all of these games communication is the key factor for maintaining cooperation among selfish individuals. We show that communication and information exchange is necessary for the emergence of costly altruism, and to maintain cooperation in the group there should be minimum rate of communication between individuals. We quantify this minimum amount of information exchange, which is necessary for individuals to exhibit cooperative behavior, by defining a noisy communication channel between them in iterated stochastic games and measuring the communication rate (in bits) during the break down of cooperation. I dedicate this to my mother, father, brother, and my beloved wife. Thanks for all the sacrifices and being always there for me.

In memory of Prof. Caro Lucas. You left fingerprints of grace on my life. You shan't be forgotten.

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I should use this opportunity to thank Prof. Chris Adami and Dr. Arend Hintze. These years has definitely become part of me, and I will have these precious experiences with me for ever. I never forget the exciting moments we had after solving a problem. Thank you for all your support. I could not achieve anything without your help and guidance. I indeed enjoyed these years working with you, thinking with you, and laughing with you.

PREFACE

A man is a success if he gets up in the morning and gets to bed at night, and in between he does what he wants to do.

-Bob Dylan

I grew up among an ordinary family. All of us had completely different interests. My father was a banker and a totally "not-religious" Muslim! On the other hand, my mother was a very religious school teacher. My brother and I were something intermediate. In this family, my brother and I learned how to challenge everything and do not believe everything without a solid proof. My brother and I as the descendants of this family chose different careers in our life. My brother first decided to study in medical school; however, after he realized that he does not have the devotion to this career, he quit and became a movie critique since being "movie buff" runs in our family. I, on the other hand, went to an engineering school, and studied electrical engineering since my father wanted me to learn fixing his VHS player! Instead of learning how to fix a video player, there I learned how to model any dynamic with an input-output system. I also practiced calligraphy, screen writing, and movie directing and wrote short stories and short screen plays; studied control engineering and Artificial Intelligence (A.I.) and taught many advanced courses in electrical engineering and artificial intelligence.

Since I began my study in University of Tehran as an A.I. graduate student, I established an ever-growing passion toward evolution. As a control engineer, I was trying to apply biologically inspired models to model and predict exotic phenomena in nature. I was amazed to see the complexity among natural and biological dynamics, and I was always seeking the origin of this complexity. I wanted to know how species exhibit complex behavior and interact with each other in very intricate ways. I wanted to understand under what conditions simple organisms evolve to complicated multi-cellular organisms.

Through years of my study at the University of Tehran under supervision of late "Prof. Caro Lucas" I got familiarize to evolutionary processes and different forms of species interaction in nature. Joining BEACON at Michigan State University and the "Adami Lab", I officially became an ecologist and evolutionary biologist. Ecology and evolutionary biology is so immense and challenging, and I still, as a novice researcher in this broad field need to study and experience a lot. Yet I have learned a lot. From a control engineer that simple design is always one of his objectives and always tries to approximate and model any nonlinear natural dynamic with a time-invariant linear input-output grey box model, now I try to observe species' interaction in their niche and develop a nonlinear model, which includes the nonlinear effects of the environments to these species. I try to understand how complexity evolves over the course of evolution, how natural selection that favors to selfish members of a population maintains cooperation and altruistic behavior, or how cooperation emerges in a group of selfish animals and stabilize their despotic society.

These days, I get up early in the morning, and go to bed very late at night, and in between do what I always liked to do: investigate species interaction, hypothesize how they maintain cooperation in their group, develop a model and design experiments to test the validity of model, write a program to test my hypotheses, analyze the results, compare the results with the well-established theories in the corpus of published literature, read about evolutionary game theory, generate colorful plots for articles and presentations, video chat to my beloved wife in California and my family back in Iran, and I feel happily successful because these things give me energy and hope to live and enjoy the life.

Masoud Mirmomeni June 2015

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Chapter 1 Introduction

Nothing truly valuable can be achieved except by the unselfish cooperation of many individuals.

-Albert Einstein The World as I See It

Shaun: As Bertrand Russell once said, "the only thing that will redeem mankind is cooperation." I think we can all appreciate the relevance of that now. Liz: Was that on a beer mat? Shaun: Yeah, it was Guinness Extra Cold. Liz: I won't say anything. Shaun: Thanks.

Shaun of the Dead, E. Wright, 2004

One of the fundamental characteristics of human behavior is cooperation [3, 4, 5, 6, 7, 8]; yet, no problem is more puzzling in evolutionary biology than the evolution of cooperation since evolution is based on a hostile and savagely wild competition between individuals and should therefore be favored by only selfish behavior [7, 9]. The quest for ubiquitous complex dynamics originated by different forms of cooperation in nature is as old as origin of species since Darwin found cooperative behavior as a challenge to his theory and noticed that natural selection cannot directly promote cooperation; therefore, he postponed the publication of *The Origin of Species* for 20 years to find a solution for this dilemma [9, 10]. As of today, we have discovered a great deal about the evolution of altruistic behavior from genes' cooperation in genome and cells' cooperation in multicellular organisms to many social behavior in animals; however, there still exist many deep questions about evolution of cooperation that need to be investigated by us as the champion of cooperation.

1.1 Motivation

Why do humans help other humans to obtain food or defend territory even if there exists cost such as risking life? Why do honeybees sacrifice their own fecundity to serve the colony and queen by protecting the hive and collect nectar? What mechanism maintains cooperation among a large group of strangers [9]? How does the fierce competition of natural selection often lead to altruistic behavior, in which individuals bear a cost to give a benefit to other members of the group [7]? To understand how societies are robust and stable, we have to address these questions. We know that whenever new form of organization emerges by natural selection, cooperation is involved [11]. We also know that natural selection favors defection over cooperation. Thus, consequently it reduces the average fitness of the population in iterative evolutionary games (fig. 1.1) [7].

A cooperator is an individual who pays a cost, c, in a competition for resources and declines some of its reproductive potentials and short-term benefits to the hope of helping other individuals and gaining long-term benefit, b. On the other hand, a defector does not pay any cost and does not deal out benefits. Cost and benefit are usually measured in terms of fitness or reproduction rate. Reproduction rate can be genetic or cultural [7]. In any mixed population, defectors have higher average fitness than cooperators. However, a group of cooperators does better than a group of defectors, yet a single cooperator is vulnerable to the existence of defectors, and as a result, each individual is tempted to defect; therefore there should be other mechanisms which allow natural selection to favor cooperation over defection [11].



Natural selection reduces the average fitness by favoring the defectors



Course of the evolution

Figure 1.1: Cooperation is vulnerable to invasion of defection: (a) Natural selection favors defectors, which are created by mutation. In a well-mixed population, defector, D, has higher fitness than cooperator, C. Thus, natural selection continuously reduces the abundance of cooperators and as a result it reduces the average fitness of the population. (b) fitness to the cooperator, fitness to the defector, and average fitness over the course of evolution.
For several decades this conundrum engrossed scientists. Many research institutes were occupied finding how cooperation emerges among a group of selfish individuals until around 50 years ago W. D. Hamilton qualitatively addressed evolution of cooperation among group of relatives in his "inclusive fitness theory", and since then numerous theories have been proposed to address conundrum of cooperation in evolutionary biology [4, 12, 13]. Among these theories, evolutionary game theory, which was developed by John Maynard Smith and George Price as the biological version of John von Neumann's theory of games, has been the leading metaphor for the evolution of altruism [14, 15, 16]. By using this idea, researchers have been trying to model and study the mechanisms that yield to the altruism (e.g. assortment [17], spatial arrangement [2, 18], reciprocity [19], kin selection [7], and inclusive fitness [13]).

Cooperation emerges in a group of selfish individuals, when these self-centered members of group initiate communication and exchange information. This information can be about the current state of members (their average payoff from previous interactions with other members), about history of their interactions and their visited opponents, or about the environment. After this information was obtained after communication between members, it will be saved into the memory of members in different ways. For example, individuals can act conditionally on their previous gains and their competitors' previous actions [14, 20, 21, 22, 23, 24, 25]. They can also act conditionally on opponents visible phenotypic properties [26], or they can conditionally interact on the type of visited opponent, and as a result, form spatial arrangements of close relatives in the group [2, 27]. In this research, we discuss different mechanisms that can maintain cooperation over the course of evolution, and for each mechanism we derive the necessity conditions for the evolution of altruistic behavior. The ultimate goal of this research is to find an answer for the following question: "How much information is necessary to be exchanged between members of a group before they successfully initiate cooperation in a dog eats dog environment, in which for survival individuals should compete for limited resources with other individuals in the group?"

To quantify this minimum amount of information (measured in bit), we analyze different evolutionary games to find the conditions that favor cooperation. In these games, individuals randomly interact with other members of group, and based on their action in every iteration (or generation), they receive payoff that indicates their average fitness or reproductive success. By repeating these games and tracking the evolution of these individuals, we can quantify the role of information in the emergence of altruism. In the remaining parts of this chapter, I will briefly review some basic definitions, which is required throughout the course of this thesis. More detailed discussion on the developing history of the research about the biological complexity, information content, and stochastic iterated games, as well as evolutionary game theorys state of the art will be conducted in the next chapter.

1.2 What is evolution?

The word *evolution* comes from the Latin word *evolvere*, which means "to unfold", "to unroll", or "to reveal or manifest" hidden potentialities. Nowadays, "evolution" simply means *change*. In biology, "evolution" means *variation in the features of groups of individuals over the course of generation* [28]. In other words, evolution is about *descent with modification* [29]. Evolution is not about the modification of an individual organism. It is about the variation of group of individuals, called *population*, over the generations. Therefore, the ontogeny of an individual is not evolution. Those changes in the population that are heritable are considered evolutionary. In nature, heritable characteristics are passed from ancestors

to descendants via DNA, a molecule that encodes genetic information [30]. Evolution occurs when there is change in the frequencies of alleles within a population of interbreeding individuals [31]. Mechanisms that can lead to changes in allele frequencies include natural selection, genetic drift, sexual recombination, mutation and gene flow. Recombination makes alleles on the same strand of DNA separated. However, the recombination rate is low, and as a result, genes that are close together on a chromosome may not always be shuffled away from each other and consequently tend to be inherited together. Mutation is the change in the DNA sequence of a cell's genome. Mutation can be neutral (have no effect on the gene frequency), alter the frequency of a gene, or prevent the gene from functioning. Natural selection is an evolutionary process by which genetic mutants that have enhanced reproduction become and remain more common in successive generations of the population. Genetic drift is another evolutionary process, which randomly changes allele frequency from one generation to the next generation. This evolutionary force occurs when selective forces are absent or relatively weak, and as a result, allele frequencies tend to "drift" upward or downward randomly since alleles are subject to sampling error [32]. Gene flow is the exchange of genes between populations and between species [33].

1.3 Information exchange and communication channel

Entropy and information are two related concepts that have been used frequently in biology to model the dynamics of living systems; thus, to understand these dynamics it is necessary to understand entropy and information by heart [34]. Information theory is an approach that can link complexity in living systems and their ability to store *information* [34]. Information theory was initially developed to model transmitting data or messages through noisy



Figure 1.2: Process of transmitting information through a noisy channel.

communication channels. Figure (1.2) shows a typical communication channel.

For every block of the figure (1.2), we can find a precise analogy in living systems [34]. For example, the source of the transmitted information can be the environment in which the organism lives and to which it tries to adapt. Through the adaptation, genome of the organism becomes correlated to this environment and there will be a "mutual information" between them. Mutation makes the encoding process of this environmental information inside the genome a *stochastic* process. The mutated genome is transmitted to the next generation. Therefore, one possible transmission channel would be the transferring heritable information from ancestors to descendants. Another possible channel can be the mechanism that translates DNA/RNA to protein, which again is a noisy channel. The destination of this noisy biological communication channel is the environment, where the organism needs to survive [34].

1.4 Evolutionary game theory

Evolutionary game theory is a perspective about evolution at the phenotypic level when the fitness values of phenotypes depend on the relative abundance or concentration of various phenotypes in the population (e.g. the concentration of cooperators and defectors [16, 26]). The dynamic of evolutionary games in well-mixed populations follows the replicator equation [35, 36, 37]. Replicator equation is a system of nonlinear ordinary differential equations. This equation describes how the relative concentration of strategies varies over the course of evolution as a consequence of frequency-dependent selection that is proportional to their fitness. Scientists applied evolutionary game theory to explain mechanisms that maintain cooperation in viruses, bacteria, plants, animals, and humans [6, 26, 38, 39, 40, 41].

1.4.1 Kin selection and inclusive fitness

The idea of kin selection is simple:

"I risk my life and jump into the river only for my family and close relatives. Why should I risk my life for someone I don't know?"

Natural selection favors cooperation if the donor and the recipient of an altruistic act are genetically related. Relatedness is defined as the probability of sharing a gene [7]. The probability that two brothers share the same gene is 1/2 and for the first cousins is 1/8. Hamilton construed the idea of relatedness in promoting the evolution of cooperation [12, 42]. His theory is widely known as "kin selection" or "inclusive fitness" [7, 43, 44]. *Inclusive fitness* considers the effects of a phenotype on its kin who might carry the same gene that induces the phenotype. Thus, this "extended phenotype of cooperation" could be the result of "selfish genes" [45, 46].

1.4.2 Direct and indirect reciprocity

Cooperation and altruism are not only among relatives. Nature is also abundant with cooperation between unrelated individuals or even between members of different species. Such observations led Robert Trivers to develop a theory that explains a new mechanism for the evolution of altruism [3]. He called this mechanism "direct reciprocity". The idea of *direct reciprocity* is simple: "I will scratch your back if you scratch mine". Direct reciprocity is considered to be a powerful mechanism when human being is the understudied species for evolution of cooperation. In Axelrod tournaments the "winning strategy" was "tit-fortat" which followed the idea of direct reciprocity. This simple strategy always starts with cooperation, and then it does whatever the opponent has done in the previous round.

Although direct reciprocity is a powerful mechanism for the evolution of cooperation, it does not address a certain aspect of human behavior. In this mechanism the same individuals should meet repeatedly, and they must be able to provide help, which is less costly for the donor than it is beneficial for the recipient. However, generally the interactions among humans are asymmetric. We generally help strangers who are in need. We donate to charities and they do not donate to us. The mechanism that can address these situations is "indirect reciprocity". Helping someone establishes a good reputation, which will be noticed, remembered, and rewarded by others. In our actions, we usually take into account the possible consequences for our reputation. We feel strongly about events that influence us directly, but we also take a keen interest in the affairs of others, as demonstrated by the contents of gossip [7].

1.4.3 Spatial arrangements

In spatial games, individuals play with their neighbors in a spatial domain. These games describe the evolutionary change of the strategy profile of individuals over space [47]. In each round of game, every player "plays the game" with a defined set of its immediate neighbors. Then, each site is occupied either by its original player or by one of its neighbors, depending on who has the highest payoff or fitness in that round. By repeating this game, we can see self-organized spatial patterns in the arena of game, which some are relatively static and the others are chaotically dynamic in every round of game [2, 27].

1.5 Evolutionary game dynamics

Evolutionary game dynamics applies population dynamical modeling to evolutionary game theory [36]. Generally speaking, in some biological populations growth rate is a continuous function in time and usually generations overlap; thus, the appropriate mathematical description of such population dynamics involves nonlinear differential equations. Darwinian dynamics based on mutation and selection is the core of mathematical models for adaptation and coevolution of biological processes [48]. The evolutionary outcome of such nonlinear processes is often not a fitness-maximizing equilibrium but can include oscillations and chaos. For analyzing such nonlinear dynamics with frequency-dependent selection, game-theoretic approaches with their replicator dynamics are more appropriate than optimization algorithms [48, 49]. Replicator and replicator mutator dynamics give an accurate short and long-term description of large populations' evolutionary dynamics in phenotypic space. These dynamical models have been applied to many biological and sociological problems ranging from animal behavior and ecology to speciation, macroevolution, and human language [48].

1.6 Organization of the thesis

In Chapter 2, the literature review is given. Chapter 3 discusses the evolution of information contents among digital organisms (avidians). The purpose of this chapter is to see how information content (also referred as genomic complexity), stored in the genome of avidians, is selectable and correlated to biological fitness. We are also interested in information contents variation over the course of evolution. Afterwards, in chapter 4 we discuss the evolution of cooperation and the role of information in maintaining altruism in stochastic games. In chapter 5, I introduce Iterated Trust Dilemma (ITD) as a new game that describes how super cooperation can evolve among group of selfish players by establishing trust among players via communication and information exchange. Moreover, we analyze how noise in communication channel between players, mutation as noise between generations, and temptation payoff affect the established super cooperation. Chapter 6 addresses the social behavior in animals by using a new game as an extension of standard "Public Goods Game". Chapter 7 includes summary and concluding remarks.

Chapter 2 Literature Review

An eye for an eye only ends up making the whole world blind. -Mahatma Gandhi

- Sir, if any of my circuits or gears will help, I'll gladly donate them!

-C3PO

Star Wars: A New Hope, G. Lucas, 1977

Our astonishing capacity to cooperate, which does not have any place in traditional Darwinian's perspective, is one of the main reasons that makes us survivor of any ecosystem on the Earth [46]. Cooperation is not just limited to us; in fact it is abundant among other species on our planet. Altruistic behavior is irrational and it is against the base of selfinterest from the perspective of Darwin's formulation for the struggle to survive. Scientists from a wide range of disciplines have pursued for more than a century to address the rise of cooperation and altruism in our "dog-eat-dog" world [46]. Among these disciplines, evolutionary game theory, developed by J. Maynard Smith and G. Price, gives a better description of species' inter and intra group conflict for the limited resources.

Evolutionary game theory has become more and more influential in modeling important biological processes since its development in 1973. The key concept in biological games is *Evolutionary Stable Strategy* (ESS), which resists invasion by all other strategies once it has dominantly established in the population. Here, by applying evolutionary game theory we are interested in those mechanisms that make cooperation and altruism evolutionary stable in a population of selfish individuals.

2.1 History of evolutionary games

People have been playing games such as chess, backgammon, or noughts and crosses for thousands of years, and are still interested in how to optimally play these games. Finding optimal strategies for games with uncertainty has a long history [50]. Probability theory as a mathematical theory of random events has been found to be very useful in gambling applications [51]. Operational research methodology, such as linear programming has been applied to complex problems of military logistics during the World War II and now are very popular in modern industry applications [50, 52].

It was only recently that scientists realized that there are many applications to game theory in biology, where the Darwinian fitness is the representation of reward and the evolutionary force of natural selection is equivalent to rationality force in game theory. Charles Darwin in *The Descent of Man and Selection in Relation to Sex* implicitly applied game theory to explain why natural selection should act to equalize the sex ratio [50]. Dusing in 1884 and Fisher in 1930 presented a precise mathematical explanation to the sex ratio problem; however, their method was not a game theoretic approach. In 1967, Hamilton for the first time applied game theory to describe this problem [53].

The first implementation of game theory to evolutionary biology happened six years earlier than Hamilton's game theoretic solution to sex ratio problem when R. C. Lewinton for the first time applied game theory in his paper, *evolution and the theory of games*, which involved a single species game rather than a game between individuals and nature. It is worth mentioning that the mentioned approach is generally accepted as the "wrong standing point" by modern evolutionary biologists [50]. Another fundamental branch of evolutionary game theory was the concept of relatedness and inclusive fitness, initiated by Hamilton in 1964 [12] and Trivers in 1971 [3]. The idea of relatedness, in which the behavior of an organism is not just a function of its personal fitness (number of its own offspring), but also the benefit of its siblings should be included provides a plausible explanation for much altruistic behavior in nature. The next and the most important contribution to evolutionary game theory was the concept of "evolutionary stable strategy" as an equivalence to Nash equilibrium in terms of importance, developed by John Maynard Smith and George Price in 1973 [54]. Following Maynard Smith and Price contribution to evolutionary game theory, Haigh developed the general theory of matrix games in 1975 [55] and proposed a way to find all the ESSs of a matrix game. Later, Bishop and canning proved the possibility to co-existence of ESSs [56], and followed by their discovery was a series of papers that established this idea [57, 58, 59, 60, 61]. While most of the mathematical theories of evolutionary games address linear games, where rewards are related to the interaction of a set of independent competitors, biological processes are nonlinear. To extend the existing linear games, Hamilton [12] and Parker [62] included nonlinearity in their models to address sex ratio problem and patch foraging models respectively. The theory of nonlinear evolutionary games is still in its rudimentary state; however, some important aspects of this theory have been discovered [63].

Parallel to nonlinear evolutionary games, Palm developed the theory of multi-player evolutionary games, which is related to nonlinear games [50]. Haigh and Cannings used nonlinear evolutionary games in their multiplayer war of attrition. Moreover, this approach was used by Broom et al. in their multiplayer matrix games [63, 64, 65, 66]. The first step of modeling biological processes is to consider the process in a well-mixed infinite population size of identical members. However, in nature this assumption does not quite hold and natural populations usually contain individuals with different traits. This problem has been addressed by Maynard Smith and Parker [67]. Furthermore, Houston and McNamara developed a methodology to model a population where the strategies of players were highly affected by the state of players in the arena of the game [68]. Moran addressed the problem of games in finite population and introduced the Moran process to model interaction of species in finite populations [69, 70]. Taylor et al. applied Moran's discovery to develop games in finite populations [71]. The structural effects of populations on evolutionary games was popularized with the concept of "cellular automata" in the game of life [72], and later was extended by Lieberman [73] and Nowak [74] in their graphic and spatial games.

Standard game theory modeling is interested in the optimal strategies, and in these games rational individuals have the ability to change their strategy as they explore the game. In the theory of static evolutionary games, it is also assumed that a given strategy has been found by the population with the aid of some stability and invasion analysis [63]. Nonetheless we know that populations evolve gradually and to track their evolution, one should consider a dynamic for this process. This is the subject of evolutionary dynamics.

The most commonly used dynamics in evolutionary games is the continuous replicator equation, developed by Taylor and Jonker [35]. May be the breathtaking development in evolutionary game dynamics was given by Zeeman [37, 75], who showed that any ESS is an attractor of the replicator equation; thus any set of initial concentration of individuals in the population will converge to one ESS [37]. Bomze and Cressman analyzed the stability properties of the replicator equation [76, 77]. A related dynamic is the replicator mutator equation of Page and Nowak [78]. To address the effect of mutation, Helbing proposed a different model, called the imitation dynamics where players adjust their strategy according to the visited opponent [79]. Another approach for modeling these processes is adaptive dynamics and was developed around 1980s. These models study how a population varies when new strategies similar to current strategies emerge within a population [36, 80].

2.2 Inclusive fitness theory and evolution of cooperation

Inclusive fitness is one of the most important explanations for the evolution of cooperation and altruism. This theory has been widely used since its development in 1964 to analyze and study social behavior of species, and it has been justified by many different population genetic and quantitative models [7, 13, 17, 19, 21, 22, 1]. Before Hamilton's mathematical proof of his kin selection, which is equivalent to inclusive fitness theory, scientists generally believed that species succeed the "evolutionary war" by leaving behind the maximum number of copies of themselves in the population. By using Wrights "coefficient of relationship", r, as the measure of genetic relatedness, Hamilton developed the "inclusive fitness" theory in 1964 as a mechanism for the evolution of cooperation. Kin selection theory, which is also known as Hamilton's rule, mathematically describes whether or not altruism is favored by natural selection:

$$r > \frac{c}{b}$$

where r is the degree of relatedness (coefficient of relatedness), b is the benefit of the altruism to the recipient of cooperation, and c is the cost of altruism to the altruist. Using cost and benefit helped Hamilton to have an economic view point to natural selection as an optimizer that tries to maximize fitness yet let the altruists exist in the population [81]. Although Hamilton became one of the leading evolutionary biologists of the 20th century because of his works on kinship and altruism, nobody took his work on "kin selection" seriously unless an ingenious chemist, who quit his job at IBM and began his new career as an evolutionary biologist at the Galton Laboratory, London noticed this paper and used this rule to develop his marvelous theory at mid-1970s. This man was George Price and became Hamilton's close friend until he committed suicide in January 1975 in his apartment. He applied Hamilton's idea to extend Fisher's fundamental theorem, and the result was a novel covariance model for evolutionary changes of traits. By applying the "Price equation" to check the variation of cooperative traits and altruistic behavior, we find that when altruists are surrounded by many blood kin in the population as carriers of altruistic genes, natural selection favors altruism and number of offspring produced by an individual carrying the altruistic genes increases over the generations. In other words, if the mean relatedness within the population is less than the mean genetic relatedness within the population, then malevolent behavior can evolve. Price's novel idea was published in Nature in 1970 and later was used by David C. Queller to extend the Hamilton's inclusive fitness theory [81].

Despite its reputation, Hamilton's rule has been often criticized being ambiguous or inadequately general [17, 82, 83, 84, 85, 86]; thus, various corrections have been given to this theory, which on the one hand, increase the generality of the theory, and on the other hand, erode the simplicity of the Hamilton's rule [13, 87, 88, 89]. In most of these extended versions of Hamilton's rule, assortment and non-additivity were added to the model as necessity conditions to maintain cooperation [13, 90]. Having assortment in the population helps altruists to interact mostly with altruists, which makes the benefit of cooperation be distributed mostly to altruistic carriers. At the same time defectors or non-cooperators are stuck interacting with each other and suffering the absence of cooperation. Non-additivity has similar effects on altruism. Cooperation can evolve even in the absence of positive assortment whenever collective cooperation yields synergistic benefits [90]. Queller in his extension to inclusive fitness theory clearly demonstrated the roles of positive assortment and non-additivity to the evolution of cooperation [13, 91].

In Hamilton's original form of kin selection theory, r is the coefficient of relatedness between donors and recipients; however, this measure in Queller's inclusive fitness theory is generalized to a measure of assortment between individuals with cooperative genotype and the recipient's character with which donors interact [13, 91]. In Queller's inclusive fitness theory r is a covariance measure of assortment:

$$r = \frac{Cov(g, z')}{Cov(g, z)}$$
(2.1)

where g is the self genotype, z is the self phenotype (0 for defection and 1 for cooperation), and z' is the average phenotype of recipient [13, 91]. Substituting this ratio in to the Hamilton's form of kin selection theory, we have:

$$Cov(g, z') b > Cov(g, z) c$$

$$(2.2)$$

which simply says that natural selection favors cooperation when assortment between those with cooperative genotype and characters of recipients, scaled by the benefit of altruism on average be greater than the assortment between the cooperative genotype and donor's character, scaled by the cost of the altruism [13, 91]. This extended version of Hamilton's kin selection theory is applicable to interactions among relatives, non-relatives, and even across species [91], as well as accommodating the genotype/phenotype differences that result from conditional behavior (e.g. in iterated interactions [91]). It is worth mentioning that inclusive fitness theory in both original and extended form is only applicable to problems with directional selection, and when selection is disruptive, this rule is not a proper model of social behavior [91]. By adding another covariance term to measure the assortment between altruistic genotype and the degree to which cooperative behavior is mutual, scaled by the amount of deviation from additivity, Queller also included non-additivity into his inclusive fitness formulation of Hamilton's rule as:

$$Cov(g, z')b + Cov(g, zz')d > Cov(g, z)c$$

$$(2.3)$$

where d > 0 represents the synergy factor, d < 0 represents diminishing returns, d = 0represents additivity. Inequality (2.3) depicts two fundamental ways to compensate for an average carrier's local sacrifice [91]:

- Sufficient help from others, and/or
- Sufficient synergistic fitness rewards for mutual cooperation

Inclusive fitness theory in its many general forms has been applied to address a wide range of biological problems and widely accepted as a general model to explain the evolution of social behavior [92, 93, 94, 95, 96, 97, 98, 99]; however, all of these generalizations over the years distorted the initial idea of inclusive fitness and created an erratic language for this theory, which have led to significant misunderstanding and meaningless argument [100]. The strongest criticisms concern how specific genetic variations alter the outcome of selection, and how inclusive fitness theory can be predictive and provide vital perspective on evolutionary process [89, 101, 102, 103, 104]. These criticisms claim that inclusive fitness theory is a limited concept and works only for a small subset of evolutionary processes in nature since it assumes personal fitness to be additive to the individual actions; however,



Figure 2.1: Result of regression analysis of a hypothetical change in allele frequency. Allen et al. used this example to show regression analysis could be misleading. In this analysis the starting ingredients are the genetic types represented by colors (blue: cooperator (g = 1), grey: defector (g = 0)), interaction between partners is represented by arrows, and numbers of eventual offspring as an fitness indicator is represented by numbers of each individual present at a particular time. It is possible to calculate the change in allele frequency from these data. They fitted a linear model of offspring number based on each individuals own genotype and partners genotype to this data set. For this process, they obtained B, C > 0and BR - C > 0, which indicates the rise in frequency of the cooperator type is due to costly cooperation between closely related partners. Without having further information, there is no statistical or scientific reason to conclude that this interpretation is correct [1].

we know that this is at least not true for the Queller's extension to inclusive fitness theory since he added the synergy factor as a non-additive term to personal fitness [1]. Moreover, the predictability power of inclusive fitness theory has been under researchers criticism since it includes the linear regression bases to avoid additivity restraint (Fig. (2.1) and (2.2)). Researchers have shown that this theory not useful if the objective is to analyze whether mutations that modify social behavior are favored or opposed by natural selection [1].

In sum, inclusive fitness theory with its generalization forms is a kind of causal analysis that analyzes the evolutionary causes of social phenotypes [100]. In its original form, three forces are involved to evolutionary changes: the cost as a direct component that affects



Figure 2.2: Regression is not capable of identifying the causes of frequency change. In this example Allen et al. demonstrated how regression methods can be misleading in characterizing the reason of change in allele frequency. Their three hypothetical examples depict how the regression method leads to wrong interpretations. (a) A hanger-on (indicated by purple) interacts with a high-fitness partner. The regression recipe misinterprets this behavior as mutually beneficial cooperation (B > 0, C < 0). (b) A jealous individual (indicated by red) attacks an individual of high fitness, which reduces the recipients fitness from 5 to 4, and the attackers fitness from 1 to 0. The regression recipe misinterprets this attack as costly cooperation (B, C > 0). (c) A nurse (indicated by blue) helps an individual of low fitness, which as a result increases the recipients fitness from 0 to 0.5 (this gives an extra 50% chance of having an offspring), and decreases the nurses fitness from 1 to 0.5. The regression recipe again misinterprets this aid as costly harming or spite (B < 0, C > 0) [1].

the altruists, the benefit as an indirect component that affects social partners influenced by the focal individual's phenotype, and the coefficient of relatedness as an adjustment between these two components [100]. Misunderstanding inclusive fitness theory is the result of distortion of Hamilton's rule [100]. Hamilton's original formulation in terms of direct and indirect causes provides a useful partition that works for simple biological processes. On the other hand, the modern forms of this theory provide more comprehensive causal analysis to the social behavior that includes more direct and indirect components to the fitness. In the modern inclusive fitness theory costs and benefits are context dependent, and coefficients of relatedness in their generalized form translate all fitness components into common units of total using multiple regression techniques [100]. However, it is worth mentioning that the limitations of this theory with its causal analysis are reasonably well known. The causal analyses yield to enhance understanding rather than alternatives to more complex and detailed mathematical analyses of particular problems [100].

2.3 Evolution of cooperation in stochastic games

People will most likely act differently in different situations [25]. The situation could be the state of the environment, the partners attitude, or the availability of resources, etc. Therefore, the action of an individual is a random variable conditioned on environmental parameters. Using this idea, we can extend the standard game theory to conditional games or more generally to stochastic games. Iterative games are more interesting since in each interaction, players gain information about the visited opponents. This information can be exploited for the next rounds by acting conditionally on this gained information. In evolutionary game theory, conditional strategies have shown a great potential in surviving difficult situations. It is obvious that to have conditional strategy, individuals should have information about the state of the game and memory to save this information to recall for future actions. Conditional strategy of a player could be a random variable of its previous actions, the opponent's previous actions, received payoffs, or a combination of them. For example, "Tit For Tat" (TFT) is a strategy conditioned on the opponent's previous action; thus it is only need to have one unit of memory (for two player games this unit is one bit). Although this strategy is very simple and defeated all of its complicated strategies in Axelrod's famous tournament and scored extremely well, it has an "Achilles heel" [4, 5]. In a noisy and error-prone arena in which is hard for players to observe the opponent's action, a single error between two TFT players leads to a sequence of mutual recriminations, which can only be broken by another mistake. In such environment, the performance of TFT reduces a lot and two TFT players act as two All Defectors (AllD). Therefore, to solve this problem it is good to add forgiveness and generosity to the players. The new Generous TFT (GTFT) is more resistant to the noise and has a better performance in a noisy environment compare to standard TFT. To solve TFT problem in noisy environment, Nowak and Sigmund also proposed a similar strategy that performs well in noisy environment [15]. This strategy is Win-Stay Lose-Shift (WSLS) strategy. In this strategy, player acts in the next round the same if his payoff is higher than a given threshold and switches to the other strategy otherwise [15]. Similar to TFT, this strategy needs one unit of memory to save its own previous action. The action of player with WSLS strategy is conditioned directly on its previous action and indirectly on its opponent's action, since the payoff of the player is a function of both players' actions. The performance of simple conditional strategies such as TFT, GTFT and WSLS encouraged biologists to explain the evolution of altruism by *reactive strategies* or reciprocal interactions based on repeated encounters and decision makings. Since natural interactions compare to artificial interactions between computer programs is full of uncertainty, the reactions of individuals are generally stochastic: they cooperate with a probability conditioned on their own and opponents' previous actions [105]. Another reason that makes the interaction of biological organisms stochastic is the population size. In population dynamics and standard evolutionary game theory when the interaction between individuals is modeled by replicator equation, the population size is assumed to be infinite; however, biological systems are subject to all sorts of other random effects and are inherently stochastic. For example, not every encounter for a special type of individual has the same effect on fitness. Moreover, the biological dynamics are affected by many other random sources such as variability in mating success, foraging success, infant mortality, etc. This stochasticity is widely accepted by scientists, usually it is ignored and not included in the biological models since it is assumed that the effect of this stochasticity is negligible [106]. While ignoring this stochasticity might be reasonable in some situations, it is shown that, in general, even if the effects of this stochasticity are arbitrarily small, they may qualitatively change the asymptotic behavior of the system [107]; thus, they should be included in the model, and one way to consider this stochasticity is to use stochastic evolutionary games in which individuals act completely conditionally on their state and their opponents' previous actions.

Lloyd Stowell Shapley introduced stochastic games in 1953 as a dynamical game with probabilistic transitions played by one or more players. Similar to standard games, stochastic games are sequential. In this kind of games, players select actions and receive a payoff based on the current state and the chosen actions. The game then moves to a new random state, whose distribution depends on the previous state and the actions chosen by the players, and this procedure is repeated for a finite or infinite number of stages. Similar to the standard games, the total payoff to an individual is usually the discounted sum of the stage payoffs or the limit inferior of the averages of the stage payoffs [108]. Two players stochastic games are widely used in evolutionary game theory to model finite population size dynamics [18, 23, 109, 110, 111, 112, 113].

To model species interaction in finite population, stochastic games are usually combined with graphical models, called stochastic evolutionary graphical game. These graphical models have been used to analyze discrete systems that operate on stochastic (adversarial) environments [74]. In evolutionary graph theory possible configurations of a system and its environment are represented as vertices, and the transitions correspond to interactions between individuals that change the state of the system or the environment are represented as edges. A run of the game corresponds to an infinite path in this stochastic graph. Similar to standard games, in many cases, there exists a stable stochastic strategy or an equilibrium fixed point; however, optimal strategies for both players may not exist.

2.4 Altruism in multiplayer game

The "tragedy of the common" is a social dilemma in which members of a group seeking the maximum self-interest by exploiting a public good, and by doing so they often harm their own and other members' long-term interest [114, 115]. As of today, tragedy of the common is not only well-known in social sciences and politics [114] but also plays an important role to model and study the evolution of social behavior in biology [116, 117, 118, 119]. One way to study and model such social dilemmas in animal behavior is evolutionary game theory, which describes pairwise or group wise interactions of a population with defined payoffs for different strategies, and among famous games in evolutionary game theory "public goods

game" has been most commonly used to describe social dilemmas similar to the tragedy of the common.

In experimental economics the public goods game is a classic laboratory standard for studying collective action problems [120, 121, 122, 123]. In this game, members of the group decide to invest the amount of their possessed tokens into a pot or common good. Then, the total contributed tokens in the pot are multiplied by a factor (called "synergy factor"), which is greater than one and less than the number of players in the game. At the end, this public good payoff is equally distributed among the players in the group, no matter whether they invested their token into the common good or not. Ideally, the group exploits maximal investment from the common good if everybody contributes the maximum amount and take advantage of the synergy; however, this strategy is vulnerable to the existence of defectors or "free riders", those who receive share from the common good yet do not invest their tokens. It can be easily shown that in this dilemma, the rational Nash equilibrium is the self-interested strategy because not contributing anything clearly dominates all other players regardless of their strategy.

Interestingly, in reality what is observed frequently is not the rational Nash equilibrium, and people tend to share their tokens into the common good. The actual levels of contribution found is variable [124], and the average contribution typically is a function of the synergy factor [125]. Several solutions have been proposed to address this dilemma. For example Capraro suggested a solution to this dilemma based on the idea that members of the group can forecast if acting cooperatively pays, and then they cooperate in a rate that depends on their forecast (similar to quorum sensing mechanism in microbial communities). According to his model, increasing the synergy factor will increase level of cooperation [126]. Hardin in his paper suggested that the tragedy of the commons can only be avoided if defectors or free riders receive punishment for not participating in the investment [114], and since then punishment has shown its potential in maintaining cooperation in public goods game [127, 128, 129, 130, 131, 132, 133]. On the other hand, punishing cooperators or moralists [133] do not perform very well in well-mixed populations since they lose the competition against the non-punishing cooperators, or secondary defectors, since moralists acquire an additional cost for punishing defectors, and as a result, defectors can invade the population of non-punishing cooperators [115]. Therefore, there should be other ways that stabilize cooperation since punishment is a costly process [8]. Dreber et al. showed in their experiment that although the option of costly punishment increases the rate of cooperation, punishment does not alter the average payoff of the group. Moreover, they discovered a strong negative correlation between total payoff and use of costly punishment. This observation confirms that those people who win the competition and receive the highest total payoff tend not to use the costly maladaptive punishment [8]. Therefore, there might be other reasons that costly punishment still exists over the course of evolution. Deng and chu in their paper proposed that the non-linearity of the structures of public goods might be the force that maintains cooperation within the well-mixed populations [134]. Wakano et al. found that the spatial evolutionary dynamics of ecological public goods in "selection-diffusion" systems might promote cooperation [135].

The research on social behavior is still going and different versions of public goods game play important roles in this field.

2.5 Altruism in spatial games

In evolutionary spatial games, players play the game with their defined neighbors in an arena. Evolutionary spatial games concern the evolution of different strategies over space [47]. Despite having John von Neumann as the same father, the theory of spatial games and the theory of cellular automata, at first glance, seem to be totally unrelated; however, after recent development in both fields, these two uncorrelated disciplines have been merged together [136]. In iterated evolutionary spatial games, the players are distributed on a two or higher dimensional array, called arena of the game. Then, in every round every player plays the game against its immediate neighbors. Based on the payoff of players, each site is occupied by the original owner or one of its neighbors. Several standard evolutionary games have been extended to spatial games, and in many of these cases, cooperation emerges in games in which is not possible to maintain cooperation in their standard forms [2, 25, 27, 66, 132, 133, 135]. Moreover, it is seen that the spatial effects greatly change the result of the frequency-dependent game dynamics, and as a result, one can find many fascinating mathematical phenomena such as spatial chaos, fractal patterns, and kaleidoscope like shapes [2, 27, 74]. For example, Nowak and May showed that Spatial Iterated Prisoner's Dilemma (S-IPD) with the following payoff matrix:

$$E = \begin{array}{cc} C & D \\ C & \left(\begin{array}{cc} 1 & 0 \\ b & \epsilon \end{array} \right) \qquad b > 1, \qquad 0 < \epsilon \ll 1 \end{array}$$
(2.4)

depicts spatial chaos if 1.8 < b < 2 (Fig. (2.3)). In this game, game favors defector if b > 1.8, and as a result, big clusters of defectors expand in the arena until they conquer the arena. On the other hand, cooperator has advantage to the defector if b < 2, and big clusters of cooperators expand in the arena. Chaotic patterns emerge for 1.8 < b < 2 (Fig. (2.3)), when both defectors and cooperators have chance to expand their clusters in the background of the opposite strategy (Fig. (2.3)).

They also noticed that if the dynamic is chaotic (1.8 < b < 2.0), these spatial games can generate fractal and kaleidoscope patterns that change abruptly over generations (Fig. (2.4)). To generate the kaleidoscopes, they insert a defector in the center of a 200 × 200 arena with all cooperators. The similar patterns can be generated if we substitute IPD with other games such as hawk-dove game (coordination game).

2.6 Chapter summary

In this chapter, I reviewed some studies related to my research. First, I reviewed the historical development of evolutionary game theory by first reviewing the Richard Lewinton's paper on the evolution and the theory of games as its "wrong standing point". Then, I focused on the concept of relatedness and inclusive fitness theory by reviewing pillars of behavioral evolutionary biology written by Hamilton and Trivers. To my knowledge Hamilton's works were the first evolutionary investigation of emerging cooperation among selfish individuals. Constructing a foundation for such investigations, Queller extended Hamilton's kin selection theory and conducted his seminal research in 1985 and developed his inclusive fitness theory. Queller's inclusive fitness theory predicts that cooperation emerges in the population when the assortment between those with the cooperative genotype and the recipient's phenotype (modeled by a covariance term), scaled by the benefit factor be greater than the assortment between the cooperative genotype and phenotype of donor, scaled by the cost of the altruism.



Figure 2.3: The spatial iterated prisoner's dilemma depicts marvelous chaotic patters. In this example the size of arena is 200×200 . The edges are wrapped around to avoid boundary conditions. The color code is as follows: blue indicates cooperator to cooperator transition; red represents a defector to defector transition; green represents a cooperator with a defector as parent, and yellow indicates a defector with a cooperator as parent. The more green or yellow in the picture, the more variation occurs from generation to generation. All blue and all red arena is completely static. (a) b = 1.35, this situations is advantageous to cooperator (b) 1.7 < b < 1.8, this situations favors cooperator; however, the dynamic is slower than the previous case since we are closer to the critical point. (c) 1.8 < b < 2.0, the spatial game in this situation is chaotic since both cooperators and defectors can expand in the background of defectors and cooperators respectively. (d) b = 2.01, this situations is advantageous to defector [2].





(a)



(d)

Figure 2.4: The spatial iterated prisoner's dilemma generates fractal patters. In this example the size of arena is 99×99 , and one defector is added to the center of all cooperators, and b is chosen to be in the chaotic interval. (a) generation 30 (b) generation 217 (c) generation 219, and (d) generation 221 [2].

Moreover, by adding a synergy factor to his theory, Queller extended Hamilton's rule for nonadditive problems.

Then, I discussed John Maynard Smith's and George Price's marvelous research that yielded to the new field of "evolutionary game theory" by reviewing their paper in 1973 which describes "evolutionary stable strategies" as equivalence to Nash equilibrium in evolutionary processes. Followed that, I reviewed stochastic games and multiplayer games as two possible mechanisms that can maintain cooperation among a group of selfish individuals. I finished my review by studying the effect of population structure on spatial games, and I reviewed some papers that represent evidence of cooperation and defection coexistence in some spatial games in which there is no chance for emergence of cooperation in the standard form of these games.

In the following chapters, I will use what we have learned so far from literature review to study necessity conditions for emergence of altruism and try to develop theories for the evolution of cooperation and altruistic behavior.

Chapter 3

Evolution of Information Content in Digital Organisms

Genetics is about how information is stored and transmitted between generations.

-John Maynard Smith

Fools ignore complexity. Pragmatists suffer it. Some can avoid it. Geniuses remove it.

-Alan J. Perlis

- The most valuable commodity I know of is information! -Gordon Gekko Wall Street, O. Stone, 1987

What is the role of communication and information flow on emergence of complex behavior such as altruism? Is information content stored in genomic sequences increased over the course of evolution? How does evolution as a directed random process increase the level of complexity from simple single-celled organisms to complex animals? In this chapter, to address these questions and investigate the effect of evolution on genomic complexity or *information content*, we designed multiple experiments in Avida [34, 137, 138], a digital evolution platform, which contains a population of evolving and self-replicating "digital organisms," to study how information content is correlated to the fitness of organisms as a measure of organism's behavioral complexity. To do so, the "Price equation" is used to track changes in avidians during various phases of punctuated evolution. Investigating the correlation between information content and fitness over the course of evolution is necessary to understand how altruism and cooperation emerge as a result of evolutionary processes. This analysis is the first step of having an information theoretic form of kin selection and inclusive fitness theory. Details on the Price equation and Avida software are described in appendices A and B respectively.

3.1 What is information and how is it related to complexity?

The concept of *information* has been around since the mid 20^{th} century when Claude Shannon [139] and Robert Wiener [140] worked separately to define it in terms of statistical concepts such as entropy. In biology, information is a broad fundamental concept from the information carried by DNA as series of nucleic acids to the information obtained, analyzed, and transferred in the swarm of insects or clan of animals [141, 142]. While informationtheoretic measures have been used frequently in some branches of biology such as neuroscience and bioinformatics, these measures are less common in ecology, evolutionary biology, and behavioral sciences, since information-theoretic measures quantify the amount of stored or transferred information, while evolutionary and behavioral biologists mostly concern about the quality of information stored and transferred within or between the populations. What evolutionary biologists and behavioral scientists need is a measure that quantitatively measures the amount of information in the system yet qualitatively measures the relationship between the information and the fitness. In other words, instead of just calculating the autocorrelation of the genome, or estimating the correlation between symbols in the genome and organism's behavior, we should look for the correlation between the symbols in the genomic sequence and the environment's features in which the sequence is functional [143, 144].

Here, information content, also called genomic complexity, reflects the amount of infor-

mation stored in a sequence [143, 145] especially as it applied to the **fitness** of organisms over time as they exist in a particular environment. This measure of information content is defined as the mutual information [146] between a sequence of symbols, and the representation of the environment in which that sequence is to be interpreted [144]. Mutual information gives the difference between the entropy of the population in the absence of selection, and the entropy of the population given the environment, that is, given the selective forces that the environment engenders [144, 147].

The information content is defined based on Shannon's definition of entropy. The quantity entropy (H) in Shannon's information theory represents the required number of bits to indicate the state of a random variable given a distribution of probabilities [143, 148]. In other words, Shannon's entropy measures how much information can be stored in this random variable. In a biological genome, for a given site i, we can have four nucleotides with probabilities:

$$\{p_A(i), p_C(i), p_G(i), p_T(i)\}$$
(3.1)

The Shannon's entropy can be calculated as:

$$H_i = -\sum_j^{A,C,G,T} p_j(i) \times \log(p_j(i))$$
(3.2)

The maximum entropy for each site happens when the distribution of nucleotides follows uniform distribution. This means that the probabilities of occurrence of each nucleotide for a given site is equal to $\frac{1}{4}$. In this case, maximum entropy would be equal to one. A site in a genome has maximal information if, in DNA, it is perfectly conserved across an equilibrated ensemble [143]. Therefore, the probability of the conserved bases would be one and the probability of the remaining bases would be zero, rendering $H_i = 0$ for this site according to equation (3.2). Thus, the amount of information per site can be measured by:

$$I(i) = H_{max} - H_i \tag{3.3}$$

and by applying equation (3.3) to all ℓ sites and summing over the sites, the information content of an organism's sequence can be estimated as:

$$C = \ell - \sum_{i} H(i) \tag{3.4}$$

which can only be an approximation to the true information of a genome in an environment.

In Avida the complexity of an adapted digital organism can be obtained by measuring substitution frequencies at each instruction across the population. The easiest way to measure genomic complexity or information content is to fix the genome size, as is done in the experiments reported here, although this constraint can be relaxed by implementing a suitable alignment procedure. To correctly assess the information content of the ensemble of sequences, we need to obtain the substitution probabilities at each position, which go into the calculation of the per-site entropy.

3.2 Experimental Setup

The experiments run in the logic environment, in which the logic resources associated with each function are unlimited (as was true in the early Avida experiments). The population size is limited to 1600 organisms, and avidians compete in a toroidal environment 1 . The

¹The experiments reported in this research were performed using version 2.12 of the Avida software which is freely available from devolab.cse.msu.edu/ software/avida

genome length of the ancestral organism (organism.heads) is fixed at 50 instructions. As with the original logic experiment, the ancestral organism can self-replicate but is not able to accomplish any logical computations. Experiments run under the Linux operating system on an Intel10 1536 cluster of 192 dual core Intel 2200+ processors (High Performance Computing Laboratory, Michigan State University http:/hpcc.msu.edu).

The population size of 1600 is smaller than the earlier logic experiments. This is due to the fact that to analyze each organism in the population over all the generations, a very computationally intensive endeavor need to be done. The world topology is a 40×40 torus like grid in which X and Y wrap at the edges. A typical Avida experiment reports fitness every *update*, an arbitrary unit of time in which $30 \times N$ instructions are executed globally. In these experiments, instead of measuring and recording the features of digital organisms update by update, these features are measured generation by generation since the Price equation addresses the variation of a specific characteristic generation by generation. To find the variation of characters in consecutive generations, the parent ID of those descendant existed in both populations is changed from their original parent ID to their own ID since this is the result of self-replication.

3.2.1 Experiment 1

In this experiment, we track how avidians perform different logic tasks. In other words, how often a logic task is performed by an avidian is considered as a trait, and since performing each task increases the fitness of avidians, these traits are positively selected. Despite the earlier Avida experiments, which performing a task multiple times is not rewarding, here there is benefit in repeating a logic task up to ten times for avidians. Besides these logic tasks, in this experiment we analyze the variation of three other traits over the course of evolution: fitness, information content, or genomic complexity, and the difference between the frequency of two alleles of no logic task operation (NopA - NopC). It is assumed that the latter is a neutral trait and is uncorrelated to information content and fitness, and thus is not under pressure of selection. Here, the idea is to apply the Price equation to see how traits with different level of selectability (from zero (NopA - NopC) to one (fitness)) evolve over the course of evolution. Table (3.1) briefly describes the traits used in this experiment.

Table 3.1: Description of traits that are analyzed for the first Avida experiment.

Trait	Description
And	This task is triggered when two 32 bit numbers are input, the values are "anded" together in a bitwise fashion, and the result is output. The and operation returns a one if and only if both inputs are one; otherwise it returns a zero
AndNat	This task is triggered when two 20 bit numbers are input the values are "ordered" together in a hitrige
AndNot	This task is triggered when two 32 bit humbers are input, the values are andn-ed together in a bitwise factor of the result is activity. The AufVict operation check for and net. It shows a considered the second s
	ashion, and the result is output. The Androi operation stands for and-not. It only returns a one if for each
Nond	bit part one input is a one and the other input is not a one. Otherwise it returns a zero.
Nand	This task is triggered when two 32 bit humbers are input, the values are named together in a bitwise factor of the result is autout. Nand atomda for "act and "" The non-discretistic restriction are if and an it is the second secon
	assion, and the result is output. Name scans for not and . The hand operation returns a zero if and only if
Nor	both inputs are one; otherwise it returns a one.
NOT	In its task is triggered when two 32 bit numbers are input, the values are inored together in a bitwise fashion, and the result is output. The new energies strong for not and struggered with the inputs, are gree
	and the result is output. The hor operation stands for not-or and returns a one only it both inputs are zero.
Not	Otherwise a zero is returned. This task is simpled when an approximation inputs a 22 bit number to release life the bits and outputs the rough
NOL	This task is triggered when an organism inputs a 52 bit number, toggies an of the bits, and outputs the result.
	and outproving one The latter approach only used in the number are strend in these dependence to itself, of negating it
OrNet	and subtracting one. The latter applicant only works since numbers are stored in twos-complement notation.
Ornot	In its task is triggered when two 32 bit numbers are input, the values are orn together in a bitwise fasmon, and the result is output. The one operation strong for on pot. It is not used thus if for each bit pois one input is
	and the result is output. The off operation stands for or-not. It is fetunis true if for each off pair one input is
Or	This task is triggered when two 22 bit numbers are input the values are "ared" together in a bitwise fachion
	and the result is output it returns a one if either the first input or the second input is a one otherwise it
	and the issue is output. It returns a one if effect the mat input of the second input is a one, otherwise it returns a zero
Xor	This task is triggered when two 32 bit numbers are input the values are "vored" together in a bitwise fashion
	and the result is output. The vor operation stands for "exclusive or" and returns a one if one but not both of
	the inputs is a one. Otherwise a zero is returned.
Fitness	Fitness is defined as the metabolic
	rate divided by gestation. Metabolic rate refers to how fast an organism can execute instructions (letters of
	its genome) while gestation refers to the number of instructions it takes for an organism to reproduce.
FrNeut	Fraction of Neutral Mutations
InfCon	Information content or Physical Complexity of Organism
NTasks	Total number of tasks done
NDTask	Number of different tasks done
NopAC	The difference between frequency of NopA and NopC instruction in avidian's genome. The instructions
	Nop-A, Nop-B, and Nop-C are no-operation instructions, and will not do anything when executed. They will,
	however, modify the behavior of the instruction preceeding it (by changing the CPU component that it
	affects) or act as part of a label to denote positions in the genome.

In this experiment, the genome length of avidians is fixed at 50. The treatments have one point mutation rates μ , with a frequency of 0.0005/site. We record the variation of traits for 10,000 generations.

3.2.2 Experiment 2

Here, the variation of genome length as a feature, which is assumed to be correlated to the information content, is considered. The genome length of avidian's is not fixed and varies over the course of evolution. The point mutation rates μ , of 0.0075/site, and the rates of insertion and deletion were set to 0.01 per genome per generation respectively, and divide insertion and deletion probabilities are set to 0.05. Similar to the previous experiment the genomes, genome length, and fitness of the organisms are recorded for 10000 generations.

3.3 Results

In this section, the effect of mutation as a random process on characters that are highly correlated to fitness (e.g. information content), characters that are weakly correlated to fitness (e.g genome length), and characters that are uncorrelated to fitness as the control is given. Here, other evolutionary processes are ignored, and the focus is on mutation as the random force that changes traits of avidians over the course of evolution.

3.3.1 Price equation and fitness as a trait over the course of evolution

First, we apply the "Price equation" to fitness. If we treat fitness as a trait and ignore the second term of this equation, the Price equation reformulates the "Fisher's fundamental theorem". Figure (3.1) shows log of mean fitness over the course of evolution. As we expect, the mean fitness increases over generations.

Figure (3.2) shows the scatter plot of left hand side vs. right hand side of the Price


Figure 3.1: Log mean fitness over 10000 generations

equation applied to fitness as a trait.

Fig. (3.3) shows the effects of two terms of right hand side of the Price equation, selection and mutation, on the fitness over the course of evolution, and how they balance on the left hand side.

3.3.2 Evolution of logic tasks as correlated characters to fitness

Here, we apply the Price equation to see how often avidians perform a logic task over the course of evolution. Figure (3.4-3.8) present the number of logic tasks performed by avidians over the generations. By comparing figures (3.4-3.8) and (3.1), we see that number of performed logic tasks increases over the generations (there are some rare exceptions in AndNot, Nand, and Not, where the number of performed tasks decreases abruptly over a short period; however, the general trend is increasing), and thus these logic tasks and fitness are highly correlated. This depicts the positive selectability of these traits over the course of evolution.



Figure 3.2: Left hand side vs. right hand side of the Price equation. Here, we applied the price equation to avidians fitness and we treated fitness as a trait. The small box in this figure demonstrates deviation from identity line.

Figure (3.9-3.13) show the scatter plot of two terms of left hand side vs. right hand side of the Price equation when applied to each performed logic task as a trait.

Fig. (3.14-3.23) demonstrate the effects of two terms of right hand side of Price equation, selection and mutation, on the logic tasks over the course of evolution, and how they balance on the left hand side. In other words, these figures show how selection (first term) and mutation (second term) specify together the direction of variation of logic tasks in consecutive generations. According to Fig. (3.14-3.23) (a), it is clear that all logic tasks (except Xor, which is not performed by avidians in all these 10,000 generations) are positively selected as the first term is usually positive. As expected, mutation for all logic tasks except "Not" usually is deleterious for logic tasks. Not is a simple logic task (almost all avidians perform this task from early generations), and it seems that mutation has neutral effect on this task on average. Finally, we see that the first term and the second term usually cancel out each



Figure 3.3: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on fitness as a trait. X-axis shows the components of right hand side and Y-axis demonstrates the left hand side of the Price equation: (a) scatter plot of selection (blue asterisks) and mutation (red squares) vs. left hand side of the Price equation, (b) box plot of the components of right hand side of the Price equation.



Figure 3.4: And and AndNot logic tasks as two selectable traits in a population of avidians over the course of evolution: (a) And, (b) And-Not



Figure 3.5: Nand and Nor lagic tasks as two selectable traits in a population of avidians over the course of evolution: (a) Nand, (b) Nor



Figure 3.6: And and AndNot logic tasks as two selectable traits in a population of avidians over the course of evolution: (a) Or, (b) Or-Not



Figure 3.7: Not and Xor lagic tasks as two selectable traits in a population of avidians over the course of evolution: (a) Not, (b) Xor



Figure 3.8: Number of different performed tasks and total number of performed tasks as two selectable traits in a population of avidians over the course of evolution: (a) Number of different performed tasks, (b) Total number of performed tasks



Figure 3.9: Left hand side, right hand side of the Price equation, and their deviation from identity line for And and AndNot as to selectable logic tasks: (a) And, (b) And-Not (the small box in each sub figure shows the distribution of deviation from identity line. In other words, it presents the estimation error of the evolutionary dynamic of And and AndNot as two selectable traits modeled by the Price equation.)



Figure 3.10: Left hand side, right hand side of the Price equation, and their deviation from identity line for Nand and Nor as two selectable logic tasks: (a) Nand, (b) Nor (the small box in each sub figure shows the distribution of deviation from identity line. In other words, it presents the estimation error of the evolutionary dynamic of Nand and Nor as two selectable traits modeled by the Price equation.)



Figure 3.11: Left hand side, right hand side of the Price equation, and their deviation from identity line for Or and OrNot as to selectable logic tasks: (a) Or, (b) Or-Not (the small box in each sub figure shows the distribution of deviation from identity line. In other words, it presents the estimation error of the evolutionary dynamic of Or and OrNot as two selectable traits modeled by the Price equation.)



Figure 3.12: Left hand side, right hand side of the Price equation, and their deviation from identity line for Not and Xor as two selectable logic tasks: (a) Not, (b) Xor (the small box in each sub figure shows the distribution of deviation from identity line. In other words, it presents the estimation error of the evolutionary dynamic of Not and Xor as two selectable traits modeled by the Price equation.)



Figure 3.13: Left hand side, right hand side of the Price equation, and their deviation from identity line for number of types of performed tasks and total number of performed tasks as two highly selectable logic tasks: (a) number of types of performed tasks, (b) total number of performed tasks (the small box in each sub figure shows the distribution of deviation from identity line. In other words, it presents the estimation error of the evolutionary dynamic of number of types of performed tasks and total number of performed tasks as two highly selectable traits modeled by the Price equation.)

other.

3.3.3 Evolution of information content

Here, we apply the "Price equation" to check the selectability of information content in genomes of digital organisms and its correlation to fitness. Figure (3.24) shows the avidian's information content, stored in avidians genome, over 10000 generations. By comparing figures (3.24) and (3.1), we see that both fitness and information content are highly correlated, and they increase over the course of evolution.

Figure (3.25) shows left hand side, right hand side, and their deviation from the identity line.

Fig. (3.26) shows the effects of two terms of right hand side of Price equation, selection and mutation, on the information content over the course of evolution, and how they balance on the left hand side. Similar to logic traits, this figure describes how selection and mutation specify together the direction of information content in consecutive generations. According to Fig. (3.26) (a), it is clear that information content is strongly selected as the first term is usually positive. As expected, mutation usually is deleterious and it reduces the information content (increases entropy). Finally, we see that the first term and the second term usually cancel out each other.

3.3.4 Price equation and uncorrelated characters to the fitness

In this experiment the Price equation is applied to study the two characters (no-ops and frac-neut) that are assumed to be uncorrelated to the fitness and information content. We hypothesize that as fitness increases and avidians' genome become more complicated (as



Figure 3.14: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on And and AntNot as two selectable logic tasks: (a) And, (b) And-Not



Figure 3.15: Box plots of the first term of right hand side (selection) and the second term of right hand side (mutation) of the Price equation when applied to And and AndNot as two selectable logic tasks: (a) And, (b) AndNot



Figure 3.16: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on Nand and Nor as two selectable logic tasks: (a) Nand, (b) Nor



Figure 3.17: Box plots of the first term of right hand side (selection) and the second term of right hand side (mutation) of the Price equation when applied to Nand and Nor as two selectable logic tasks: (a) Nand, (b) Not



Figure 3.18: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on Or and OrNot as two selectable logic tasks: (a) Or, (b) Or-Not



Figure 3.19: Box plots of the first term of right hand side (selection) and the second term of right hand side (mutation) of the Price equation when applied to Or and OrNot as two selectable logic tasks: (a) Or, (b) OrNot



Figure 3.20: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on Not and Xor as two selectable logic tasks: (a) Not, (b) Xor



Figure 3.21: Box plots of the first term of right hand side (selection) and the second term of right hand side (mutation) of the Price equation when applied to Not and Xor as two selectable logic tasks: (a) Not, (b) Xor



Figure 3.22: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on number of types of performed tasks and total number of performed tasks as two selectable logic tasks: (a) number of types of performed tasks, (b) total number of performed tasks



Figure 3.23: Box plots of the first term of right hand side (selection) and the second term of right hand side (mutation) of the Price equation when applied to number of types of performed tasks and total number of performed tasks as two selectable logic tasks: (a) number of types of performed tasks, (b) total number of performed tasks



Figure 3.24: Information content in a population of avidians over the course of evolution.



Figure 3.25: Left hand side vs. right hand side of the Price equation, and their deviation from the identity line when applied to information content as a highly selectable trait (the small box in this figure shows the estimation error of the Price equation as an evolutionary model of highly selectable trait (information content). This distribution demonstrates how left hand side and right hand side are identical according to the Price equation for information content.)



Figure 3.26: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on the information content as a highly selectable trait: (a) scatter plot of selection (blue asterisks) and mutation (red squares) vs. left hand side, (b) box plot of the components of right hand side of the Price equation.

what we saw in the previous experiments), these characters, the different between frequency of NopA and NopC instructions and fraction of neutral mutation, should not change dramatically. Fig. (3.27) shows the variation of these traits over the course of evolution.

Fig. (3.28) demonstrates the scatter plot of left hand side vs. right hand side of the "Price equation" and their deviation from the identity line for these neutral traits.

Figure (3.29) and (3.30) show the scatter plots of the terms of right hand side vs. left hand side of the Price equation. In other words, these figures demonstrate the effects of selection (first term) and mutation (second term) on these features.

By comparing fig. (3.14-3.22), fig. (3.26), and fig. (3.29), we see that for the no-ops the left hand side and the right hand side of the Price equation around are almost identical since their deviation from the identity line is very narrow. We also see that there is no positive or negative selection against this feature. According to the box plot of figure (3.29), it is obvious that the two terms of right hand side are statistically zero. The distribution of the scatter plot of the right hand side and the left hand side of the Price equation demonstrates that even for these features, which are uncorrelated to fitness and information content, this equation holds.

3.3.5 Genome length as a weakly selectable trait over the generations

In this experiment, the Price equation is applied to a population of avidians to study how genome length varies over 10000 generations. If there is no penalty for genome length, it is hypothesized that as avidians fitness increases (learn more logic functions), their genome length should increase to provide enough space to save the necessary information for those



Figure 3.27: Neutral traits in a population of avidians over the course of evolution: (a) fraction of neutral mutation as neutral trait, (b) mean frequency of NopA minus mean frequency of NopC genes in avidians' genomes.



Figure 3.28: Left hand side vs. right hand side of the "Price equation" applied to fraction of neutral mutation and difference between frequency of NopA and NopC genes as two neutral and uncorrelated characters to the fitness (the small boxes in subfigures show the estimation error of the Price equation as an evolutionary model of neutral traits (fraction of neutral mutation and difference between frequency of NopA and NopC genes). These distributions demonstrate how left hand side and right hand side are identical according to the Price equation for neutral traits): (a) fraction of neutral mutation, (b) difference between frequency of NopA and NopC genes.



Figure 3.29: Effects of selection (first term of right hand side) and mutation (second term of right hand side) on fraction of neutral mutation and difference between frequency of NopA and NopC genes as two neutral and uncorrelated characters to the fitness: (a) scatter plot of selection (blue asterisks) and mutation (red squares) vs. left hand side of the "Price equation" applied to "fraction of neutral mutation" trait, (b) scatter plot of selection (blue asterisks) and mutation (red squares) vs. left hand side of the "Price equation" applied to "fraction of neutral mutation" trait, (b) scatter plot of selection (blue asterisks) and mutation (red squares) vs. left hand side of the "Price equation" applied to the "difference between frequency of NopA and NopC genes" trait.



Figure 3.30: Box plot of the components of right hand side of the "Price equation" (selection and mutation) on two neutral and uncorrelated characters to the fitness: (a) fraction of neutral mutation, (b) difference between frequency of NopA and NopC genes.

complicated tasks.

Figure (3.31) presents the fitness and the genome length of avidians over 10000 generations. Figure (3.31) shows that as fitness increases, the genome length fluctuates (the red dashed line has a negligible negative slope). This fluctuation reflects the tension between increasing genome length to accommodate more difficult tasks, and the implicit penalty of longer genome lengths, requiring more CPU cycles to copy. Thus a genome that learns a new logic function may generate a longer genome, but that genome is pressured to become shorter so as to maximize the increase in fitness.

Fig. (3.32) and (3.33) show the scatter plot of left hand side vs. right hand side of the "Price equation" and the effects of selection (first term) and mutation (second term) on genome length.

By comparing figures (3.14-3.22), (3.26), (3.29) and (3.32), we see that similar to logic task "Not" and neutral trait "NopA - NopC", mutation has Brownian distribution, and it does not have huge effects on the evolution of genome length; however, on average this term is slightly greater than zero. This shows that in this experiment mutation on average was not deleterious, and overall slightly increases the fitness of avidians. On the other hand, we see that the first term is negative, which shows that there is a weak negative selection against genome length. According to fig. (3.32), the variation of genome length is mostly derived by the first term of Price equation (selection). Moreover, we see that both first term and second term of the right hand side are distributed around zero; however, their deviation from zero is considerable.



Figure 3.31: Fitness and genome length in a population of avidians over the course of evolution: (a) log of mean fitness, (b) mean genome length (the dashed red line demonstrates the fitted linear model to genome length over generation (intercept: 52.565, slope: -0.0005)



Figure 3.32: Left hand side vs. right hand side of the Price equation, and their deviation from the identity line when applied to genome length as a weakly selectable trait (the small box in this figure shows the estimation error of the Price equation as an evolutionary model of weakly selectable trait (genome length). This distribution demonstrates how left hand side and right hand side are identical according to the Price equation for genome length.)

3.4 Discussion

In this study, experimental evolution in Avida as an alternative approach to experimental evolutionary design was applied to investigate the evolution of characters with different correlation levels to fitness. To track the evolution of information content and other traits, weakly correlated and uncorrelated traits to fitness and information content, the Price equation was used.

First, these experiments depict a strong correlation between the left hand side and the right hand side of the Price equation for all of the characters examined. This shows that the Price equation is a good linear estimator for features that are highly, weakly or unlikely correlated to fitness (figures (3.3), (3.14-3.22), (3.26), (3.32), and (3.29)). Moreover, the Price equation demonstrates the role of selection and mutation as two evolutionary forces on



Figure 3.33: Effect of selection (first term of right hand side) and mutation (second term of right hand side) on genome length:(a) scatter plot of selection (blue circles) and mutation (red squares) vs. left hand side of the "Price equation" applied to the genome length as a weakly selectable trait, (b) box plot of the components of right hand side of the "Price equation".

the variation of characters with different level of character-fitness correlation over the course of evolution. For highly correlated characters to fitness like information content, "number of performed tasks", "or-not", or "nor" that are highly positively selected, the distribution of the first term (selection) and the distribution of the second term (mutation) are normal and highly separated. For these traits, the average of the first term is positive showing that these characters are positively selected, and the average of the second term are negative showing that mutations are mostly deleterious. On the other hand, if the character is uncorrelated to fitness like "fraction of neutral mutation" or "difference between frequency of NopA and NopC alleles", both selection term and mutation term of the Price equation have small Brownian random distribution, and the distribution of the character over the generation is narrow normal distribution around origin (fig. (3.29)). In addition, if the feature is correlated but not highly correlated to fitness like "not task", "and task" or the genome length, the distribution of the first term (selection) and the distribution of the second term (mutation) are normal with zero mean. The first term is more scattered around origin and shows more power to shape the variation of these characters. On the other hand, the mutation term has a narrow Brownian random distribution around origin and does not have major effect on the left hand side or the variation of the character over generations. Moreover, the distribution of the right hand side and the left hand side of the equation around the identity line is more scattered in comparison to the other characters. This can be measured by calculating the R^2 of the linear model of the right hand side vs. left hand side of the Price equation (table (3.2)).
Table 3.2: \mathbb{R}^2 of left hand side vs. right hand side of the Price equation for different characters.

	Information content	Genome length	ΔNOP frequency
R^2	0.973	0.6787	0.9929

In this study, to probe the forces acting on characters in different states of a population dynamic, the Price equation is applied in different states of population from highly unstable take-over state in which huge changes in mean fitness and mean character occur to a stable state in which the average of fitness and character remain constant. To identify these different states, a measure similar to the Fisher's ratio for each of these experiments is measured. Fig. (3.34) and (3.35) show the variation of this Fisher's like ratio for each experiment [149].

Tables (3.3) and (3.4) show the chosen generation intervals for this analysis.

generation interval	state
[181, 240]	take over event
[951, 1000]	take over event
[1591, 1640]	take over event
[3901, 3950]	stasis
[7001, 7050]	stasis
[9751, 9800]	stasis

Table 3.3: Different states for the population dynamics during the first experiment.



Figure 3.34: Fisher like ratio for the first experiment: (a) Fisher like ratio for different states of the first experiment based on the variation of Fisher like ratio, (b) log mean fitness over the generation (the dashed color lines present the selected regions based on the peaks of Fisher like ratio).



Figure 3.35: Fisher like ratio for the second experiment: (a) Fisher like ratio for different states of the second experiment based on the variation of Fisher like ratio, (b) log mean fitness over the generation (the dashed color lines present the selected regions based on the peaks of Fisher like ratio).

generation interval	state
[601, 110]	take over event
[1801, 2300]	Stasis
[3101, 3600]	take over event
[4301, 4800]	stasis
[5301, 5800]	take over event
[8001, 8800]	stasis

Table 3.4: Different states for the population dynamics during the second experiment.

Fig. (3.36-3.44) and (3.37-3.45) show the statistical properties of selection and mutation forces on the evolution of some highly (e.g. "or" and "number of different tasks") and weakly (e.g. "and", "nand", and "not") correlated characters to fitness during the different states of experiments.

Fig. (3.46-3.53) show the statistical properties of selection and mutation forces on the evolution of information content, genome length, fraction of neutral mutation, and difference between number of nop-A and nop-C alleles in the genome of avidians as highly, weakly, and none correlated characters to fitness during the different states of experiments.

These figures clearly exhibit that whenever there is a major variation in the characteristic of population and the fitness of population increases (take over events), the variance of the first term and the second term decreases due to the effect of advantageous mutation (especially for the experiments which analyze characters highly correlated to fitness). Moreover, due to the beneficial mutations that suppress the average effect of deleterious mutations, for selectable traits such as information content or number of performed tasks, the absolute value of second term is less than the first term. This yields to an increase to the value of the trait over the take over events. If the traits are weakly selected or are uncorrelated to fitness, first term and second term are small and on average they don't have any effect on



Figure 3.36: Dispersal of the right hand side of the "Price equation" applied to And as a selectable logic task and a correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.37: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to And as a selectable logic task and a correlated trait to fitness, as a linear function of current mean value of trait (average number of performed And in the current population) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for And logic task, (b) slopes of linear models for And logic task.



Figure 3.38: Dispersal of the right hand side of the "Price equation" applied to Nand as a weakly selectable logic task and a correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i\Delta z_i)$ (the mutation term).



Figure 3.39: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to Nand as a selectable logic task and a correlated trait to fitness, as a linear function of current mean value of trait (average number of performed Nand in the current population) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for Nand logic task, (b) slopes of linear models for Nand logic task.



Figure 3.40: Dispersal of the right hand side of the "Price equation" applied to Not as a weakly selectable logic task and a weakly correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.41: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to Not as a weakly selectable logic task and a weakly correlated trait to fitness, as a linear function of current mean value of trait (average number of performed Not in the current population) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for Not logic task, (b) slopes of linear models for Not logic task.



Figure 3.42: Dispersal of the right hand side of the "Price equation" applied to average number of performed tasks as a highly selectable logic task and a correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.43: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to average number of performed tasks as a highly selectable trait and a highly correlated trait to fitness, as a linear function of current mean value of trait (average number of performed tasks in the current population) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for average number of performed tasks, (b) slopes of linear models for average number of performed tasks.



Figure 3.44: Dispersal of the right hand side of the "Price equation" applied to Or as a weakly selectable logic task and a highly correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.45: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to Or as a highly selectable logic task and a highly correlated trait to fitness, as a linear function of current mean value of trait (average number of performed Or in the current population) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for Or logic task, (b) slopes of linear models for Or logic task.



Figure 3.46: Dispersal of the right hand side of the "Price equation" applied to information content of genome as a highly selectable trait and a highly correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.47: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to information content of genome as a highly selectable trait and a highly correlated trait to fitness, as a linear function of current mean value of trait (average information content of genome) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for information content of genome, (b) slopes of linear models for information content of genome.



Figure 3.48: Dispersal of the right hand side of the "Price equation" applied to genome length as a weakly selectable trait and a weakly correlated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.49: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to genome length as a weakly selectable trait and a weakly correlated trait to fitness, as a linear function of current mean value of trait (mean genome length) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for genome length, (b) slopes of linear models for genome length.



Figure 3.50: Dispersal of the right hand side of the "Price equation" applied to fraction of neutral mutation as a neutral trait and an uncorrelated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.51: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to fraction of neutral mutation as a neutral trait and an uncorrelated trait to fitness, as a linear function of current mean value of trait (average fraction of neutral mutation) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for fraction of neutral mutation, (b) slopes of linear models for fraction of neutral mutation.



Figure 3.52: Dispersal of the right hand side of the "Price equation" applied to difference between frequency of nop-A and nop-C alleles in genome as a neutral trait and an uncorrelated trait to fitness in different states of the population dynamic (take over events and stasis): (a) $cov(w_i, z_i)$ (the selection term), (b) $E(w_i \Delta z_i)$ (the mutation term).



Figure 3.53: Slopes and intercepts of different fitted linear models to the right hand side of the "Price equation", applied to difference between frequency of nop-A and nop-C alleles in genome as a neutral trait and an uncorrelated trait to fitness, as a linear function of current mean value of trait (average difference between frequency of nop-A and nop-C alleles in genome) in different states of the population dynamic (take over events and stasis): (a) intercepts of linear models for difference between frequency of nop-A and nop-C alleles in genome, (b) slopes of linear models for difference between frequency of nop-A and nop-C alleles in genome.

the trait. On the other hand, if population is in a stable state (generation [7001, 7500] for the first experiments and generation [8000, 8800] for the second experiment), the variance of the first term and the second term is very high, especially for highly correlated traits to the fitness, and on average first term is a high positive value (the trait is highly selectable) and the second term is a low negative value (all mutations are deleterious); however, on average the first term and second term are almost equal and they cancel out each other in the right hand side of the equation (since we are in stasis, and we do not expect a dramatic change in trait values). It is obvious that at the beginning of the experiments, the mutation term (second term of the right hand side) has significant effects on the evolution of character. This pattern is repeated whenever we have major variation in the population. On the other hand, when the population becomes stable, the effect of the mutation term reduces and first term and the second term cancel out each other.

3.5 Chapter Summary

In this chapter, we ran experiments on Avida and by applying the Price equation we analyzed the variation of characters with different level of correlation to fitness. Moreover, we investigated the effects of selection and mutation as two major evolutionary forces on the variation of these characters. Understanding the mechanisms and evolutionary dynamics, which increase the information content that consequently helps the emergence of complex behavior, is the groundwork to study the evolution of cooperation. In the next chapter, we apply the Queller's inclusive fitness theory, which uses the Price equation to extend Hamilton's kin selection theory, to conditional games and investigate the necessity conditions for maintaining cooperation among groups of selfish individuals.

Chapter 4

Evolution of Cooperation in Conditional Games

The moment there is suspicion about a person's motives, everything he does becomes tainted.

-Mahatma Gandhi

- Reciprocity, Mr. Hudgens, is the key to every relationship. -Captain Dudley Smith L.A. Confidential, C. Hanson, 1997

Since 1964 after Hamilton developed his theory for the evolution of cooperation among relatives based on the idea of inclusive fitness, evolutionary biologists have been working on theories to address the evolution of cooperation [4, 12, 13]. Among these theories, evolutionary game theory has been the leading metaphor for the evolution of altruism [14, 16, 36]. By using this idea, researchers have been trying to model and understand the mechanisms that yield to cooperation (e.g. assortment, reciprocity, kin selection, and group selection) [7, 17, 19]. Interestingly, all of these mechanisms fail to maintain cooperation when the environment is noisy in which it is hard to communicate and increase the level of trust between the individuals [46]. This shows the importance of information and communication for the emergence of cooperation among selfish individuals.

In this chapter, to quantify the effect of information on the evolution of altruism, we analyze the variation of information, entropy, mutual information, fitness, and distribution of different strategies or phenotypes in unconditional and unconditional two players games. These players randomly play or interact with each other in every generation, and based on their action, they receive payoff, which indicates their average fitness. Then, based on this average fitness, they will reproduce offspring for the next generation. By repeating these random games and tracking the evolution of different strategies, we can quantify the role of information for the emergence of altruism. The ultimate goal of this research would be answering the following question:

"What is the lower bound of information flow among selfish individuals to make cooperation evolutionary stable?"

4.1 Evolution of cooperation in unconditional games: a review

Scientists usually use two ways to describe mechanisms, which yield to cooperation. Population geneticists usually use personal fitness to model evolution of cooperation; however, this approach is not useful for complex social behavior. The other model is to define an inclusive fitness for individuals in the population. In this section, by defining an inclusive fitness between players with pure cooperative or defective strategies, a game theoretic approach is used to address evolution of cooperation in unconditional games. Here, we try to derive the well-established theories of evolution of cooperation with our formulation. This helps us to have a better understanding of our theory of evolution of cooperation in conditional game in section (4.3). Table (4.1) presents the notation, used in this chapter.

In unconditional games even if there exists information about the opponents' next action or the current state of the game, players close their eyes to this information and don't adapt themselves to the current state and adjust their next move in the next round of game. In

Random variable	Definition in the iterated game
g	self genotype (0: defector, 1: cooperator)
g'	opponent's genotype
z	self phenotype, strategy, or action
z'	opponent's phenotype, strategy, or action
P_z	self payoff after one game
$P_{z'}$	opponent's payoff after one game
$\tilde{w_j(z)}$	fitness of the player "z" after j^{th} game
$\check{G_i}$	iterated game played in generation "i"
p_i	frequency of the cooperator type in generation " i "

Table 4.1: List of random variables used in iterated stochastic games

other words, in such games genotype-phenotype transformation is an identity function and their channel is noiseless. We have:

$$z = g, \qquad z' = g' \tag{4.1}$$

The payoff matrix for such unconditional iterated game is:

$$E = \begin{array}{c} C & D \\ C \begin{pmatrix} R & S \\ D \end{pmatrix}$$

Considering this payoff matrix, the payoff to type z after an interaction against type z' is:

$$P_{z}(z, z') = Rzz' + Sz(1-z') + T(1-z)z' + P(1-z)(1-z')$$
(4.2)

and the payoff to the cooperator and defector in these iterated games is:

$$P^{C}(z') = Rz' + S(1 - z') = (S + P_{0}) + (R - S)z'$$
$$P^{D}(z') = Tz' + P(1 - z') = (P + P_{0}) + (T - P)z'$$
(4.3)

The fitness to the cooperator and defector in generation "i" after "j" rounds of games is:

$$w_{ij}^{C} = \frac{1}{j} \left(\sum_{k=1}^{j} \left(Rz'_{k} + S\left(1 - z'_{k}\right) \right) \right)$$
$$w_{ij}^{D} = \frac{1}{j} \left(\sum_{k=1}^{j} \left(Tz'_{k} + P\left(1 - z'_{k}\right) \right) \right)$$
(4.4)

For infinitely large rounds of games the fitness values of these types would be:

$$w_i^C = \lim_{j \to +\infty} \left(\frac{1}{j} \left(\sum_{k=1}^j \left(R z'_k + S \left(1 - z'_k \right) \right) \right) \right) \approx p_i R + (1 - p_i) S$$
$$w_i^D = \lim_{j \to +\infty} \left(\frac{1}{j} \left(\sum_{k=1}^j \left(T z'_k + P \left(1 - z'_k \right) \right) \right) \right) \approx p_i T + (1 - p_i) P \qquad (4.5)$$

where p_i is the fraction of cooperator in the population at generation "*i*". By combining these equations, the fitness of a random player with strategy "*z*" after "*j*" rouns of games can be written as:

$$w_{ij}(z) = \frac{1}{j} \left[z \left(\sum_{k=1}^{j} \left(Rz'_k + S\left(1 - z'_k\right) \right) \right) + (1 - z) \left(\sum_{k=1}^{j} \left(Tz'_k + P\left(1 - z'_k\right) \right) \right) \right] \quad (4.6)$$

As "j" goes to infinity, the fitness of this player would be:

$$w_i(z) = z \left(p_i R + (1 - p_i) S \right) + (1 - z) \left(p_i T + (1 - p_i) P \right)$$
(4.7)

or:

$$w_i(z) = \left[P + (T - P)p_i\right] + \left[(S - P) + (R - S - T + P)p_i\right]z$$
(4.8)

and the mean fitness of the population is:

$$\bar{w}_i(z) = P + (S - 2P + T)p_i + (R - S - T + P)p_i^2$$
(4.9)

which is positive for the games that we discuss in this chapter.

Here, we are interested in conditions that maintain cooperation in well-mixed population of cooperators and defectors. There are multiple ways to address this problem (e.g. invasion analysis, stability analysis of equilibrium points, or directly comparing the mean fitness of different strategies). Among the mentioned approaches, comparing the fitness of players in a competition for limited resources yields to better understanding of the dynamic of the game. To do so, we can apply simpler version of the "Price equation" (this equation does not have the mutation term) to a population of cooperators and defectors. This yields to a covariance equation, which is equivalent to right hand side of "replicator equation". In fact, both invasion analysis and stability analysis of fixed points (steady state analysis) are special case of this equation. By applying the "Price equation" without its second term, we can investigate the conditions that favor cooperation in mixed populations of cooperators and defectors. To write the "Price equation" for this problem, we have to treat fitness of players as a random variable, which depends on type of player and payoff matrix of the game. We have:

$$w_{j}(z) = \frac{1}{j} \left[z \sum_{k=1}^{j} \left(Rz'_{k} + S\left(1 - z'_{k}\right) \right) + (1 - z) \sum_{k=1}^{j} \left(Tz'_{k} + P\left(1 - z'_{k}\right) \right) \right]$$

$$= \frac{1}{j} \sum_{k=1}^{j} \left[Rzz'_{k} + Sz - Szz'_{k} + Tz'_{k} + P - Pz'_{k} - Tzz'_{k} - Pz + Pzz'_{k} \right]$$

$$= \frac{1}{j} \sum_{k=1}^{j} \left[\left(P + (S - P)z + (T - P)z'_{k} \right) + (R - S - T + P)zz'_{k} \right]$$

$$= P + (S - P)z + \frac{(T - P)}{j} \sum_{k=1}^{j} z'_{k} + \frac{(R - S - T + P)}{j} \sum_{k=1}^{j} zz'_{k}$$
(4.10)

which is similar to the condition that David Queller derived in 1985 [13]. Since it is assumed that genotype-phenotype mapping is a noiseless identity mapping; genotype and phenotype are identical random variables. By applying the "Price equation" we derive the condition that favors cooperation in a well-mixed population of defectors and cooperators:

$$\bar{w}\bar{\Delta z} = cov\left(z,w\right) = cov\left(g,w\right) \ge 0 \tag{4.11}$$

We have:

$$cov (g, w) = \overbrace{cov (g, P)}^{0} + (S - P) cov (g, z) + \frac{(T - P)}{j} \sum_{k=1}^{j} cov (g, z'_{k}) + \frac{(R - S - T + P)}{j} \sum_{k=1}^{j} cov (g, zz'_{k}) = (S - P) cov (g, z) + \frac{(T - P)}{j} \sum_{k=1}^{j} cov (g, z'_{k}) + \frac{(R - S - T + P)}{j} \sum_{k=1}^{j} cov (g, zz'_{k}) \ge 0$$

Therefore, the necessity condition that makes cooperation positively selected over defection is:

$$\frac{1}{j} \sum_{k=1}^{j} \left[(S-P) \cos(g,z) + (T-P) \cos(g,z'_k) + (R-S-T+P) \cos(g,zz'_k) \right] \ge 0(4.12)$$

or:

$$\frac{1}{j}\sum_{k=1}^{j} \left[(S-P) + (T-P)\frac{\cos\left(g, z_{k}'\right)}{\cos\left(g, z\right)} + (R-S-T+P)\frac{\cos\left(g, z_{k}'\right)}{\cos\left(g, z\right)} \right] \ge 0$$
(4.13)

Equation (4.13) is written in personal fitness formulation since all the fitness in this equation are assigned to the central player. By taking into account the viewpoint of opponent, we have an inclusive fitness representation for this condition. Since, genotype and phenotype are identical random variables for noiseless genotype phenotype channel, we have:

$$\sum_{k=1}^{j} cov\left(g, z_{k}'\right) = \sum_{k=1}^{j} cov\left(z, g_{k}'\right)$$

Moreover, it is easy to show that:

$$cov(g, zz') = cov(g', zz')$$

$$(4.14)$$

The proof of this equation is given in appendix C. Now, by substituting these equivalencies, the necessity condition (4.14) can be written in inclusive fitness formulation as:

$$\frac{1}{j} \sum_{k=1}^{j} \left[(S-P) + (T-P) \frac{\cos\left(g'_{k}, z\right)}{\cos\left(g, z\right)} + (R-S-T+P) \frac{\cos\left(g'_{k}, zz'_{k}\right)}{\cos\left(g, z\right)} \right] \ge 0 \quad (4.15)$$

For infinitely large rounds of game, this condition would be:

$$(S-P) + (T-P)\frac{\cos(g',z)}{\cos(g,z)} + (R-S-T+P)\frac{\cos(g',zz')}{\cos(g,z)} \ge 0$$
(4.16)

which is identical to Queller's inclusive fitness formulation [13]. In the following, this necessity condition is applied to Iterated Prisoners Dilemma (IPD) as a benchmark game among unconditional games to investigate the conditions that maintain cooperation in the population. In unconditional games genotype and phenotype are identical random variables; thus, for these unconditional iterated games we have:

$$cov(g, z) = var(g) = var(z) = p_i(1 - p_i)$$

Moreover, it is easy to show that in these unconditional games (without any assortment) there is no correlation between the genotype of the player and phenotype of opponent. We have:

$$cov(g, z') = cov(g', z) = cov(z, z') = 0$$

Therefore, the necessity condition (4.16) for these games would be:

$$(S-P) + (T-P) \underbrace{\overbrace{cov(g',z)}^{0}}_{p_i(1-p_i)} + (R-S-T+P) \frac{p_i^2(1-p_i)}{p_i(1-p_i)} \ge 0$$
(4.17)

or:

$$(S - P) + (R - S - T + P) p_i \ge 0 \tag{4.18}$$

4.1.1 Iterated Prisoners Dilemma (IPD)

The Iterated prisoners dilemma is a benchmark in game theory, and it is a game played between two random players in which both individuals have to make a decision whether to cooperate or defect. After players chose their actions - to cooperate (C) or to defect (D) - their actions are revealed and players receive a payoff according to a payoff matrix. The payoffs in the payoff matrix define the type of the game; in the prisoners dilemma, the payoffs should follow the following inequality:

For example, Axelrod used the following set of values in his tournament [4]:

$$R = 3, S = -1, T = 5, \text{ and } P = 0$$

We use the same payoffs here, and based on these payoffs, the payoff matrix for IPD game is:

$$E_{IPD} = \begin{pmatrix} 3 & 0 \\ \\ 5 & 1 \end{pmatrix} \tag{4.19}$$

which makes defection an evolutionary stable strategy. This means that after defection is established in the population, any invasion of cooperation, resulted by mutation, will be unsuccessful. By applying the necessity condition (4.18) to this game, we have:

$$-1 + (4 - 5 + 0) p_i \ge 0 \quad \Rightarrow \quad p_i \le -1$$

which makes it impossible to make cooperation evolutionary stable.

4.2 Stability analysis of fixed points in unconditional games: a review

One other equivalent way to selectability analysis of strategies to investigate the faith of cooperation in a given game is to derive the dynamics that rule the variation of strategies over the competition. Then, by finding the equilibrium points of the dynamics, which are usually nonlinear ordinary differential equations, we can check their stability properties. The evolutionary games of well-mixed populations generally have replicator dynamics. In this section, replicator equation is applied to check the stability of possible equilibrium points in unconditional two player games. Moreover, the equivalency of replicator equation and the "Price equation" in its simpler form is given. Replicator equation has been used to describe the variation of strategies' concentration in a given population. If the population is very large, and if the generations blend continuously into each other, we can assume that the increase rate \dot{p}_i/p_i is a function of its evolutionary success. Therefore, we have:

$$\frac{\bar{p}_i}{\bar{p}_i} = w_i - \bar{w} \tag{4.20}$$

This yields to the replicator equation as:

$$\dot{p}_i = p_i \left(w_i - \bar{w} \right) \tag{4.21}$$

If the payoff matrix of a game is anti-diagonal as:

$$E = \begin{array}{c} C & D \\ C & a \\ D & b & 0 \end{array}$$
(4.22)

the replicator equation (4.21) is written as:

$$\dot{p}_i = p_i (1 - p_i) \left[-(b + a) p_i + a \right]$$
(4.23)

By doing simple matrix operation, such as column-wise operations that do not change the game properties [36], the payoff matrix (4.2) can be written as the following anti-diagonal matrix:

$$E = \begin{array}{cc} C & D \\ C & S - P \\ D \\ T - R & 0 \end{array}$$
(4.24)

Therefore, the replicator equation for this game would be:

$$\dot{p_i} = p_i \left(1 - p_i\right) \left[\left(S - P\right) - \left(S - P + T - R\right) p_i \right]$$
(4.25)

In appendix C we show that the right-hand side of this equation is the covariance between genotype and fitness, which is the selection force in the "Price equation" in steady state.

Thus, we have:

$$\dot{p}_i = cov(g, w) = p_i \left(1 - p_i\right) \left[\left(S - P\right) - \left(S - P + T - R\right) p_i \right]$$
(4.26)

The replicator equation of unconditional two players games has three equilibrium points. To check the stability of each equilibrium, we should take the derivative of this equation respect to " p_i and check the sign of this derivative in each equilibrium. We have:

$$\frac{d\dot{p_i}}{dp_i} = (1 - p_i) \left[(S - P) - (S - P + T - R) p_i \right] - p_i \left[(S - P) - (S - P + T - R) p_i \right] - (S - P + T - R) p_i (1 - p_i)$$

Defector $(p_i = 0)$ is a stable equilibrium, if:

P > S

Cooperator $(p_i = 1)$ is a stable equilibrium, if:

R > T

Mixed strategy $p_i = \frac{(S-P)}{(S-P+T-R)}$ is stable equilibrium, if:

$$\frac{(S-P)(T-R)}{S-P+T-R} > 0$$



Figure 4.1: Phase diagram of replicator equation for iterated prisoner dilemma.

4.2.1 Iterated prisoners dilemma

For this game, the replicator equation (4.25) is:

$$\dot{p_i} = -p_i \left(1 - p_i^2\right) \tag{4.27}$$

In this game we have two equilibrium points, and among these two points $p_i = 0$ is evolutionary stable. Figure (4.1) shows the phase diagram of this game. According to this figure, it is obvious that defector is an evolutionary stable strategy.

4.3 Evolution of cooperation in conditional games

In standard iterated games, players play unconditionally. If players do not have information about each other, or there is not any environmental relatedness or clustering in the population, players play unconditionally, and it is hard to evolve complicated cooperative behavior out of these standard games in which usually defection is conqueror of the competition. Many
researchers tried new ideas to address evolution of cooperation and altruism by introducing external terms to these iterated games [7, 17, 19]. These approaches have at least one thing in common: to evolve cooperation in the population, there should be at least a minimum level of communication in which information is exchanged between, which as a result will increase the level of trust between individuals. This information can be about the players' previous actions or the state of the game. In this section, we analyze the performance of conditional strategies in two players conditional games. To do so, we introduce assortment term "q", as the probability of cooperation when a cooperator faces a defector or vice versa. In other words, assortment q can be seen as one strategys error rate in recognizing the other type, or it can be the faith rate of one type to the other type. Here, we also investigate the role of communication and information exchange between players with these conditional strategies over the course of evolution. It is worth mentioning that for any given strategy q is a fixed continuous parameter. Thus, the cooperation rate of a cooperator with an assortment term q = 0.5 when facing a defector is fixed and equals to 50 percent.

Similar to the previous section, we use the payoff matrix given in equation (4.2) for these conditional games. For simplicity, first we consider a game between a conditional cooperative strategy and an unconditional defector. In other words, no matter what the opponents strategy is, defectors always defect, and probability of cooperation for conditional cooperative strategy, while interacting with a cooperator, is one and is q, while interacting with a defector. Later, we discuss fully stochastic game. We can summarize the players' strategies (one semi-conditional and the other pure strategy) in the following "strategy matrix":

$$Z = \begin{array}{c} C & D \\ C & \begin{pmatrix} 1 & q \\ 0 & 0 \end{pmatrix}$$
(4.28)

The elements of this matrix represent the probability of cooperation in any type of interaction. According to this strategy matrix, we can calculate the probability of each type of interaction. By using the elements of strategy matrix, we can calculate the probability of any type of interaction in a population in which the concentration of conditional cooperative strategy is p_i . We can summarize these probabilities is a new matrix, called "Game Matrix" as:

$$G = \begin{array}{c} C & D \\ C & p_i^2 & p_i (1 - p_i) q \\ D & p_i (1 - p_i) q & (1 - p_i)^2 + 2p_i (1 - p_i) (1 - q) \end{array} \right)$$
(4.29)

Considering these probabilities of interactions, for a given population, we can treat fitness of each strategy and each of these interactions as a random variable and calculate the probability and values of each random variable during rounds of conditional game. Table (4.2) summarizes the probabilities and values of these random variables in these conditional games.

As we know, the conditions that favor cooperation in two players game are:

$$cov (g, w) > 0$$

$$(S - P) + (T - P) \frac{cov (g', z)}{cov (g, z)} + (R - S - T + P) \frac{cov (g', zz')}{cov (g, z)} \ge 0$$
(4.30)

G_i	Probability	g	g'	z	z'	P_z	$P_{z'}$
CC	p_i^2	1	1	1	1	R	R
DD	$(1-p_i)^2$	0	0	0	0	Р	Р
CD	$p_i \left(1 - p_i\right) q$	1	0	1	0	S	T
DD	$p_i \left(1 - p_i\right) \left(1 - q\right)$	1	0	0	0	Р	Р
DC	$(1-p_i)p_iq$	0	1	0	1	T	S
DD	$(1-p_i)p_i(1-q)$	0	1	0	0	P	P

Table 4.2: List of random variables in the conditional iterated game.

These necessity conditions are equivalent. The second condition just has the inclusive fitness formulation of the first condition. The equivalency of these conditions is given in appendix C.

For this conditional game, the fitness of each strategy (conditional cooperative strategy and pure defection) can be written as:

$$\bar{w}_{C} = p_{i} \left[p_{i}R + q \left(1 - p_{i} \right) S + \left(1 - q \right) \left(1 - p_{i} \right) P \right]$$

$$\bar{w}_{D} = \left(1 - p_{i} \right) \left[p_{i}qT + \left(p_{i} \left(1 - q \right) + \left(1 - p_{i} \right) \right) P \right]$$
(4.31)

By plugging table (4.2) into the necessity conditions (4.30), we have:

$$cov(g, w) = p_i \left((-R + P + (S + T - 2P)q) p_i^2 \right) + p_i (R - P + (3P - 2S - T)q) p_i + (S - P)q = \underbrace{\frac{\geq 0}{p_i (1 - p_i)}}_{i} \left[(R - P - (S + T - 2P)q) p_i + (S - P)q \right]$$

Therefore, the necessity condition that favors conditional cooperative strategy is:

$$(R - P - (S + T - 2P)q)p_i + (S - P)q > 0$$
(4.32)



Figure 4.2: Isocline and domain of attraction for conditional cooperation and defection strategies in IPD.

4.3.1 Conditional cooperation in iterated prisoners dilemma

By plugging the payoff matrix of IPD into the necessity condition (4.32), conditional cooperative strategy is a stable fixed point if and only if:

$$(2 - 3q) p_i > q \tag{4.33}$$

or:

$$q < \frac{2p_i}{1+3p_i} \tag{4.34}$$

Figure (4.2) shows the region in which the conditional cooperative strategy is stable. According to this figure, it is obvious that if $q \in [0.5, 1]$, defection is evolutionary stable strategy, and it resists against any introduced concentration of conditional cooperative strategy with q > 0.5. However, if we let conditional cooperative strategies have lower assortment values, defection cannot be evolutionary stable strategy anymore since in this game, a very low concentration of conditional cooperative strategy with a low assortment term is enough to invade a population of pure defectors. In fact, if mutation introduces a conditional cooperative strategy with assortment q = 0, this strategy will conquer any population of defectors. This strategy is the evolutionary stable strategy of this game. If assortment q is less than 0.5, both conditional cooperative strategy and pure defection strategy are resistant to invasion of the opposite strategy, introduced by mutation (very low concentration); thus, in this case IPD between conditional cooperative strategy and pure defection is similar to coordination game in which the winner of the game will be the one with higher initial concentration. In such conditions, the domain of attraction between these strategies is a function of assortment. The lower the assortment term is, the bigger the domain of attraction of conditional cooperative strategy would be.

4.4 Evolution of cooperation in conditional games: stability analysis

Here, we apply replicator equation as an equivalent approach to selectability analysis to check the stability of possible equilibrium points in these conditional games. Using this approach gives us better understanding of assortment's effects on the game dynamic and the stability of fixed points. Considering the conditional cooperative strategy and pure defection strategy, we can write the conditional payoff matrix as:

$$E = \begin{pmatrix} C & D \\ R & qS + (1-q)P \\ D \begin{pmatrix} qT + (1-q)P & P \end{pmatrix} \end{pmatrix}$$
(4.35)

By doing simple matrix operation, we can convert the payoff matrix (4.35) to an anti-diagonal matrix as:

$$E = \begin{array}{cc} C & D \\ C & (S-P)q \\ D \\ (P-R) + (T-P)q & 0 \end{array} \right)$$
(4.36)

Therefore, the replicator equation for this game would be:

$$\dot{p}_{i} = p_{i} \left(1 - p_{i}\right) \left[\left[\left(R - P\right) + q \left(-S + 2P - T\right) \right] p_{i} + q \left(S - P\right) \right]$$
(4.37)

which is identical to the covariance between genotype and fitness (or the selection force in the "Price equation"). By taking the derivative of this equation respect to the concentration of conditional cooperative strategy in the population, we have:

$$\frac{d\dot{p}_{i}}{dp_{i}} = (1-p_{i}) \left[\left[(R-P) + q(-S+2P-T) \right] p_{i} + q(S-P) \right]
- p_{i} \left[\left[(R-P) + q(-S+2P-T) \right] p_{i} + q(S-P) \right]
+ \left[(R-P) + q(-S+2P-T) \right] p_{i} (1-p_{i})$$
(4.38)

Defection $(p_i = 0)$ is evolutionary stable strategy if and only of:

$$(S-P)q < 0$$

Conditional cooperative strategy $(p_i = 1)$ is evolutionary stable if and only if:

$$(T-P)q < (R-P)$$

Mixed strategy $p_i = \frac{(q(S-P))}{(P-R) + (S-2P+T)q}$ is stable fixed point if and only if:

$$\frac{q\,(S-P)\,((P-R)+(T-P)\,q)}{(P-R)+(S-2P+T)\,q} > 0$$

4.4.1 Stability of conditional cooperative strategy in IPD

Considering the conditional and pure strategies of cooperator and defector, for this game the replicator equation (4.37) would be:

$$\dot{p}_i = p_i \left(1 - p_i\right) \left((2 - 3q) \, p_i - q\right) \tag{4.39}$$

In this game, we can have two to three equilibrium points. Figure (4.3) shows the phase diagram of this game for different q. According to this figure, both conditional cooperator and pure defector can be evolutionary stable. Defector is evolutionary stable strategy if only if $q \ge 0.5$. Conditional cooperative strategy can be a stable fixed point, if and only if q < 0.5. In this game, mixed strategy cannot be evolutionary stable. For small assortment terms (q < 0.5), the only evolutionary stable strategy is conditional cooperative strategy with assortment q = 0.



Figure 4.3: Phase diagram of replicator equation for conditional iterated prisoner dilemma. blue: q = 0 or complete conditional game, red: q = 0.2, green: q = 0.4, light blue: q = 0.6, yellow: q = 0.8, and black: q = 1.0 or unconditional game.

4.5 Communication and information exchange in con-

ditional games

In this section, we try to quantify the amount of information that conditional cooperator gains about the opponent's type during the game. Moreover, by adding noise into the communication channel, we try to analyze the effect of communication noise on fate of the game. Finally, we consider conditional strategy for both cooperation and defection. Conditional defective strategies on average have lower payoffs in comparison to the pure defector strategy in one interaction; however, this lower payoff pays back when they gain more payoff in long run by confusing vigilant/conditional cooperators. Our hypothesis is that in such cases both strategies can co-exist.

4.5.1 Communication between conditional cooperator and pure defector in noiseless environment

Here, we have two random variables: action of conditional cooperator and opponent's type. The strategy matrix of conditional cooperator and pure defector can be written as:

$$S_{C} = \begin{array}{ccc} C & D & C & D \\ C & p_{C|C} & p_{C|D} \\ p_{D|C} & p_{D|D} \end{array} = \begin{array}{ccc} C & 1 & q \\ D & 0 & 1-q \end{array}$$
(4.40)

where $p_{C|C}$ is probability of cooperation for a conditional cooperator when it interacts with another conditional cooperator, $p_{C|D}$ is probability of cooperation for a conditional cooperator when it interacts with a pure defector, where $p_{D|C}$ is probability of defection for a conditional cooperator when it interacts with another conditional cooperator, and $p_{D|D}$ is probability of defection for a conditional cooperator when it interacts with a pure defector.

$$S_{D} = \begin{array}{ccc} C & D & C & D \\ \\ C \begin{pmatrix} p_{C|C} & p_{C|D} \\ p_{D|C} & p_{D|D} \end{pmatrix} &= \begin{array}{ccc} C \begin{pmatrix} 0 & 0 \\ 1 & 1 \end{pmatrix}$$
(4.41)

where $p_{C|C}$ is probability of cooperation for a pure defector when it interacts with a conditional cooperator, $p_{C|D}$ is probability of cooperation for a pure defector when it interacts with another pure defector, where $p_{D|C}$ is probability of defection for a pure defector when it interacts with a conditional cooperator, and $p_{D|D}$ is probability of defection for a pure defector when it interacts with another pure defector. Based on these strategy matrixes, the action probabilities of conditional cooperator is:

$$P_{C}^{C} = p_{i} + q (1 - p_{i})$$

$$P_{C}^{D} = (1 - q) (1 - p_{i})$$
(4.42)

Consequently, by using equation (4.42) the entropy of conditional cooperator's action is:

$$H(A_{C}) = -\left(p_{i} + q(1 - p_{i})\right) \log\left(p_{i} + q(1 - p_{i})\right) - (1 - q)(1 - p_{i}) \log\left((1 - q)(1 - p_{i})\right)$$

Similarly, the conditional entropy of action given opponent's type is:

$$H(A_C|O) = \sum_{j \in \{C,D\}} p_j H(A_C|O=j)$$

= $-(1-p_i) \left(q \log q + (1-q) \log (1-q)\right)$ (4.43)

Therefore, the mutual information between action of conditional cooperator and type of opponent is:

$$I(A_C; O) = H(A_C) - H(A_C|O)$$

= $-(p_i + q(1 - p_i)) \log(p_i + q(1 - p_i))$
 $-(1 - q)(1 - p_i) \log((1 - q)(1 - p_i))$
 $+(1 - p_i)(q \log q + (1 - q) \log(1 - q))$



Figure 4.4: Effect of assortment on mutual information between action of conditional cooperator and opponent type. X-axis is assortment term (q), Y-axis is the concentration of conditional cooperation in population, and Z-axis is mutual information between action of conditional cooperator and opponent type.

Figure (4.4) shows this mutual information for different q and concentration of conditional cooperator.

4.5.2 Communication between conditional cooperator and pure defector in noisy environment

To model the effect of environmental noise on the action of conditional cooperator, we define the following error matrix:

$$\Xi = \begin{array}{cc} C & D \\ \Xi = \begin{array}{c} C \begin{pmatrix} 1 - \epsilon & \epsilon \\ \\ D \begin{pmatrix} \epsilon & 1 - \epsilon \end{pmatrix} \end{array}$$
(4.44)

Error matrix Ξ shows how conditional cooperator estimates the frequency of each type during the game. By applying this error matrix to the actual concentration of players, the estimated concentrations by conditional cooperator would be:

$$\begin{pmatrix} \hat{\rho_C} \\ \hat{\rho_D} \end{pmatrix} = \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon & 1 - \epsilon \end{pmatrix} \begin{pmatrix} \rho_C \\ 1 - \rho_C \end{pmatrix}$$

$$= \begin{pmatrix} \epsilon + \rho_C - 2\epsilon\rho_C \\ 1 - \epsilon - \rho_C + 2\epsilon\rho_C \end{pmatrix}$$

$$(4.45)$$

By plugging estimated concentrations (4.45) into equation (4.4), we can calculate the mutual information between action of conditional cooperator and opponent's type in noisy environments. Figure (4.5) shows this mutual information for different q and concentration of conditional cooperator in environments with different levels of noise.

4.5.3 Communication between vigilant cooperator and defector in conditional games

In this section, we want to quantify the mutual information between action and type of opponents, if both types are vigilant. The strategy matrix of conditional/vigilant cooperator and defector can be written as:

$$S_{C} = \begin{pmatrix} C & D & C & D \\ p_{C|C} & p_{C|D} \\ p_{D|C} & p_{D|D} \end{pmatrix} = \begin{pmatrix} C & 1 & q_{C} \\ 0 & 1 - q_{C} \end{pmatrix}$$
(4.46)



Figure 4.5: Effect of assortment and environmental noise on mutual information between action of conditional cooperator and opponent type. X-axis is assortment term (q), Y-axis is the concentration of conditional cooperation in population, and Z-axis is mutual information between action of conditional cooperator and opponent type: (a) one percent noise, (b) two percent noise, (c) five percent noise, (d) ten percent noise, (e) twenty five percent noise, and (f) fifty percent noise.

$$S_{D} = \begin{array}{ccc} C & D & C & D \\ C \begin{pmatrix} p_{C|C} & p_{C|D} \\ p_{D|C} & p_{D|D} \end{pmatrix} &= \begin{array}{ccc} C \begin{pmatrix} q_{D} & 0 \\ 1 - q_{D} & 1 \end{pmatrix}$$
(4.47)

Based on these strategy matrices, the action probabilities of conditional cooperator and defector are:

$$P_{C}^{C} = p_{i} + q_{C} (1 - p_{i})$$

$$P_{C}^{D} = (1 - q_{C}) (1 - p_{i})$$
(4.48)

$$P_D^C = p_i q_D$$

$$P_D^D = 1 - p_i q_D$$
(4.49)

Consequently, by using equations (4.48) and (4.49), we can calculate the entropy of players' actions as:

$$H(A_C) = -\left(p_i + q_C(1 - p_i)\right) \log\left(p_i + q_C(1 - p_i)\right) - (1 - q_C)(1 - p_i) \log\left((1 - q_C)(1 - p_i)\right)$$

$$H(A_D) = -p_i q_D \log\left(p_i q_D\right) - p_i (1 - q_D) \log\left(p_i \left(1 - q_D\right)\right)$$
(4.50)

Similarly, the conditional entropy of action given type of opponents for each player is:

$$H(A_{C}|O) = \sum_{j \in \{C,D\}} p_{j}H(A_{C}|O=j)$$

= $-(1-p_{i})\left(q_{C}\log q_{C} + (1-q_{C})\log(1-q_{C})\right)$ (4.51)

$$H\left(A_D|O\right) = \sum_{j \in \{C,D\}} p_j H\left(A_D|O=j\right)$$
$$= -p_i \left(q_D \log q_D + (1-q_D) \log (1-q_D)\right)$$
(4.52)

Therefore, the mutual information between action of vigilant players and type of opponent is:

$$I(A_{C}; O) = H(A_{C}) - H(A_{C}|O)$$

= $-(p_{i} + q_{C}(1 - p_{i})) \log(p_{i} + q_{C}(1 - p_{i}))$
 $-(1 - q_{C})(1 - p_{i}) \log((1 - q_{C})(1 - p_{i}))$
 $+(1 - p_{i})(q_{C} \log q_{C} + (1 - q_{C}) \log(1 - q_{C}))$

$$I(A_D; O) = H(A_D) - H\left(A_D \middle| O\right)$$

= $-p_i q_D \log\left(p_i q_D\right) - p_i (1 - q_D) \log\left(p_i \left(1 - q_D\right)\right)$
+ $p_i \left(q_D \log q_D + (1 - q_D) \log(1 - q_D)\right)$

Figure (4.6) shows this mutual information for different q and concentration of conditional cooperator. Similar to previous section, we can apply the error matrix Ξ to estimate the concentration of players, and by plugging these estimated values into equations (4.53) and (4.53) we can calculate the mutual information between action of vigilant players and type of opponent.

4.6 Chapter Summary

In this chapter, first evolutionary game theory was applied to two players games for investigating the conditions in which cooperation emerges among selfish individuals. To study the evolution of cooperation in unconditional games, we applied the Queller's inclusive fitness theory which uses the "Price equation". Moreover, the population dynamics of these games were modeled by replicator equation, and the results confirmed the inclusive fitness theory. Secondly, by introducing conditional cooperative strategy, we investigated the emergence of cooperation over the conditional games. We extended the inclusive fitness theory to conditional games and derived the necessity conditions for maintaining cooperation in such conditional games. Then, we investigated the stability of the possible evolutionary stable strategies by using replicator equation. Interestingly, our observations show emergence of cooperation in situations in which is not possible to have cooperation if the players play unconditionally. Finally, we quantified the communication rate and information exchange between individuals during these conditional games by calculating the mutual information between actions of vigilant players and type of opponents. We also analyzed how assortment and environmental noise affect this communication.



Figure 4.6: Effect of assortment on mutual information between action of vigilant players and opponent type. X-axis is assortment term (q), Y-axis is the concentration of conditional cooperation in population, and Z-axis is mutual information between action of conditional cooperator and opponent type: (a) mutual information between action of vigilant cooperator and opponent type (b) mutual information between action of vigilant defector and opponent type

Chapter 5

Evolution of Super-reciprocity in Iterated Trust Dilemma (ITD)

It will have blood; they say, blood will have blood.

-Shakespeare, Macbeth

Oliver: I remember you! Grocer: And I remember you too. Now get out of my store and stay out! Oliver: Oh, don't be like that. Let bygones be bygones. Let's help each other. You have a business, and we have a business. We'll send people to your store, and you send people to our store. What do you say? Grocer: You mind your business and I'll mind my business. Now get out before I throw you out!

Tit for Tat, C. Rogers, 1935

So far, we discussed well-established theories that explain how evolution, which favors short-term benefits, can maintain cooperation for long-term benefits. In this chapter, we explicitly discuss the role of communication in establishing trust and confidence over "blind" faith. We also try to quantify the minimum amount of information that is necessary to exchange between players for building the trust. Trust is based largely on proof, evidence, or real facts and is the basic principle of knowledge-based judgment. On the other hand, faith is "the matter of hope". It is a belief that does not require proof, evidence, or tangible facts. Here, we show that how players build trust and bring commitment during the iterated game by communication and experiencing the game.

In the classical Iterated Prisoners Dilemma (IPD), direct reciprocity as a conditional strategy on the opponents action is a form of communication leading to altruistic behavior. However, if players use stochastic strategies, a secondary form of cooperation in which players alternate in receiving the Temptation (T) and Sucker (S) rewards can emerge (superreciprocity). This reciprocal behavior will become evolutionary dominant if the reward (T) is increased above a certain threshold, but is inherently more risky than primary cooperation since it relies on trust between players in two consecutive iterations of the game. Here, we investigate how different environmental conditions such as mutation rate, environmental noise, and reward T affect the evolution of reciprocity. Super-reciprocal strategies rely on the synchronization of two genes and are thus much more sensitive to environmental changes that affect the accuracy of players prediction of opponents' future moves. We find that increasing the environmental noise or mutation rate is deleterious to super-reciprocity, while increasing T stabilizes its evolution. Conversely, in environments that are highly predictable and where there is no payoff advantage to engage in reciprocal cooperation, basic cooperation via reciprocal communication remains the strategy of choice.

5.1 Iterated Trust Dilemma

In standard iterated prisoners dilemma of equation (4.2), if $R < \frac{S+T}{2}$, IPD gets replaced by a new game previously referred to as the Iterated Lift Dilemma (ILD) [150, 151]. Here, we call this game as "Iterated Trust Dilemma (ITD)", since to maintain the dominant strategy there should be trust and commitment between players. Players in this game have stochastic strategies. Players choose their next move based on the game played in the previous round (Cooperation vs. Cooperation (CC), Cooperation vs. Defection (CD), Defection vs. Cooperation (DC), and Defection vs. Defection (DD)) and the probability that is saved in their genome as part of their strategy. If two players interact for the first time, their cooperation probability depends on another gene (P_C) in their genome. This gene indicates with what probability they cooperate for the first time they meet an opponent. Thus, each strategy contains five genes:

$$(P_C, P_1, P_2, P_3, P_4) \tag{5.1}$$

where P_C is the probability of cooperation for the first interaction, P_1 is the probability of cooperation if in the previous interaction both players cooperated, P_2 is the probability of cooperation if in the previous interaction I cooperated and my opponent defected, P_3 is the probability of cooperation if in the previous interaction I defected and cheated on my opponent while my opponent cooperated, and P_4 is the probability of cooperation if in the previous interaction both players defected and cheated on each other. For example, if the genome or the strategy of one player is:

(0.2, 0.6, 0.05, 0.75, 0.35)

the chance of cooperation for this player in the first interaction is 20 percent. Moreover, this player will cooperate with the probabilities 0.6, 0.05, 0.75, and 0.35 in the next round of game, if the game between its opponent in the current round is cooperationcooperation, cooperation-defection, defection-cooperation, and defection-defection respectively. It is worth mentioning that the strategy of players is fixed during their lifetime. For instance, if P_1 gene of a player is 0.4, the chance of cooperation for this player is always 40 percent, if in the previous this player and its opponent both played cooperatively. In ITD, unlike IPD, players by switching from defection to cooperation and exchanging T rewards with S rewards maximize their mean fitness. This strategy, called secondary cooperation, is a super-reciprocal strategy and has a periodic pattern in which after a player receives the T reward by cheating on its opponent, it will receive an S reward in the next round by cooperating and being cheated from the opponent. To engage in secondary cooperation, players should have a strategy as:

$$(P_C, x, 0.0, 1.0, y)$$

, where x and y can be any arbitrary continues value in [0, 1]. In the next section, we mathematically prove that such strategy is optimal and the player of this type of strategy will have the maximum mean fitness, if $R < \frac{S+T}{2}$. Now, the question if this strategy is evolvable in an evolutionary game or not, and how do random processes such as mutation or environmental noise affect the evolution of secondary cooperation? It is obvious that the secondary cooperation is inherently more risky than the primary cooperation since it relies on trust between players in two consecutive iterations of the game (compared to the primary cooperation which has to deal with a single move). Moreover, primary cooperation suffers less by withdrawing from the reciprocation of cooperative moves in comparison to this secondary cooperation.

Initial research on this game was limited to the simple recognition of secondary cooperation as an alternative to primary cooperation or defection strategies [4] and how error correction can lead to short phases of secondary cooperation within cooperative IPD regimes [152]. Delahaye et al. for the first time investigated the properties of secondary cooperation both within the classical IPD payoff scheme (R = 3, S = 0, T = 5 and P = 1), by introducing a secondary cooperating capable strategy called "Reason", as well as within the ITD payoff

scheme (R = 3, S = 0, T > 6, and P = 1) [151]. The strategies used in this study had a memory depth equal to one with a random first move and deterministic moves there after. Delahaye et al. limited their strategies to up to three strategies at a time and they used well-mixed population in their analysis [151].

Here, we take a different approach to Delahay et al. and evolve strategies capable of playing secondary cooperation to investigate the conditions that make secondary cooperation a stable evolutionary attractor in addition to primary cooperation and defection. We hypothesize that the stability of secondary cooperation depends both on the player's ability to predict future moves as well as the payoff advantage that secondary cooperation have over other strategies. We also investigate the effect of temptation reward, environmental noise, and mutation rate on strategy dominance within an evolving population to determine the parameter settings that trigger transitions between strategies. Finally we investigate the rate of communicated information between players in two consecutive round of games to find in what information rate, controlled by environmental noise, the secondary and primary cooperation collapse to defection.

5.2 Secondary cooperation as the optimal strategy in ITD

Before we discuss the experiments and our agent based modeling, here I discuss the optimality of secondary cooperation in ITD. To do so, I assume a homogenous population of agents, and I find the optimal strategy for a given game.

5.2.1 Optimal strategy among a group of players that completely engage in secondary cooperation play

To completely engage in secondary cooperation, players should have the following genome:

$$(P_C, P_1, 0.0, 1.0, P_4) \tag{5.2}$$

Thus a group of secondary cooperators should have a gene pool consists of genes as (5.2). Here, the objective is to use optimization technique to find the optimal values for P_C , P_1 , and P_4 genes that maximize fitness of the secondary cooperators. To do so, assume genes of super cooperators be (q, x, 0, 1, y). Gene q, as we know, is the probability of cooperation in the first move. Considering this genome, the probability of each type of game (CC, CD, DC, DD) in the first interaction is:

$$\pi_1(0) = \pi_{CC}(0) = q^2,$$

$$\pi_2(0) = \pi_{CD}(0) = q(1-q),$$

$$\pi_3(0) = \pi_{DC}(0) = q(1-q),$$

$$\pi_4(0) = \pi_{DD}(0) = (1-q)^2$$
(5.3)

As we know, the payoff matrix for this game is:

$$E = \begin{array}{c} C & D \\ C & R & S \\ D & T & P \end{array}$$
(5.4)

Therefore, the mean fitness after the first interaction over the population is:

$$\bar{w}(0) = Rq^2 + (S+T)q(1-q) + P(1-q)^2$$
(5.5)

By taking the derivative of $\bar{w}(0)$ respect to q, we can find the optimal value for the probability of cooperation in the first interaction. Using this idea, the optimal value for this probability is:

$$P_C = \frac{S + T + 2P}{2(S + T - R - P)}$$
(5.6)

Since this term appears once in the mean fitness of players after rounds of iterated games, it does not affect the mean fitness of players; thus, as we see later, over the course of evolution this term vanishes, and mostly players prefer to defect during the first interaction. Now, let's assume the frequency of each type of interaction is known after "t" rounds of games. We can recursively calculate the frequency of each type of interaction for the next round as:

$$\pi_{1}(t+1) = x^{2}\pi_{1}(t) + y^{2}\pi_{4}(t)$$

$$\pi_{2}(t+1) = \pi_{2}(t) + x(1-x)\pi_{1}(t) + y(1-y)\pi_{4}(t)$$

$$\pi_{3}(t+1) = \pi_{3}(t) + x(1-x)\pi_{1}(t) + y(1-y)\pi_{4}(t)$$

$$\pi_{4}(t+1) = (1-x)^{2}\pi_{1}(t) + (1-y)^{2}\pi_{4}(t)$$
(5.7)

By looking at equation (5.7), we see that the frequency of CD and DC games increase over generations, and these games act as attractors in game space since over generations these games are seen more often; therefore, no matter what the values of x and y are, eventually we just see CD and DC games in the population, and the mean fitness of the population converges to:

$$\lim_{t \to +\infty} \bar{w}(t) = \frac{S+T}{2} \tag{5.8}$$

In fact, x and y just determine the speed of getting to the attractor of this game. The only cases that make CC and DD games stable are the extreme values for x and y (0 and 1). If both of these genes are zero, we have oscillations from CC to DD games.

5.2.2 Optimal strategy among a homogenous group of players in both IPD and ITD regimes

Now, let's assume that the population is homogeneously filled with players with (q, x, v, z, y)gene, where the probability of cooperation in the first move is q. This scenario is quite different of our agent based modeling in which population is heterogeneous and different strategies are competing with each other to conquer the population. The optimal probability of first interaction is identical to what we had in the previous case (equation (5.6)). Similar to the previous case, given the frequency of each type of interaction after "t" rounds of game, we can recursively calculate the frequency of each type of interaction for the next round as:

$$\pi_{1}(t+1) = x^{2}\pi_{1}(t) + vz\pi_{2}(t) + vz\pi_{3}(t) + y^{2}\pi_{4}(t)$$

$$\pi_{2}(t+1) = x(1-x)\pi_{1}(t) + v(1-z)\pi_{2}(t) + z(1-v)\pi_{3}(t) + y(1-y)\pi_{4}(t)$$

$$\pi_{3}(t+1) = x(1-x)\pi_{1}(t) + z(1-v)\pi_{2}(t) + v(1-z)\pi_{3}(t) + y(1-y)\pi_{4}(t)$$

$$\pi_{4}(t+1) = (1-x)^{2}\pi_{1}(t) + (1-v)(1-z)\pi_{2}(t) + (1-v)(1-z)\pi_{3}(t) + (1-y)^{2}\pi_{4}(t)$$
(5.9)

This dynamic can be modeled as a Markow process with the following transition matrix:

$$M = \begin{pmatrix} x^2 & vz & vz & y^2 \\ x(1-x) & v(1-z) & z(1-v) & y(1-y) \\ x(1-x) & z(1-v) & v(1-z) & y(1-y) \\ (1-x)^2 & (1-v)(1-z) & (1-v)(1-z) & (1-y)^2 \end{pmatrix}$$
(5.10)

The stable state of this Markov process is the right eigenvector of transition matrix that corresponds to eigenvalue $\lambda = 1$, which would be:

$$\boldsymbol{V_{1}} = \begin{pmatrix} \frac{y(y(1-v-z)+2vz)}{(1-x)(1+x-v-vx-z(x-2v+1))} \\ \frac{y(1+y-x)}{1+x-v-vx-z(x-2v+1)} \\ \frac{y(1+y-x)}{1+x-v-vx-z(x-2v+1)} \\ 1 \end{pmatrix}$$
(5.11)

Since this eigenvector shows the distribution of actions after infinite number of iterated games, it should sum up to one; therefore, to have the proper eigenvector we need to normalize this vector:

$$\boldsymbol{X}(\infty) = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \\ v_4 \end{pmatrix} = \begin{pmatrix} \frac{y(y(1-v-z)+2vz)}{1-v+2y-z+2vz+vx^2-vy^2+2xy^2-2x^2y+x^2z-y^2-z^2-y^2-2vxz+2vzy} \\ \frac{y(1-x)(1+y-x)}{1-v+2y-z+2vz+vx^2-vy^2+2xy^2-2x^2y+x^2z-y^2z-x^2-y^2-2vxz+2vzy} \\ \frac{y(1-x)(1+y-x)}{1-v+2y-z+2vz+vx^2-vy^2+2xy^2-2x^2y+x^2z-y^2-x^2-y^2-2vxz+2vzy} \\ \frac{(1-x)(1+x-v-z-vx-xz+2vz)}{1-v+2y-z+2vz+vx^2-vy^2+2xy^2-2x^2y+x^2z-y^2z-x^2-y^2-2vxz+2vzy} \end{pmatrix} 5.12$$

The mean fitness of the population after infinite number of iterated games is:

$$\bar{w}(\infty) = Rv_1 + Sv_2 + Tv_3 + Pv_4 \tag{5.13}$$

To find the optimal value of genome that gives the maximum mean fitness, we should have:

$$\frac{\partial \bar{w}}{\partial x} = \frac{\partial \bar{w}}{\partial v} = \frac{\partial \bar{w}}{\partial z} = \frac{\partial \bar{w}}{\partial y} = 0$$

$$0 \le x \le 1, \quad 0 \le v \le 1, \quad 0 \le z \le 1, \quad 0 \le y \le 1$$
(5.14)

which gives us:

$$\begin{split} \left[1 + (v + z - 2y - 1)x^{2} + (2x - v - z - 1)y^{2} + 2(1 - x + y)vz + 2y - v - z\right], \\ \left[y(2x - y - 2)(S + T) + 2((v + z - 1)x + vz)P\right] \\ -2(vx + y^{2} - 2xy + xz - x - vz)\left[y(y(1 - v - z) + 2vz)R + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \left[1 + (v + z - 2y - 1)x^{2} + (2x - v - z - 1)y^{2} + 2(1 - x + y)vz + 2y - v - z\right], \\ \left[(1 + 2vz - vy - zy)R + (1 - x)(1 + 2y - x)(S + T)\right] \\ -2(1 - vy + 2xy - x^{2} - yz - y + vz)\left[y(y(1 - v - z) + 2vz)R + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \left[1 + (v + z - 2y - 1)x^{2} + (2x - v - z - 1)y^{2} + 2(1 - x + y)vz + 2y - v - z\right], \\ \left[y(2z - y)R + (1 - x)(2z - x - 1)P\right] \\ + (1 - 2z - x^{2} + y^{2} + 2xz - 2yz)\left[y(y(1 - v - z) + 2vz)R + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \left[1 + (v + z - 2y - 1)x^{2} + (2x - v - z - 1)y^{2} + 2(1 - x + y)vz + 2y - v - z\right], \\ \left[y(2v - y)R + (1 - x)(2v - x - 1)P\right] \\ + (1 - 2v - x^{2} + y^{2} + 2vx - 2vy)\left[y(y(1 - v - z) + 2vz)R + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \\ \left[1 + (v + z - 2y - 1)x^{2} + (2x - v - z - 1)y^{2} + 2(1 - x + y)vz + 2y - v - z\right], \\ \left[y(2v - y)R + (1 - x)(2v - x - 1)P\right] \\ + (1 - 2v - x^{2} + y^{2} + 2vx - 2vy)\left[y(y(1 - v - z) + 2vz)R + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \\ + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \\ + y(1 - x)(1 + y - x)(S + T) + (1 - x)(1 + x - v - z - vx - xz + 2vz)P = 0 \\ \end{array} \right]$$

Since finding a closed form analytical solution for this nonlinear optimization problem with constraints (5.14) is exhaustive, we used computational methods to find the optimal solution for a given payoff matrix. To do so, we applied **fmincon(.)** package in **MatLab** software to this nonlinear optimization problem. Table (5.1) shows the results for different payoff

matrices.

Temptation reward (T)	P_1	P_2	P_3	P_4
2	1.0 ± 0.0	0.79 ± 0.1	0.79 ± 0.08	0.65 ± 0.12
4	1.0 ± 0.0	0.88 ± 0.04	0.88 ± 0.04	0.90 ± 0.03
5	0.88 ± 0.09	0.82 ± 0.07	0.72 ± 0.13	0.93 ± 0.01
6	0.70 ± 0.16	0.64 ± 0.16	0.72 ± 0.17	0.96 ± 0.001
7	0.60 ± 0.23	0.22 ± 0.08	0.99 ± 0.0	0.38 ± 0.23
8	0.5 ± 0.25	0.06 ± 0.02	1.0 ± 0.0	0.5 ± 0.25
9	0.56 ± 0.25	0.02 ± 0.006	1.0 ± 0.0	0.44 ± 0.25
10	0.46 ± 0.25	0.02 ± 0.016	1.0 ± 0.0	0.54 ± 0.25
11	0.54 ± 0.25	0.01 ± 0.006	1.0 ± 0.0	0.46 ± 0.25
12	0.48 ± 0.25	0.01 ± 0.004	1.0 ± 0.0	0.52 ± 0.25
13	0.54 ± 0.25	0.02 ± 0.01	1.0 ± 0.0	0.46 ± 0.25
14	0.48 ± 0.25	0.005 ± 0.0	1.0 ± 0.0	0.52 ± 0.25
15	0.52 ± 0.25	0.0 ± 0.0	1.0 ± 0.0	0.48 ± 0.25

Table 5.1: Optimal genome of a general player in iterated trust game. Each row contains the mean and variance of optimal values over twenty runs.

According to table (5.1), it is obvious that the optimal strategies are:

$$P_1 = (0.0, 1.0, 0.0, 1.0)$$
, master slave strategy
 $P_2 = (0.0, 0.0, 1.0, 1.0)$, super cooperation strategy (5.16)

Since population is homogenous, there is no competition between any types; thus, master slave and super cooperation both yield to maximum mean fitness, and they are both optimal strategies; however, if population is not homogenous, master slave strategy would be very poor strategy, and it will be extinct over generations.

5.3 Quantifying communication and information exchange by calculating mutual information between random variables in consecutive iterations of ITD game

Here, we want to quantify the communication rate and the amount of exchanged information between players over the consecutive interactions in rounds of ITD. In our simulations, we let a strategy plays against itself, the evolved strategy in noiseless environment, and a random strategy; however, here all the derivations are written for general strategies.

After deriving the probability distributions of each type of interaction and plays of players (cooperation (C) or defection (D)), we can calculate the mutual information between these random variables at consecutive rounds of game. This mutual information is our measure to quantify the exchanged information between players during iterated games. Moreover, by adding noise to the communication channel, we quantify the effect of noise on exchanged information and consequently on the evolution of cooperation, hoping to find the break points of the cooperative strategies in IPD and ITD regimes. Since the probability of cooperation over the first interaction does not play an important role on average fitness of players, we ignore this gene for the entire analysis of this section. Thus, the strategies of players has four genes as:

$$\widetilde{S}_{S} = \left(P_{1}^{S}, P_{2}^{S}, P_{3}^{S}, P_{4}^{S}\right)$$
$$\widetilde{S}_{O} = \left(P_{1}^{O}, P_{2}^{O}, P_{3}^{O}, P_{4}^{O}\right)$$
(5.17)

In equation (5.17), the opponent's strategy is written according to opponent's viewpoint. Since we write everything in central player's viewpoint, we have to modify opponent's strategy as:

$$\widetilde{S}_{O}^{*} = (P_{1}^{O}, P_{3}^{O}, P_{2}^{O}, P_{4}^{O})$$
(5.18)

We can define the following random variables:

$$A_{S}(t) \in \{C, D\}$$

$$A_{O}(t) \in \{C, D\}$$

$$G(t) \in \{CC, CD, DC, DD\} = \{g_{1}, g_{2}, g_{3}, g_{4}\}$$
(5.19)

where A_S , A_O , and G stand for central players action, opponent's action, and game played respectively at time "t". The probability of each event is:

$$\widetilde{P_{S}^{A}} = \left[P_{C}^{S}(t), P_{D}^{S}(t)\right]'$$

$$\widetilde{P_{O}^{A}} = \left[P_{C}^{O}(t), P_{D}^{O}(t)\right]'$$

$$\widetilde{P_{G}^{t}} = [\pi_{1}(t), \pi_{2}(t), \pi_{1}(t), \pi_{4}(t)] = [\pi_{1}(t), \pi_{2}(t), \pi_{3}(t), \pi_{4}(t)]'$$
(5.20)

5.3.1 Mutual information between G(t) and other random variables at "t + 1"

Here we want to calculate the mutual information between game played at round "t" and all other random variables at "t + 1". In this situation, players know what game has been played at round "t" and based on this available information they want to choose their action. In other words, players remember their own and opponent's previous actions. This is the maximum information one player can have about the previous round of game and based on this available information it is easier for the player to decide what to do. We want to calculate the mutual information between G(t) and $A_S(t+1)$, $A_O(t+1)$, and G(t+1).

5.3.1.1 Mutual information between $G\left(t\right)$ and $A_{S}\left(t+1\right)$

First, we have to calculate the transition matrices. We have:

$$\mathbf{T_{GS}} = \begin{array}{cccc} CC & CD & DC & DD \\ C \begin{pmatrix} P_1^S & P_2^S & P_3^S & P_4^S \\ D \begin{pmatrix} 1 - P_1^S & 1 - P_2^S & 1 - P_3^S & 1 - P_4^S \end{pmatrix}$$
(5.21)

Therefore, we have:

$$H(A_{S}(t+1)) = - P_{C}^{S}(t+1)\log_{2}(P_{C}^{S}(t+1)) - P_{D}^{S}(t+1)\log_{2}(P_{D}^{S}(t+1))$$
(5.22)

where:

$$P_{C}^{S}(t+1) = P_{1}^{S}\pi_{1}(t) + P_{2}^{S}\pi_{2}(t) + P_{3}^{S}\pi_{4}(t) + P_{4}^{S}\pi_{4}(t)$$

$$= \widetilde{G}_{S}\widetilde{P}_{G}^{t}$$

$$P_{D}^{S}(t+1) = \left(1 - P_{1}^{S}\right)\pi_{1}(t) + \left(1 - P_{2}^{S}\right)\pi_{2}(t) + \left(1 - P_{3}^{S}\right)\pi_{3}(t) + \left(1 - P_{4}^{S}\right)\pi_{4}(t)$$

$$= \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}$$
(5.23)

Thus, we have:

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{P}_{G}^{t}\log_{2}\left(\widetilde{G}_{S}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{4}\mathbf{T}_{\mathbf{GS}}(i,j)\widetilde{P}_{G}^{t}(j)\log_{2}\left(\sum_{j=1}^{4}\mathbf{T}_{\mathbf{GS}}(i,j)\widetilde{P}_{G}^{t}(j)\right) \quad (5.24)$$

The conditional entropy between $G\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$H(A_{S}(t+1)|G(t)) = \sum_{i=1}^{4} \pi_{i} H(A_{S}(t+1)|G(t) = g_{i})$$

= $-\sum_{i=1}^{4} \sum_{j=1}^{2} \widetilde{P}_{G}^{t}(i) \mathbf{T}_{\mathbf{GS}}(j,i) \log_{2} \mathbf{T}_{\mathbf{GS}}(j,i)$ (5.25)

Therefore, the mutual information between $G\left(t\right)$ and $A_{S}\left(t+1\right)$ is:

$$I(A_{S}(t+1); G(t)) = H(A_{S}(t+1)) - H(A_{S}(t+1)|G(t))$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{T}_{\mathbf{GS}}(i, j) \widetilde{P}_{G}^{t}(j) \log_{2} \left(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{GS}}(i, j) \widetilde{P}_{G}^{t}(j)\right) + -\sum_{i=1}^{4} \sum_{j=1}^{2} \widetilde{P}_{G}^{t}(i) \mathbf{T}_{\mathbf{GS}}(j, i) \log_{2} \mathbf{T}_{\mathbf{GS}}(j, i)$$
(5.26)

5.3.1.2 Mutual information between G(t) and $A_O(t+1)$

To find the mutual information between G(t) and $A_O(t+1)$ we should follow the same idea. We have:

$$\mathbf{T_{GO}} = \begin{array}{cccc} CC & CD & DC & DD \\ C \begin{pmatrix} P_1^O & P_3^O & P_2^O & P_4^O \\ D \begin{pmatrix} 1 - P_1^O & 1 - P_3^O & 1 - P_2^O & 1 - P_4^O \end{pmatrix} \end{array}$$
(5.27)

Therefore, we have:

$$H(A_O(t+1)) = -\widetilde{G_O^*}\widetilde{P_G^t}\log_2\left(\widetilde{G_O^*}\widetilde{P_G^t}\right) - \left(1 - \widetilde{G_O^*}\right)\widetilde{P_G^t}\log_2\left(\left(1 - \widetilde{G_O^*}\right)\widetilde{P_G^t}\right)$$
$$= -\sum_{i=1}^2\sum_{j=1}^4 \mathbf{T_{GO}}(i,j)\widetilde{P_G^t}(j)\log_2\left(\sum_{j=1}^4 \mathbf{T_{GO}}(i,j)\widetilde{P_G^t}(j)\right) \quad (5.28)$$

The conditional entropy between G(t) and $A_O(t+1)$ similar to previous subsection is given by:

$$H(A_{O}(t+1)|G(t)) = \sum_{i=1}^{4} \pi_{i} H(A_{O}(t+1)|G(t) = g_{i})$$

= $-\sum_{i=1}^{4} \sum_{j=1}^{2} \widetilde{P_{G}^{t}}(i) \mathbf{T_{GO}}(j,i) \log_{2} \mathbf{T_{GO}}(j,i)$ (5.29)

Therefore, the mutual information between G(t) and $A_O(t+1)$ is:

$$I(A_{O}(t+1); G(t)) = H(A_{O}(t+1)) - H(A_{O}(t+1)|G(t))$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{T}_{\mathbf{GO}}(i, j) \widetilde{P}_{G}^{t}(j) \log_{2} \left(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{GO}}(i, j) \widetilde{P}_{G}^{t}(j)\right) + \sum_{i=1}^{4} \sum_{j=1}^{2} \widetilde{P}_{G}^{t}(i) \mathbf{T}_{\mathbf{GO}}(j, i) \log_{2} \mathbf{T}_{\mathbf{GO}}(j, i)$$
(5.30)

It is worth mentioning that here we derive the mutual information between round t and t + 1 based on self player's view point. In other words, $\pi_2(.)$ is the action that self player cooperates and opponent defects. To write the equations for opponent, we use the same random variables. For example, if opponent is central player and it cooperates, and self player as the opponent in this view point defects, we use $\pi_3(.)$ to derive the equations.

5.3.1.3 Mutual information between $G\left(t\right)$ and $G\left(t+1\right)$

The transition matrix between G(t) and G(t+1) is:

$$\mathbf{T_{GG}} = \begin{pmatrix} CC & CD & DC & DD \\ P_1^S P_1^O & P_2^S P_3^O & P_3^S P_2^O & P_4^S P_4^O \\ P_1^S (1 - P_1^O) & P_2^S (1 - P_3^O) & P_3^S (1 - P_2^O) & P_4^S (1 - P_4^O) \\ (1 - P_1^S) P_1^O & (1 - P_2^S) P_3^O & (1 - P_3^S) P_2^O & (1 - P_4^S) P_4^O \\ (1 - P_1^S) (1 - P_1^O) & (1 - P_2^S) (1 - P_3^O) & (1 - P_3^S) (1 - P_2^O) & (1 - P_4^S) (1 - P_4^O) \end{pmatrix}$$
(5.31)

Therefore, we have:

$$H(G(t+1)) = -\sum_{i=1}^{4} \sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}(i,j) \widetilde{P}_{G}^{t}(j) \log_{2}\left(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}(i,j) \widetilde{P}_{G}^{t}(j)\right)$$
(5.32)

The conditional entropy between G(t) and G(t+1) is:

$$H(G(t+1)|G(t)) = -\sum_{i=1}^{4} \sum_{j=1}^{4} \widetilde{P}_{G}^{t}(i) \operatorname{\mathbf{T}_{\mathbf{GG}}}(j,i) \log_{2} \operatorname{\mathbf{T}_{\mathbf{GG}}}(j,i)$$
(5.33)

Thus, the mutual information between $G\left(t\right)$ and $G\left(t+1\right)$ is:

$$\begin{split} I\big(G\left(t+1\right);G\left(t\right)\big) &= H\big(G\left(t+1\right)\big) - H\big(G\left(t+1\right)\left|G\left(t\right)\right) \\ &= -\sum_{i=1}^{4}\sum_{j=1}^{4}\mathbf{T}_{\mathbf{GG}}\left(i,j\right)\widetilde{P}_{G}^{t}\left(j\right)\log_{2}\big(\sum_{j=1}^{4}\mathbf{T}_{\mathbf{GG}}\left(i,j\right)\widetilde{P}_{G}^{t}\left(j\right)\big) \\ &+ \sum_{i=1}^{4}\sum_{j=1}^{4}\widetilde{P}_{G}^{t}\left(i\right)\mathbf{T}_{\mathbf{GG}}\left(j,i\right)\log_{2}\mathbf{T}_{\mathbf{GG}}\left(j,i\right) \\ \end{split}$$
(5.34)

5.3.2 Mutual information between $A_{S}(t)$ and other random variables at "t + 1"

To find the mutual information between $A_S(t)$ and $A_S(t+1)$, $A_O(t+1)$, and G(t+1), first we have to derive the transition matrices. It is obvious that these random variables are functions of $A_O(t)$ as well; therefore, $A_O(t)$ can be seen as the hidden state of Markov process between these random variables which needs to be estimated. There are two ways to estimate $A_O(t)$: one way is to recursively calculate $A_O(t)$ from t = 1, ... and the other way would be the estimation of G(t) in steady state from the right eigen vector of transition matrix corresponding to eigenvalue equals to one and using this steady state to estimate $A_O(t)$.

5.3.2.1 Mutual information between $A_{S}(t)$ and $A_{S}(t+1)$

The transition matrix between $A_{S}(t)$ and $A_{S}(t+1)$ is given by:

$$\mathbf{T_{SS}} = \frac{C}{D} \begin{pmatrix} P_1^S P(A_O^C(t) | A_S^C(t)) + P_2^S P(A_O^D(t) | A_S^C(t)) & P_3^S P(A_O^C(t) | A_S^D(t)) + P_4^S P(A_O^D(t) | A_S^D(t)) \\ (1 - P_1^S) P(A_O^C(t) | A_S^C(t)) + (1 - P_2^S) P(A_O^D(t) | A_S^C(t)) & (1 - P_3^S) P(A_O^C(t) | A_S^D(t)) + (1 - P_4^S) P(A_O^D(t) | A_S^D(t)) \end{pmatrix}$$
(5.35)

or:

$$\mathbf{T}_{SS} = \begin{array}{c} C & D \\ \frac{P_1^S \pi_1 + P_2^S \pi_2}{\pi_1 + \pi_2} & \frac{P_3^S \pi_3 + P_4^S \pi_4}{\pi_3 + \pi_4} \\ \frac{(1 - P_1^S) \pi_1 + (1 - P_2^S) \pi_2}{\pi_1 + \pi_2} & \frac{(1 - P_3^S) \pi_3 + (1 - P_4^S) \pi_4}{\pi_3 + \pi_4} \end{array} \right)$$
(5.36)
Therefore, we have:

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{P}_{G}^{t}\log_{2}\left(\widetilde{G}_{S}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}(t)\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\mathbf{T}_{\mathbf{SS}}(i,j)\widetilde{P}_{S}^{A}(j)\log_{2}\left(\sum_{j=1}^{2}\mathbf{T}_{\mathbf{SS}}(i,j)\widetilde{P}_{S}^{A}(j)\right)$$
(5.37)

The conditional entropy between $A_{S}\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$H\left(A_{S}(t+1)|A_{S}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(A_{S}(t+1)|A_{S}(t)=i\right)$$

$$= -\left\{\overline{\left\{P_{A_{S}(t)=C}\right\}}\sum_{i=1}^{2} \mathbf{T}_{\mathbf{SS}}(i,1)\log_{2}\left(\mathbf{T}_{\mathbf{SS}}(i,1)\right)$$

$$-\left\{\overline{\left\{P_{A_{S}(t)=D}\right\}}\sum_{i=1}^{2} \mathbf{T}_{\mathbf{SS}}(i,2)\log_{2}\left(\mathbf{T}_{\mathbf{SS}}(i,2)\right)$$

$$= -\sum_{i=1}^{2}\sum_{j=1}^{2} (\pi_{2i-1} + \pi_{2i})\mathbf{T}_{\mathbf{SS}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{SS}}(j,i)\right)$$
(5.38)

Therefore, the mutual information between $A_{S}\left(t\right)$ and $A_{S}\left(t+1\right)$ is:

$$I(A_{S}(t+1); A_{S}(t)) = H\left(A_{S}(t+1)\right) - H\left(A_{S}(t+1)|A_{S}(t)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{SS}}(i, j) \widetilde{P_{S}^{A}}(j) \log_{2}\left(\sum_{j=1}^{2} \mathbf{T}_{\mathbf{SS}}(i, j) \widetilde{P_{S}^{A}}(j)\right) + \sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{2i-1} + \pi_{2i}) \mathbf{T}_{\mathbf{SS}}(j, i) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(j, i)\right)$$
(5.39)

5.3.2.2 Mutual information between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$

To find the mutual information between $A_O(t+1)$ and $A_S(t)$, we should follow the same idea. We have:

$$\mathbf{T}_{SO} = \begin{pmatrix} C & D \\ P_1^O P(A_O^C(t) | A_S^C(t)) + P_3^O P(A_O^D(t) | A_S^C(t)) & P_2^O P(A_O^C(t) | A_S^D(t)) + P_4^O P(A_O^D(t) | A_S^D(t)) \\ (1 - P_1^O) P(A_O^C(t) | A_S^C(t)) + (1 - P_3^O) P(A_O^D(t) | A_S^C(t)) & (1 - P_2^O) P(A_O^C(t) | A_S^D(t)) + (1 - P_4^O) P(A_O^D(t) | A_S^D(t)) \end{pmatrix}$$
(5.40)

or:

$$\mathbf{T_{SO}} = \begin{array}{c} C & D \\ \frac{P_1^O \pi_1 + P_3^O \pi_2}{\pi_1 + \pi_2} & \frac{P_2^O \pi_3 + P_4^O \pi_4}{\pi_3 + \pi_4} \\ \frac{(1 - P_1^O) \pi_1 + (1 - P_3^O) \pi_2}{\pi_1 + \pi_2} & \frac{(1 - P_2^O) \pi_3 + (1 - P_4^O) \pi_4}{\pi_3 + \pi_4} \end{array} \right)$$
(5.41)

Therefore, we have:

$$H(A_O(t+1)) = -\widetilde{G_O^*} \widetilde{P_G^t} \log_2\left(\widetilde{G_O^*} \widetilde{P_G^t}\right) - \left(1 - \widetilde{G_O^*}\right) \widetilde{P_G^t} \log_2\left(\left(1 - \widetilde{G_O^*}\right) \widetilde{P_G^t}\right)$$
$$= -\sum_{i=1}^2 \sum_{j=1}^2 \mathbf{T_{SO}}(i,j) \widetilde{P_S^A}(j) \log_2\left(\sum_{j=1}^2 \mathbf{T_{SO}}(i,j) \widetilde{P_S^A}(j)\right)$$
(5.42)

The conditional entropy between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$ is given by:

$$H\left(A_{O}(t+1)|A_{S}(t)\right) = \sum_{i\in\{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(A_{O}(t+1)|A_{S}(t)=i\right)$$

$$= -\overbrace{\left\{P_{A_{S}(t)=C}\right\}}^{\pi_{1}+\pi_{2}} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SO}}(i,1)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(i,1)\right)$$

$$-\overbrace{\left\{P_{A_{S}(t)=D}\right\}}^{\pi_{3}+\pi_{4}} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SO}}(i,2)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{2i-1} + \pi_{2i}) \mathbf{T}_{\mathbf{SO}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(j,i)\right)$$

(5.43)

Thus, the mutual information between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$ is:

$$I(A_{O}(t+1); A_{S}(t)) = H(A_{O}(t+1)) - H(A_{O}(t+1)|A_{S}(t))$$

= $-\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{SO}(i, j) \widetilde{P_{S}^{A}}(j) \log_{2} \left(\sum_{j=1}^{2} \mathbf{T}_{SO}(i, j) \widetilde{P_{S}^{A}}(j)\right)$ (5.44)
+ $\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{2i-1} + \pi_{2i}) \mathbf{T}_{SO}(j, i) \log_{2} \left(\mathbf{T}_{SO}(j, i)\right)$

5.3.2.3 Mutual information between $A_{S}\left(t\right)$ and $G\left(t+1\right)$

The transition matrix between $A_S(t)$ and G(t+1) is:

$$\mathbf{T_{SG}} = \begin{pmatrix} P_1^S P_1^O P(A_O^C(t) | A_S^C(t)) + P_2^S P_3^O P(A_O^D(t) | A_S^C(t)) \\ P_3^S P_2^O P(A_O^C(t) | A_S^D(t)) + P_4^S P_4^O P(A_O^D(t) | A_S^D(t)) \\ P_1^S \left(1 - P_1^O\right) P(A_O^C(t) | A_S^C(t)) + P_2^S \left(1 - P_3^O\right) P(A_O^D(t) | A_S^C(t)) \\ P_3^S \left(1 - P_2^O\right) P(A_O^C(t) | A_S^D(t)) + P_4^S \left(1 - P_4^O\right) P(A_O^D(t) | A_S^D(t)) \\ \left(1 - P_1^S\right) P_1^O P(A_O^C(t) | A_S^C(t)) + \left(1 - P_2^S\right) P_3^O P(A_O^D(t) | A_S^C(t)) \\ \left(1 - P_1^S\right) P_2^O P(A_O^C(t) | A_S^D(t)) + \left(1 - P_4^S\right) P_4^O P(A_O^D(t) | A_S^D(t)) \\ \left(1 - P_1^S\right) \left(1 - P_1^O\right) P(A_O^C(t) | A_S^C(t)) + \left(1 - P_2^S\right) \left(1 - P_3^O\right) P(A_O^D(t) | A_S^C(t)) \\ \left(1 - P_3^S\right) \left(1 - P_2^O\right) P(A_O^C(t) | A_S^D(t)) + \left(1 - P_4^S\right) \left(1 - P_4^O\right) P(A_O^D(t) | A_S^D(t)) \end{pmatrix}$$
(5.45)

or:

$$\mathbf{T}_{SG} = \begin{pmatrix} C & D \\ \frac{P_1^S P_1^O \pi_1 + P_2^S P_1^O \pi_2}{\pi_1 + \pi_2} & \frac{P_3^S P_2^O \pi_3 + P_4^S P_4^O \pi_4}{\pi_3 + \pi_4} \\ \frac{P_1^S (1 - P_1^O) \pi_1 + P_2^S (1 - P_3^O) \pi_2}{\pi_1 + \pi_2} & \frac{P_3^S P_2^O \pi_3 + P_4^S (1 - P_4^O) \pi_4}{\pi_3 + \pi_4} \\ \frac{(1 - P_1^S) P_1^O \pi_1 + (1 - P_2^S) P_3^O \pi_2}{\pi_1 + \pi_2} & \frac{(1 - P_3^S) P_2^O \pi_3 + (1 - P_4^S) P_4^O \pi_4}{\pi_3 + \pi_4} \\ \frac{(1 - P_1^S) (1 - P_1^O) \pi_1 + (1 - P_2^S) (1 - P_3^O) \pi_2}{\pi_1 + \pi_2} & \frac{(1 - P_3^S) (1 - P_2^O) \pi_3 + (1 - P_4^S) (1 - P_4^O) \pi_4}{\pi_3 + \pi_4} \end{pmatrix}$$
(5.46)

We have:

$$H(G(t+1)) = -\sum_{i=1}^{4} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{SG}}(i,j) \widetilde{P_{S}^{A}}(j) \log_{2} \left(\sum_{j=1}^{2} \mathbf{T}_{\mathbf{SG}}(i,j) \widetilde{P_{S}^{A}}(j)\right)$$
(5.47)

The conditional entropy between $A_{S}(t)$ and G(t+1) is given by:

$$H\left(G\left(t+1\right)|A_{S}\left(t\right)\right) = \sum_{i\in\{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(G\left(t+1\right)|A_{S}\left(t\right)=i\right)$$
$$= -\sum_{i=1}^{2} \sum_{j=1}^{4} \left(\pi_{2i-1}+\pi_{2i}\right) \mathbf{T}_{\mathbf{SG}}\left(j,i\right) \log_{2}\left(\mathbf{T}_{\mathbf{SG}}\left(j,i\right)\right)$$
(5.48)

Thus, the mutual information between $A_{S}(t)$ and G(t+1) is:

$$\begin{split} I\big(G\left(t+1\right);A_{S}\left(t\right)\big) &= H\bigg(G\left(t+1\right)\bigg) - H\bigg(G\left(t+1\right)\big|A_{S}\left(t\right)\bigg) \\ &= -\sum_{i=1}^{4}\sum_{j=1}^{2}\mathbf{T}_{\mathbf{SG}}\left(i,j\right)\widetilde{P_{S}^{A}}\left(j\right)\log_{2}\big(\sum_{j=1}^{2}\mathbf{T}_{\mathbf{SG}}\left(i,j\right)\widetilde{P_{S}^{A}}\left(j\right)\big) \\ &+ \sum_{i=1}^{2}\sum_{j=1}^{4}\left(\pi_{2i-1} + \pi_{2i}\right)\mathbf{T}_{\mathbf{SG}}\left(j,i\right)\log_{2}\left(\mathbf{T}_{\mathbf{SG}}\left(j,i\right)\bigg) \end{split}$$

5.3.3 Mutual information between $A_O(t)$ and other random variables at "t + 1"

To find the mutual information between $A_O(t)$ and other random variables at "t + 1", we have to follow the same idea and derive the transition matrices.

5.3.3.1 Mutual information between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$

The transition matrix between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$\mathbf{T_{OS}} = \begin{pmatrix} C & D \\ P_1^S P(A_S^C(t) \mid A_O^C(t)) + P_3^S P(A_S^D(t) \mid A_O^C(t)) & P_2^S P(A_S^C(t) \mid A_O^D(t)) + P_4^S P(A_S^D(t) \mid A_O^D(t)) \\ (1 - P_1^S) P(A_S^C(t) \mid A_O^C(t)) + (1 - P_3^S) P(A_S^D(t) \mid A_O^C(t)) & (1 - P_2^S) P(A_S^C(t) \mid A_O^D(t)) + (1 - P_4^S) P(A_S^D(t) \mid A_O^D(t)) \end{pmatrix}$$
(5.49)

$$\mathbf{T_{OS}} = \begin{array}{c} C & D \\ C & \frac{P_1^S \pi_1 + P_3^S \pi_3}{\pi_1 + \pi_3} & \frac{P_2^S \pi_2 + P_4^S \pi_4}{\pi_2 + \pi_4} \\ D & \left(\frac{(1 - P_1^S) \pi_1 + (1 - P_3^S) \pi_3}{\pi_1 + \pi_3} & \frac{(1 - P_2^S) \pi_2 + (1 - P_4^S) \pi_4}{\pi_2 + \pi_4} \right) \end{array}$$
(5.50)

Therefore, we have:

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{P}_{G}^{t}\log_{2}\left(\widetilde{G}_{S}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\mathbf{T}_{\mathbf{OS}}(i,j)\widetilde{P}_{O}^{A}(j)\log_{2}\left(\sum_{j=1}^{2}\mathbf{T}_{\mathbf{OS}}(i,j)\widetilde{P}_{O}^{A}(j)\right) \quad (5.51)$$

The conditional entropy between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$H\left(A_{S}(t+1)|A_{O}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(A_{S}(t+1)|A_{O}(t)=i\right)$$

$$= -\left\{P_{A_{O}(t)=C}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OS}}(i,1) \log_{2}\left(\mathbf{T}_{\mathbf{OS}}(i,1)\right)$$

$$-\left\{P_{A_{O}(t)=D}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OS}}(i,2) \log_{2}\left(\mathbf{T}_{\mathbf{OS}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{i} + \pi_{i+2}) \mathbf{T}_{\mathbf{OS}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{OS}}(j,i)\right)$$
(5.52)

or:

Therefore, the mutual information between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$ is:

$$I(A_{S}(t+1); A_{O}(t)) = H(A_{S}(t+1)) - H(A_{S}(t+1) | A_{O}(t))$$

= $-\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{OS}(i, j) \widetilde{P}_{O}^{A}(j) \log_{2} \left(\sum_{j=1}^{2} \mathbf{T}_{OS}(i, j) \widetilde{P}_{O}^{A}(j)\right)$ (5.53)
+ $\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{i} + \pi_{i+2}) \mathbf{T}_{OS}(j, i) \log_{2} \left(\mathbf{T}_{OS}(j, i)\right)$

5.3.3.2 Mutual information between $A_{O}\left(t\right)$ and $A_{O}\left(t+1\right)$

We have:

$$\mathbf{T_{OO}} = \begin{pmatrix} C & D \\ P_1^O P(A_S^C(t) | A_O^O(t)) + P_2^O P(A_S^D(t) | A_O^O(t)) & P_3^O P(A_S^C(t) | A_O^D(t)) + P_4^O P(A_S^D(t) | A_O^D(t)) \\ (1 - P_1^O) P(A_S^C(t) | A_O^O(t)) + (1 - P_2^O) P(A_S^D(t) | A_O^O(t)) & (1 - P_3^O) P(A_S^C(t) | A_O^D(t)) + (1 - P_4^O) P(A_S^D(t) | A_O^D(t)) \end{pmatrix}$$
(5.54)

or:

$$\mathbf{T_{OO}} = \begin{array}{cc} C & D \\ C & \frac{P_1^O \pi_1 + P_2^O \pi_3}{\pi_1 + \pi_3} & \frac{P_3^O \pi_2 + P_4^O \pi_4}{\pi_2 + \pi_4} \\ D & \left(\frac{(1 - P_1^O) \pi_1 + (1 - P_2^O) \pi_3}{\pi_1 + \pi_3} & \frac{(1 - P_3^O) \pi_2 + (1 - P_4^O) \pi_4}{\pi_2 + \pi_4} \right) \end{array}$$
(5.55)

Therefore, we have:

$$H(A_{O}(t+1)) = -\widetilde{G}_{O}^{*}\widetilde{P}_{G}^{t}\log_{2}\left(\widetilde{G}_{O}^{*}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{O}^{*}\right)\widetilde{P}_{G}^{t}\log_{2}\left(\left(1 - \widetilde{G}_{O}^{*}\right)\widetilde{P}_{G}^{t}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\mathbf{T}_{\mathbf{OO}}(i,j)\widetilde{P}_{O}^{A}(j)\log_{2}\left(\sum_{j=1}^{2}\mathbf{T}_{\mathbf{OO}}(i,j)\widetilde{P}_{O}^{A}(j)\right) \quad (5.56)$$

The conditional entropy between $A_O(t)$ and $A_O(t+1)$ is given by:

$$H\left(A_{O}(t+1)|A_{O}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(A_{O}(t+1)|A_{O}(t)=i\right)$$

$$= -\left\{P_{A_{O}(t)=C}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OO}}(i,1) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(i,1)\right)$$

$$-\left\{P_{A_{O}(t)=D}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OO}}(i,2) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{i} + \pi_{i+2}) \mathbf{T}_{\mathbf{OO}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(j,i)\right)$$
(5.57)

Therefore, the mutual information between $A_{O}\left(t\right)$ and $A_{O}\left(t+1\right)$ is:

$$I(A_{O}(t+1); A_{O}(t)) = H(A_{O}(t+1)) - H(A_{O}(t+1)|A_{O}(t))$$

= $-\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{OO}}(i, j) \widetilde{P_{O}^{A}}(j) \log_{2} \left(\sum_{j=1}^{2} \mathbf{T}_{\mathbf{OO}}(i, j) \widetilde{P_{O}^{A}}(j)\right)$ (5.58)
+ $\sum_{i=1}^{2} \sum_{j=1}^{2} (\pi_{i} + \pi_{i+2}) \mathbf{T}_{\mathbf{OO}}(j, i) \log_{2} \left(\mathbf{T}_{\mathbf{OO}}(j, i)\right)$

5.3.3.3 Mutual information between $A_{O}\left(t\right)$ and $G\left(t+1\right)$

The transition matrix between $A_O(t)$ and G(t+1) is:

$$\mathbf{T_{OG}} = \begin{pmatrix} P_{1}^{S} P_{1}^{O} P\left(A_{S}^{C}(t) \mid A_{O}^{C}(t)\right) + P_{3}^{S} P_{2}^{O} P\left(A_{S}^{D}(t) \mid A_{O}^{D}(t)\right) \\ P_{2}^{S} P_{3}^{O} P\left(A_{S}^{C}(t) \mid A_{O}^{D}(t)\right) + P_{4}^{S} P_{4}^{O} P\left(A_{S}^{D}(t) \mid A_{O}^{D}(t)\right) \\ P_{1}^{S} \left(1 - P_{1}^{O}\right) P\left(A_{S}^{C}(t) \mid A_{O}^{C}(t)\right) + P_{3}^{S} \left(1 - P_{2}^{O}\right) P\left(A_{S}^{D}(t) \mid A_{O}^{D}(t)\right) \\ P_{2}^{S} \left(1 - P_{1}^{O}\right) P\left(A_{S}^{C}(t) \mid A_{O}^{C}(t)\right) + P_{3}^{S} \left(1 - P_{2}^{O}\right) P\left(A_{S}^{D}(t) \mid A_{O}^{D}(t)\right) \\ \left(1 - P_{1}^{S}\right) P_{1}^{O} P\left(A_{O}^{C}(t) \mid A_{S}^{C}(t)\right) + \left(1 - P_{3}^{S}\right) P_{2}^{O} P\left(A_{S}^{D}(t) \mid A_{O}^{O}(t)\right) \\ \left(1 - P_{1}^{S}\right) P_{1}^{O} P\left(A_{S}^{C}(t) \mid A_{O}^{O}(t)\right) + \left(1 - P_{3}^{S}\right) \left(1 - P_{2}^{O}\right) P\left(A_{S}^{D}(t) \mid A_{O}^{O}(t)\right) \\ \left(1 - P_{1}^{S}\right) \left(1 - P_{1}^{O}\right) P\left(A_{S}^{C}(t) \mid A_{O}^{O}(t)\right) + \left(1 - P_{3}^{S}\right) \left(1 - P_{2}^{O}\right) P\left(A_{S}^{D}(t) \mid A_{O}^{O}(t)\right) \\ \left(1 - P_{2}^{S}\right) \left(1 - P_{3}^{O}\right) P\left(A_{S}^{C}(t) \mid A_{O}^{O}(t)\right) + \left(1 - P_{4}^{S}\right) \left(1 - P_{4}^{O}\right) P\left(A_{S}^{D}(t) \mid A_{O}^{D}(t)\right) \end{pmatrix}$$

$$(5.59)$$

$$\mathbf{T}_{OG} = \begin{pmatrix} CC & D \\ \frac{P_1^S P_1^O \pi_1 + P_3^S P_2^O \pi_3}{\pi_1 + \pi_3} & \frac{P_2^S P_3^O \pi_2 + P_4^S P_4^O \pi_4}{\pi_2 + \pi_4} \\ \frac{P_1^S (1 - P_1^O) \pi_1 + P_3^S (1 - P_2^O) \pi_3}{\pi_1 + \pi_3} & \frac{P_2^S (1 - P_3^O) \pi_2 + P_4^S (1 - P_4^O) \pi_4}{\pi_2 + \pi_4} \\ \frac{(1 - P_1^S) P_1^O \pi_1 + (1 - P_3^S) P_2^O \pi_3}{\pi_1 + \pi_3} & \frac{(1 - P_2^S) P_3^O \pi_2 + (1 - P_4^S) P_4^O \pi_4}{\pi_2 + \pi_4} \\ \frac{(1 - P_1^S) (1 - P_1^O) \pi_1 + (1 - P_3^S) (1 - P_2^O) \pi_3}{\pi_1 + \pi_3} & \frac{(1 - P_2^S) P_3^O \pi_2 + (1 - P_4^S) P_4^O \pi_4}{\pi_2 + \pi_4} \end{pmatrix}$$
(5.60)

We have:

$$H(G(t+1)) = -\sum_{i=1}^{4} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{OG}}(i,j) \widetilde{P_{O}^{A}}(j) \log_{2} \left(\sum_{j=1}^{2} \mathbf{T}_{\mathbf{OG}}(i,j) \widetilde{P_{O}^{A}}(j)\right)$$
(5.61)

The conditional entropy between $A_O(t)$ and G(t+1) is given by:

$$H\left(G\left(t+1\right)|A_{O}\left(t\right)\right) = \sum_{i\in\{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(G\left(t+1\right)|A_{O}\left(t\right)=i\right)$$
$$= -\sum_{i=1}^{2} \sum_{j=1}^{4} \left(\pi_{i}+\pi_{i+2}\right) \mathbf{T}_{\mathbf{OG}}\left(j,i\right) \log_{2}\left(\mathbf{T}_{\mathbf{OG}}\left(j,i\right)\right) (5.62)$$

Thus, the mutual information between $A_{O}\left(t\right)$ and $G\left(t+1\right)$ is:

$$\begin{split} I(G(t+1); A_{O}(t)) &= H\left(G(t+1)\right) - H\left(G(t+1) \left|A_{O}(t)\right.\right) \\ &= -\sum_{i=1}^{4} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{OG}}(i, j) \widetilde{P_{O}^{A}}(j) \log_{2}\left(\sum_{j=1}^{2} \mathbf{T}_{\mathbf{OG}}(i, j) \widetilde{P_{O}^{A}}(j)\right) \\ &+ \sum_{i=1}^{2} \sum_{j=1}^{4} \left(\pi_{i} + \pi_{i+2}\right) \mathbf{T}_{\mathbf{OG}}(j, i) \log_{2}\left(\mathbf{T}_{\mathbf{OG}}(j, i)\right) \end{split}$$
(5.63)

In this section, we calculate the mutual information between random variables at time "t" and "t + 1" in noisy environments. To do so, we assume players have fuzzy/feeble mind. Thus, by introducing error term " ϵ ", or channel error, we can write an error matrix for what

or:

a player remembers from his previous action, his opponent's action, and previous game. This noise affects the players next move by creating an error term in estimating/remembering the previous actions. Therefore, the players next action, and consequently their mean fitness, will be affected by the error caused by environmental noise. Figure (5.1) shows the error of channels for the three random variables at time "t". Considering figure (5.1), we can define the following error matrices:

$$\mathbf{Err}_{\mathbf{S}} = \begin{pmatrix} 1 - \epsilon_1 & \epsilon_1 \\ & & \\ \epsilon_1 & 1 - \epsilon_1 \end{pmatrix}$$
(5.64)

$$\mathbf{Err}_{\mathbf{O}} = \begin{pmatrix} 1 - \epsilon_2 & \epsilon_2 \\ \\ \epsilon_2 & 1 - \epsilon_2 \end{pmatrix}$$
(5.65)

$$\mathbf{Err}_{\mathbf{G}} = \begin{pmatrix} (1-\epsilon_1)(1-\epsilon_2) & (1-\epsilon_1)\epsilon_2 & \epsilon_1(1-\epsilon_2) & \epsilon_1\epsilon_2 \\ (1-\epsilon_1)\epsilon_2 & (1-\epsilon_1)(1-\epsilon_2) & \epsilon_1\epsilon_2 & \epsilon_1(1-\epsilon_2) \\ \epsilon_1(1-\epsilon_2) & \epsilon_1\epsilon_2 & (1-\epsilon_1)(1-\epsilon_2) & (1-\epsilon_1)\epsilon_2 \\ \epsilon_1\epsilon_2 & \epsilon_1(1-\epsilon_2) & (1-\epsilon_1)\epsilon_2 & (1-\epsilon_1)(1-\epsilon_2) \end{pmatrix}$$
(5.66)

5.3.4 Mutual information between G(t) and other random variables at "t + 1"

First, we derive the mutual information between G(t) and $A_S(t+1)$. Similar to noiseless environment, we can write the transition matrices and calculate the mutual information between G(t) and $A_S(t+1)$. The transition matrix between G(t) and $A_S(t+1)$ is given at





Figure 5.1: The schematic of channel error. This error happens when players have fuzzy mind about their own and opponent's previous action (a) the binary symmetric channel error of player's self action. (b) the binary symmetric channel error of opponent's self action. (c) the channel error of chosen actions by player and its opponent (game played) at previous iteration.

equation (5.21). Therefore, we have:

$$A_S(t+1) = \mathbf{T}_{\mathbf{GS}} \hat{\widetilde{P}_G^t} = \mathbf{T}_{\mathbf{GS}} \mathbf{Err}_{\mathbf{G}} \widetilde{P_G^t}$$
(5.67)

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{P}_{G}^{t}\log_{2}\left(\widetilde{G}_{S}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{t}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{4}\mathbf{T}_{\mathbf{GS}}(i,j)\mathbf{Err_{G}}\widetilde{P}_{G}^{t}\log_{2}\left(\sum_{j=1}^{2}\mathbf{T}_{\mathbf{GS}}(i,j)\mathbf{Err_{G}}\widetilde{P}_{G}^{t}\right)$$
(5.68)

The only difference between the noiseless environment and noisy environment is using \widetilde{P}_G^t instead of \widetilde{P}_G^t , which can be substituted by $\mathbf{Err}_{\mathbf{G}}\widetilde{P}_G^t$ in equation (5.24). Similar to action entropy, we can substitute \widetilde{P}_G^t with $\mathbf{Err}_{\mathbf{G}}\widetilde{P}_G^t$ in equations (5.25) and (5.26) to calculate the mutual information between G(t) and $A_S(t+1)$ in noisy environments.

To find the mutual information between G(t) and $A_O(t+1)$ in noisy environment, we should follow the same idea. The transition matrix between G(t) and $A_O(t+1)$ is given at equation (5.27). We have:

$$A_O(t+1) = \mathbf{T}_{\mathbf{GO}} \hat{\widetilde{P}_G^t} = \mathbf{T}_{\mathbf{GO}} \mathbf{Err}_{\mathbf{G}} \widetilde{P_G^t}$$
(5.69)

$$H(A_O(t+1)) = -\widetilde{G_O}\widetilde{P_G^t}\log_2\left(\widetilde{G_O}\widetilde{P_G^t}\right) - \left(1 - \widetilde{G_O}\right)\widetilde{P_G^t}\log_2\left(\left(1 - \widetilde{G_O}\right)\widetilde{P_G^t}\right)$$
$$= -\sum_{i=1}^2\sum_{j=1}^4 \mathbf{T_{GO}}(i,j) \operatorname{\mathbf{Err}}_{\mathbf{G}}\widetilde{P_G^t}\log_2\left(\sum_{j=1}^2 \mathbf{T_{GO}}(i,j) \operatorname{\mathbf{Err}}_{\mathbf{G}}\widetilde{P_G^t}\right)$$
(5.70)

Similar to previous case, we can substitute \widetilde{P}_{G}^{t} with $\mathbf{Err}_{\mathbf{G}}\widetilde{P}_{G}^{t}$ in equations (5.29) and (5.30) and calculate the mutual information between G(t) and $A_{O}(t+1)$ in noisy environments.

To find the mutual information between G(t) and G(t+1) we have to write the tran-

sition matrix in noisy environments which is given in (5.31). The game entropy in noisy environment is:

$$\begin{split} H\big(G\left(t+1\right)\big) &= -\sum_{i=1}^{4} \sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}\left(i,j\right) \hat{\widetilde{P}_{G}^{t}} \log_{2}\big(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}\left(i,j\right) \hat{\widetilde{P}_{G}^{t}}\big) \\ &= -\sum_{i=1}^{4} \sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}\left(i,j\right) \mathbf{Err}_{\mathbf{G}} \widetilde{P}_{G}^{t} \log_{2}\big(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{GG}}\left(i,j\right) \mathbf{Err}_{\mathbf{G}} \widetilde{P}_{G}^{t}\big) (5.71) \end{split}$$

The conditional entropy between G(t) and G(t+1) is:

$$H(G(t+1)|G(t)) = -\sum_{i=1}^{4} \sum_{j=1}^{4} \widehat{\widetilde{P}_{G}^{t}}(i) \mathbf{T}_{\mathbf{GG}}(j,i) \log_{2} \mathbf{T}_{\mathbf{GG}}(j,i)$$
$$= -\sum_{i=1}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}} \widetilde{P}_{G}^{t}(i) \mathbf{T}_{\mathbf{GG}}(j,i) \log_{2} \mathbf{T}_{\mathbf{GG}}(j,i) \tag{5.72}$$

Therefore, the mutual information between G(t) and G(t+1) in noisy environment is:

$$\begin{split} I\big(G\left(t+1\right);G\left(t\right)\big) &= H\big(G\left(t+1\right)\big) - H\big(G\left(t+1\right)\big|G\left(t\right)\big) \\ &= -\sum_{i=1}^{4}\sum_{j=1}^{4}\mathbf{T}_{\mathbf{G}\mathbf{G}}\left(i,j\right)\mathbf{Err}_{\mathbf{G}}\widetilde{P}_{G}^{t}\log_{2}\big(\sum_{j=1}^{4}\mathbf{T}_{\mathbf{G}\mathbf{G}}\left(i,j\right)\mathbf{Err}_{\mathbf{G}}\widetilde{P}_{G}^{t}\big)_{(5.73)} \\ &+ \sum_{i=1}^{4}\sum_{j=1}^{4}\mathbf{Err}_{\mathbf{G}}\widetilde{P}_{G}^{t}\left(i\right)\mathbf{T}_{\mathbf{G}\mathbf{G}}\left(j,i\right)\log_{2}\mathbf{T}_{\mathbf{G}\mathbf{G}}\left(j,i\right) \end{split}$$

5.3.5 Mutual information between $A_{S}(t)$ and other random variables at "t + 1" in noisy environments

Similar to noiseless environments, to find the mutual information between $A_S(t)$ and $A_S(t+1)$, $A_O(t+1)$, and G(t+1) we have to derive the transition matrices. As we know $A_O(t)$ shows itself as a hidden random variable in the transition matrices; and since now we are in noisy environments, we have to consider the effect of noise in estimation of this hidden random variable.

5.3.5.1 Mutual information between $A_{S}\left(t\right)$ and $A_{S}\left(t+1\right)$

The transition matrix between $A_{S}(t)$ and $A_{S}(t+1)$ is given by:

$$\mathbf{T}_{SS}^{\circ} = \begin{pmatrix} P_{1}^{S}P(A_{O}^{C}(t)\hat{|}A_{S}^{C}(t)) + P_{2}^{S}P(A_{O}^{D}(t)\hat{|}A_{S}^{C}(t)) & P_{3}^{S}P(A_{O}^{C}(t)\hat{|}A_{S}^{D}(t)) + P_{4}^{S}P(A_{O}^{D}(t)\hat{|}A_{S}^{D}(t)) \\ (1 - P_{1}^{S})P(A_{O}^{C}(t)\hat{|}A_{S}^{C}(t)) + (1 - P_{2}^{S})P(A_{O}^{D}(t)\hat{|}A_{S}^{C}(t)) & (1 - P_{3}^{S})P(A_{O}^{C}(t)\hat{|}A_{S}^{D}(t)) + (1 - P_{4}^{S})P(A_{O}^{D}(t)\hat{|}A_{S}^{D}(t)) \end{pmatrix}$$
(5.74)

where:

$$P(A_{O}^{C}(t)|A_{S}^{C}(t)) = \frac{\hat{\pi}_{1}}{\hat{\pi}_{1} + \hat{\pi}_{2}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(1, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{O}^{D}(t)|A_{S}^{C}(t)) = \frac{\hat{\pi}_{2}}{\hat{\pi}_{1} + \hat{\pi}_{2}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(2, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{O}^{C}(t)|A_{S}^{D}(t)) = \frac{\hat{\pi}_{3}}{\hat{\pi}_{3} + \hat{\pi}_{4}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(3, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{O}^{D}(t)|A_{S}^{D}(t)) = \frac{\hat{\pi}_{4}}{\hat{\pi}_{3} + \hat{\pi}_{4}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(4, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i, j) \widetilde{P}_{G}^{t}(j)}$$

$$(5.75)$$

Therefore, we have:

$$\mathbf{T}_{\mathbf{SS}} = D \begin{pmatrix} C & D \\ \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)} & \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)} & 1 - \frac{\sum_{i=3}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)} & 1 - \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)} & 1 - \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \widetilde{G_{S}}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P_{G}^{t}}(j)} \end{pmatrix}$$

$$(5.76)$$

Thus, the entropy of self action is:

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{P}_{G}^{\widetilde{t}}\log_{2}\left(\widetilde{G}_{S}\widetilde{P}_{G}^{\widetilde{t}}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{\widetilde{t}}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{P}_{G}^{\widetilde{t}}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\widehat{\mathbf{T}}_{SS}(i,j)\widetilde{P}_{S}^{\widetilde{A}}(j)\log_{2}\left(\sum_{j=1}^{2}\widehat{\mathbf{T}}_{SS}(i,j)\widetilde{P}_{S}^{\widetilde{A}}(j)\right)$$
(5.77)

The conditional entropy between $A_{S}\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$H\left(A_{S}(t+1)|A_{S}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(A_{S}(\hat{t}+1)|A_{S}(t)=i\right)$$

$$= -\left\{P_{A_{S}(t)=C}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SS}}(i,1) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(i,1)\right)$$

$$-\left\{P_{A_{S}(t)=D}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SS}}(i,2) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\hat{\pi}_{2i-1} + \hat{\pi}_{2i}) \mathbf{T}_{\mathbf{SS}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(j,i)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=2i-1}^{2i} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P_{G}}(l) \mathbf{T}_{\mathbf{SS}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(j,i)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=2i-1}^{2i} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P_{G}}(l) \mathbf{T}_{\mathbf{SS}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{SS}}(j,i)\right)$$

Therefore, the mutual information between $A_{S}(t)$ and $A_{S}(t+1)$ is:

$$I(A_{S}(t+1); A_{S}(t)) = H\left(A_{S}(t+1)\right) - H\left(A_{S}(t+1) | A_{S}(t)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \widehat{\mathbf{T}}_{SS}(i, j) \widehat{\widehat{P}_{S}^{A}}(j) \log_{2}\left(\widehat{\mathbf{T}}_{SS}(i, j) \widehat{\widehat{P}_{S}^{A}}(j)\right)$$

$$+ \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=i}^{i+2} \sum_{l=1}^{4} \mathbf{Err}_{G}(k, l) \widehat{P}_{G}^{t}(l) \widehat{\mathbf{T}}_{SS}(j, i) \log_{2}\left(\widehat{\mathbf{T}}_{SS}(j, i)\right)$$
(5.79)

5.3.5.2 Mutual information between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$

To find the mutual information between $A_O(t+1)$ and $A_S(t)$, we should follow the same idea. We have:

$$\mathbf{T}_{\mathbf{SO}}^{\circ} = \begin{pmatrix} C & D \\ P_1^{O} P(A_O^{C}(t) | A_S^{C}(t)) + P_3^{O} P(A_O^{D}(t) | A_S^{C}(t)) & P_2^{O} P(A_O^{C}(t) | A_S^{D}(t)) + P_4^{O} P(A_O^{D}(t) | A_S^{D}(t)) \\ (1 - P_1^{O}) P(A_O^{C}(t) | A_S^{C}(t)) + (1 - P_3^{O}) P(A_O^{D}(t) | A_S^{C}(t)) & (1 - P_2^{O}) P(A_O^{C}(t) | A_S^{D}(t)) + (1 - P_4^{O}) P(A_O^{D}(t) | A_S^{D}(t)) \end{pmatrix}$$
(5.80)

or:

$$\mathbf{T}_{\mathbf{SO}} = D \begin{pmatrix} C & D \\ \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G}_{O}^{*}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)} & \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \widetilde{G}_{O}^{*}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G}_{O}^{*}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)} & 1 - \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G}_{O}^{*}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)} & 1 - \frac{\sum_{i=3}^{4} \sum_{j=1}^{4} \widetilde{G}_{O}^{*}(i) \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(i)} \end{pmatrix}$$

$$(5.81)$$

Thus, the entropy of opponent's action is:

$$H(A_{S}(t+1)) = -\widetilde{G_{O}^{*}} \hat{\widetilde{P_{G}^{t}}} \log_{2} \left(\widetilde{G_{O}^{*}} \hat{\widetilde{P_{G}^{t}}}\right) - \left(1 - \widetilde{G_{O}^{*}}\right) \hat{\widetilde{P_{G}^{t}}} \log_{2} \left(\left(1 - \widetilde{G_{O}^{*}}\right) \hat{\widetilde{P_{G}^{t}}}\right)$$
$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T_{SO}^{*}}(i,j) \hat{\widetilde{P_{S}^{A}}}(j) \log_{2} \left(\mathbf{T_{SO}^{*}}(i,j) \hat{\widetilde{P_{S}^{A}}}(j)\right)$$
(5.82)

The conditional entropy between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$ is given by:

$$H\left(A_{O}(t+1)|A_{S}(t)\right) = \sum_{i\in\{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(A_{O}(\hat{t}+1)|A_{S}(t)=i\right)$$

$$= -\left\{P_{A_{S}(t)=C}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SO}}(i,1)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(i,1)\right)$$

$$-\left\{P_{A_{S}(t)=D}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{SO}}(i,2)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\hat{\pi}_{2i-1} + \hat{\pi}_{2i}) \mathbf{T}_{\mathbf{SO}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(j,i)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=i}^{i+2} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P}_{G}^{t}(l) \mathbf{T}_{\mathbf{SO}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(j,i)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=i}^{2} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P}_{G}^{t}(l) \mathbf{T}_{\mathbf{SO}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{SO}}(j,i)\right)$$

Therefore, the mutual information between $A_{S}\left(t\right)$ and $A_{O}\left(t+1\right)$ is:

$$I(A_{O}(t+1); A_{S}(t)) = H\left(A_{O}(t+1)\right) - H\left(A_{O}(t+1) | A_{S}(t)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{SO}}^{2}(i, j) \widehat{P_{S}^{A}}(j) \log_{2}\left(\mathbf{T}_{\mathbf{SO}}^{2}(i, j) \widehat{P_{S}^{A}}(j)\right)$$

$$+ \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=i}^{i+2} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k, l) \widetilde{P_{G}^{t}}(l) \mathbf{T}_{\mathbf{SO}}^{2}(j, i) \log_{2}\left(\mathbf{T}_{\mathbf{SO}}^{2}(j, i)\right)$$
(5.84)

5.3.5.3 Mutual information between $A_{S}\left(t\right)$ and $G\left(t+1\right)$

The transition matrix between $A_S(t)$ and G(t+1) is:

$$\mathbf{T}_{SG}^{\circ} = \begin{pmatrix} P_{1}^{S} P_{1}^{O} P(A_{O}^{C}(\hat{t}) | A_{S}^{C}(t)) + P_{2}^{S} P_{3}^{O} P(A_{O}^{O}(\hat{t}) | A_{S}^{D}(t)) \\ P_{3}^{S} P_{2}^{O} P(A_{O}^{O}(\hat{t}) | A_{S}^{D}(t)) + P_{4}^{S} P_{4}^{O} P(A_{O}^{D}(\hat{t}) | A_{S}^{D}(t)) \\ P_{1}^{S} \left(1 - P_{1}^{O}\right) P(A_{O}^{O}(\hat{t}) | A_{S}^{C}(t)) + P_{2}^{S} \left(1 - P_{3}^{O}\right) P(A_{O}^{O}(\hat{t}) | A_{S}^{C}(t)) \\ P_{3}^{S} \left(1 - P_{2}^{O}\right) P(A_{O}^{O}(\hat{t}) | A_{S}^{C}(t)) + P_{4}^{S} \left(1 - P_{4}^{O}\right) P(A_{O}^{D}(\hat{t}) | A_{S}^{D}(t)) \\ \left(1 - P_{1}^{S}\right) P_{1}^{O} P(A_{O}^{C}(\hat{t}) | A_{S}^{C}(t)) + \left(1 - P_{2}^{S}\right) P_{3}^{O} P(A_{O}^{D}(\hat{t}) | A_{S}^{C}(t)) \\ \left(1 - P_{3}^{S}\right) P_{2}^{O} P(A_{O}^{O}(\hat{t}) | A_{S}^{C}(t)) + \left(1 - P_{4}^{S}\right) P_{4}^{O} P(A_{O}^{D}(\hat{t}) | A_{S}^{D}(t)) \\ \left(1 - P_{1}^{S}\right) \left(1 - P_{1}^{O}\right) P(A_{O}^{C}(\hat{t}) | A_{S}^{C}(t)) + \left(1 - P_{2}^{S}\right) \left(1 - P_{3}^{O}\right) P(A_{O}^{D}(\hat{t}) | A_{S}^{C}(t)) \\ \left(1 - P_{3}^{S}\right) \left(1 - P_{2}^{O}\right) P(A_{O}^{O}(\hat{t}) | A_{S}^{C}(t)) + \left(1 - P_{4}^{S}\right) \left(1 - P_{4}^{O}\right) P(A_{O}^{D}(\hat{t}) | A_{S}^{D}(t)) \right) \end{pmatrix}$$

$$(5.85)$$

or:

$$\mathbf{\hat{T}_{SG}} = \frac{CC}{DD} \begin{pmatrix} \frac{P_1^S P_1^O \vec{\pi}_1 + P_2^S P_3^O \vec{\pi}_2}{\vec{\pi}_1 + \vec{\pi}_2} & \frac{P_3^S P_2^O \vec{\pi}_3 + P_4^S P_4^O \vec{\pi}_4}{\vec{\pi}_3 + \vec{\pi}_4} \\ \frac{P_1^S (1 - P_1^O) \vec{\pi}_1 + P_2^S (1 - P_3^O) \vec{\pi}_2}{\vec{\pi}_1 + \vec{\pi}_2} & \frac{P_3^S (1 - P_2^O) \vec{\pi}_3 + P_4^S (1 - P_4^O) \vec{\pi}_4}{\vec{\pi}_3 + \vec{\pi}_4} \\ \frac{(1 - P_1^S) P_1^O \vec{\pi}_1 + (1 - P_2^S) P_3^O \vec{\pi}_2}{\vec{\pi}_1 + \vec{\pi}_2} & \frac{(1 - P_3^S) P_2^O \vec{\pi}_3 + (1 - P_4^S) P_4^O \vec{\pi}_4}{\vec{\pi}_3 + \vec{\pi}_4} \\ \frac{(1 - P_1^S) (1 - P_1^O) \vec{\pi}_1 + (1 - P_2^S) (1 - P_3^O) \vec{\pi}_2}{\vec{\pi}_1 + \vec{\pi}_2} & \frac{(1 - P_3^S) (1 - P_2^O) \vec{\pi}_3 + (1 - P_4^S) P_4^O \vec{\pi}_4}{\vec{\pi}_3 + \vec{\pi}_4} \end{pmatrix}$$
(5.86)

We can also write this transition matrix as:

$$\mathbf{T}_{SG}^{*} = \begin{pmatrix} \frac{P_{1}^{S} P_{1}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(1, i) \widetilde{P_{G}^{i}}(i) + P_{2}^{S} P_{3}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(2, i) \widetilde{P_{G}^{i}}(j) \\ \Sigma_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{G}(i, j) \widetilde{P_{G}^{i}}(j) \\ \frac{P_{3}^{S} P_{2}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + P_{3}^{S} P_{4}^{A} \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \Sigma_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{P_{1}^{S} (1 - P_{1}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(1, i) \widetilde{P_{G}^{i}}(i) + P_{2}^{S} (1 - P_{3}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(2, i) \widetilde{P_{G}^{i}}(i) \\ \frac{P_{3}^{S} (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + P_{4}^{S} (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{P_{3}^{S} (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + P_{4}^{S} (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{P_{3}^{S} (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + P_{4}^{S} (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{P_{3}^{S} (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{4}^{S}) P_{4}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{1}^{S}) P_{1}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(1, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{3}^{S}) \sum_{i=1}^{4} \mathbf{Err}_{G}(2, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{3}^{S}) P_{2}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{4}^{S}) P_{4}^{O} \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{3}^{S}) (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{3}^{S}) (1 - P_{3}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{4}^{S}) (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{3}^{S}) (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{4}^{S}) (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(4, i) \widetilde{P_{G}^{i}}(i) \\ \frac{(1 - P_{3}^{S}) (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(j) \\ \frac{(1 - P_{3}^{S}) (1 - P_{2}^{O}) \sum_{i=1}^{4} \mathbf{Err}_{G}(3, i) \widetilde{P_{G}^{i}}(i) + (1 - P_{4}^{S}) (1 - P_{4}^{O}) \sum_{i=1}^{4} \mathbf{E$$

We have:

$$H(G(t+1)) = -\sum_{i=1}^{4} \sum_{j=1}^{2} \hat{\mathbf{T}_{\mathbf{SG}}}(\mathbf{i}, \mathbf{j}) A_{S}(j) \log_{2} \left(\sum_{j=1}^{4} \hat{\mathbf{T}_{\mathbf{SG}}}(\mathbf{i}, \mathbf{j}) A_{S}(j)\right)$$
(5.88)

where:

$$\hat{A}_{S} = \begin{pmatrix} \sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(j) \\ \sum_{i=3}^{4} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(i,j) \widetilde{P}_{G}^{t}(j) \end{pmatrix}$$
(5.89)

The conditional entropy between $A_{S}(t)$ and G(t+1) is given by:

$$H\left(G\left(t+1\right)\left|A_{S}\left(t\right)\right) = -\sum_{i\in\{C,D\}} \left\{P_{A_{S}(t)=i}\right\} H\left(G\left(t+1\right)\left|A_{S}(t)=i\right)\right]$$
$$= -\sum_{i\in\{C,D\}} \sum_{j=1}^{4} \left\{P_{A_{S}(t)=i}\right\} \mathbf{\hat{T}_{SG}}\left(\mathbf{j},\mathbf{i}\right) \log_{2}\left(\mathbf{\hat{T}_{SG}}\left(\mathbf{j},\mathbf{i}\right)\right)$$
(5.90)

Thus, the mutual information between $A_{S}\left(t\right)$ and $G\left(t+1\right)$ is:

$$I(G(t+1); A_{S}(t)) = H(G(t+1)) - H(G(t+1)|A_{S}(t))$$

$$= -\sum_{i=1}^{4} \sum_{j=1}^{2} \mathbf{T}_{\mathbf{S}\mathbf{G}}(\mathbf{i}, \mathbf{j}) A_{S}(j) \log_{2} \left(\sum_{j=1}^{4} \mathbf{T}_{\mathbf{S}\mathbf{G}}(\mathbf{i}, \mathbf{j}) A_{S}(j)\right)$$

$$+ \sum_{i \in \{C, D\}} \sum_{j=1}^{4} \left\{ P_{A_{S}(t)=i} \right\} \mathbf{T}_{\mathbf{S}\mathbf{G}}(\mathbf{j}, \mathbf{i}) \log_{2} \left(\mathbf{T}_{\mathbf{S}\mathbf{G}}(\mathbf{j}, \mathbf{i})\right)$$
(5.91)

5.3.6 Mutual information between $A_O(t)$ and other random variables at "t + 1"

To find the mutual information between $A_O(t)$ and other random variables at "t + 1", we have to follow the same idea and derive the transition matrices.

5.3.6.1 Mutual information between $A_{O}(t)$ and $A_{S}(t+1)$

The transition matrix between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$ is given by:

$$\mathbf{T}_{OS}^{\circ} = \begin{pmatrix} C & D \\ P_1^{S} P(A_S^{C}(t) | A_O^{C}(t)) + P_3^{S} P(A_S^{D}(t) | A_O^{C}(t)) & P_2^{S} P(A_S^{C}(t) | A_O^{D}(t)) + P_4^{S} P(A_S^{D}(t) | A_O^{D}(t)) \\ (1 - P_1^{S}) P(A_S^{C}(t) | A_O^{O}(t)) + (1 - P_3^{S}) P(A_S^{D}(t) | A_O^{C}(t)) & (1 - P_2^{S}) P(A_S^{C}(t) | A_O^{D}(t)) + (1 - P_4^{S}) P(A_S^{D}(t) | A_O^{D}(t)) \end{pmatrix}$$
(5.92)

where:

$$P(A_{S}^{C}(\hat{t})|A_{O}^{C}(t)) = \frac{\hat{\pi}_{1}}{\hat{\pi}_{1} + \hat{\pi}_{3}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(1, i) P_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i - 1, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{S}^{D}(\hat{t})|A_{O}^{C}(t)) = \frac{\hat{\pi}_{3}}{\hat{\pi}_{1} + \hat{\pi}_{3}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(3, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i - 1, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{S}^{C}(\hat{t})|A_{O}^{D}(t)) = \frac{\hat{\pi}_{2}}{\hat{\pi}_{2} + \hat{\pi}_{4}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(2, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i, j) \widetilde{P}_{G}^{t}(j)}$$

$$P(A_{S}^{D}(\hat{t})|A_{O}^{D}(t)) = \frac{\hat{\pi}_{4}}{\hat{\pi}_{2} + \hat{\pi}_{4}} = \frac{\sum_{i=1}^{4} \mathbf{Err}_{\mathbf{G}}(4, i) \widetilde{P}_{G}^{t}(i)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i, j) \widetilde{P}_{G}^{t}(j)}$$
(5.93)

Therefore, we have:

$$\mathbf{\hat{T}_{OS}} = \begin{pmatrix} C & D \\ \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} & \sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(2i) \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)} \\ D \begin{pmatrix} 2^{2} \sum_{i=1}^{4} \sum_{j=1}^{4} \widetilde{G_{S}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} \\ 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} & 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{S}}(2i) \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} & 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)} \end{pmatrix}$$
(5.94)

Thus, the entropy of self action is:

$$H(A_{S}(t+1)) = -\widetilde{G}_{S}\widetilde{\widetilde{P}_{G}^{t}}\log_{2}\left(\widetilde{G}_{S}\widetilde{\widetilde{P}_{G}^{t}}\right) - \left(1 - \widetilde{G}_{S}\right)\widetilde{\widetilde{P}_{G}^{t}}\log_{2}\left(\left(1 - \widetilde{G}_{S}\right)\widetilde{\widetilde{P}_{G}^{t}}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\widehat{\mathbf{T}_{OS}}(i,j)\widetilde{\widetilde{P}_{O}^{A}}(j)\log_{2}\left(\sum_{j=1}^{2}\widehat{\mathbf{T}_{OS}}(i,j)\widetilde{\widetilde{P}_{O}^{A}}(j)\right) \quad (5.95)$$

where:

$$\hat{A}_{O} = \begin{pmatrix} \sum_{i=1}^{2} \sum_{j=1}^{4} \operatorname{Err}_{\mathbf{G}} (2i-1,j) \widetilde{P}_{G}^{t}(j) \\ \sum_{i=1}^{2} \sum_{j=1}^{4} \operatorname{Err}_{\mathbf{G}} (2i,j) \widetilde{P}_{G}^{t}(j) \end{pmatrix}$$
(5.96)

The conditional entropy between $A_O(t)$ and $A_S(t+1)$ is given by:

$$H\left(A_{S}(t+1)|A_{O}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(A_{S}(\hat{t}+1)|A_{O}(t)=i\right)$$

$$= -\left\{\overline{\left\{P_{A_{O}(t)=C}\right\}}\sum_{i=1}^{2} \mathbf{T}_{\mathbf{OS}}(i,1)\log_{2}\left(\mathbf{T}_{\mathbf{OS}}(i,1)\right)$$

$$-\left\{\overline{\left\{P_{A_{O}(t)=C}\right\}}\sum_{i=1}^{2} \mathbf{T}_{\mathbf{OS}}(i,2)\log_{2}\left(\mathbf{T}_{\mathbf{OS}}(i,2)\right)$$

$$= -\sum_{i=1}^{2}\sum_{j=1}^{2} (\hat{\pi}_{i} + \hat{\pi}_{i+2})\mathbf{T}_{\mathbf{OS}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{OS}}(j,i)\right)$$

$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k \in \{i,i+2\}}\sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P_{G}}(l)\mathbf{T}_{\mathbf{OS}}(j,i)\log_{2}\left(\mathbf{T}_{\mathbf{OS}}(j,i)\right)$$
(5.97)

Therefore, the mutual information between $A_{O}\left(t\right)$ and $A_{S}\left(t+1\right)$ is:

$$I(A_{S}(t+1); A_{O}(t)) = H\left(A_{S}(t+1)\right) - H\left(A_{S}(t+1) | A_{O}(t)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{T}_{OS}^{*}(i, j) \, \widehat{P_{O}^{A}}(j) \log_{2}\left(\sum_{j=1}^{2} \mathbf{T}_{OS}^{*}(i, j) \, \widehat{P_{O}^{A}}(j)\right)$$

$$+ \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k \in \{i, i+2\}} \sum_{l=1}^{4} \mathbf{Err}_{G}(k, l) \, \widehat{P_{G}^{*}}(l) \, \mathbf{T}_{OS}^{*}(j, i) \log_{2}\left(\mathbf{T}_{OS}^{*}(j, i)\right)$$
(5.98)

5.3.6.2 Mutual information between $A_O(t)$ and $A_O(t+1)$

To find the mutual information between $A_O(t+1)$ and $A_O(t)$, we should follow the same idea. We have:

$$\mathbf{T_{OO}} = \begin{pmatrix} C & D \\ P_1^O P(A_S^C(t) | A_O^C(t)) + P_2^O P(A_S^D(t) | A_O^C(t)) & P_3^O P(A_S^C(t) | A_O^D(t)) + P_4^O P(A_S^D(t) | A_O^D(t)) \\ (1 - P_1^O) P(A_S^C(t) | A_O^O(t)) + (1 - P_2^O) P(A_S^D(t) | A_O^C(t)) & (1 - P_3^O) P(A_S^C(t) | A_O^D(t)) + (1 - P_4^O) P(A_S^D(t) | A_O^D(t)) \end{pmatrix}$$
(5.99)

or:

$$\mathbf{T_{OO}} = \begin{pmatrix} C & D \\ \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i) \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)} \\ D & \begin{pmatrix} \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{G}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} \\ 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i-1) \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i) \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)} \\ 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \widetilde{G_{O}^{*}}(2i-1,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i-1,j) \widetilde{P_{G}^{t}}(j)} \\ 1 - \frac{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)}{\sum_{i=1}^{2} \sum_{j=1}^{4} \mathbf{Err}_{\mathbf{G}}(2i,j) \widetilde{P_{G}^{t}}(j)} \\ \end{pmatrix}$$
(5.100)

Thus, the entropy of opponent's action is:

$$H(A_{S}(t+1)) = -\widetilde{G}_{O}^{*}\widetilde{P}_{G}^{t} \log_{2}\left(\widetilde{G}_{O}^{*}\widetilde{P}_{G}^{t}\right) - \left(1 - \widetilde{G}_{O}^{*}\right)\widetilde{P}_{G}^{t} \log_{2}\left(\left(1 - \widetilde{G}_{O}^{*}\right)\widetilde{P}_{G}^{t}\right)$$
$$= -\sum_{i=1}^{2}\sum_{j=1}^{2}\mathbf{T}_{OO}^{*}(i,j)\widetilde{P}_{O}^{A}(j) \log_{2}\left(\sum_{j=1}^{2}\mathbf{T}_{OO}^{*}(i,j)\widetilde{P}_{O}^{A}(j)\right) \quad (5.101)$$

The conditional entropy between $A_{O}\left(t\right)$ and $A_{o}\left(t+1\right)$ is given by:

$$H\left(A_{O}(t+1)|A_{O}(t)\right) = \sum_{i \in \{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(A_{O}(\hat{t}+1)|A_{O}(t)=i\right)$$

$$= -\left\{P_{A_{O}(t)=C}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OO}}(i,1) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(i,1)\right)$$

$$-\left\{P_{A_{O}(t)=D}\right\} \sum_{i=1}^{2} \mathbf{T}_{\mathbf{OO}}(i,2) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(i,2)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} (\hat{\pi}_{i} + \hat{\pi}_{i+2}) \mathbf{T}_{\mathbf{OO}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(j,i)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k \in \{i,i+2\}}^{4} \mathbf{Err}_{\mathbf{G}}(k,l) \widetilde{P_{G}^{t}}(l) \mathbf{T}_{\mathbf{OO}}(j,i) \log_{2}\left(\mathbf{T}_{\mathbf{OO}}(j,i)\right)$$
(5.102)

Therefore, the mutual information between $A_{O}\left(t\right)$ and $A_{O}\left(t+1\right)$ is:

$$I(A_{O}(t+1); A_{O}(t)) = H\left(A_{O}(t+1)\right) - H\left(A_{O}(t+1) | A_{O}(t)\right)$$

$$= -\sum_{i=1}^{2} \sum_{j=1}^{2} \widehat{\mathbf{T}_{OO}}(i, j) \widehat{\widehat{P_{O}^{A}}}(j) \log_{2}\left(\sum_{j=1}^{2} \widehat{\mathbf{T}_{OO}}(i, j) \widehat{\widehat{P_{O}^{A}}}(j)\right)$$

$$+ \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k \in \{i, i+2\}} \sum_{l=1}^{4} \mathbf{Err}_{\mathbf{G}}(k, l) \widehat{P_{G}^{t}}(l) \widehat{\mathbf{T}_{OO}}(j, i) \log_{2}\left(\widehat{\mathbf{T}_{OO}}(j, i)\right)$$
(5.103)

5.3.6.3 Mutual information between $A_{O}\left(t\right)$ and $G\left(t+1\right)$

The transition matrix between $A_O(t)$ and G(t+1) is:

$$\mathbf{T_{OG}} = \begin{pmatrix} P_1^S P_1^O P(A_S^C(t) | A_O^C(t)) + P_3^S P_2^O P(A_S^D(t) | A_O^C(t)) \\ P_2^S P_3^O P(A_S^C(t) | A_O^D(t)) + P_4^S P_4^O P(A_S^D(t) | A_O^D(t)) \\ P_1^S (1 - P_1^O) P(A_S^C(t) | A_O^C(t)) + P_3^S (1 - P_2^O) P(A_S^D(t) | A_O^C(t)) \\ P_2^S (1 - P_3^O) P(A_S^C(t) | A_O^D(t)) + P_4^S (1 - P_4^O) P(A_S^D(t) | A_O^D(t)) \\ (1 - P_1^S) P_1^O P(A_S^C(t) | A_O^C(t)) + (1 - P_3^S) P_2^O P(A_S^D(t) | A_O^D(t)) + (1 - P_4^S) P_4^O P(A_S^D(t) | A_O^D(t)) \\ (1 - P_1^S) (1 - P_1^O) P(A_S^C(t) | A_O^C(t)) + (1 - P_3^S) (1 - P_2^O) P(A_S^D(t) | A_O^D(t)) \\ (1 - P_2^S) (1 - P_3^O) P(A_S^C(t) | A_O^D(t)) + (1 - P_4^S) (1 - P_4^O) P(A_S^D(t) | A_O^D(t)) \end{pmatrix}$$
(5.104)

or:

$$\mathbf{\hat{T}_{OG}} = \frac{CC}{DD} \begin{pmatrix} \frac{P_1^S P_1^O \hat{\pi}_1 + P_3^S P_2^O \hat{\pi}_3}{\hat{\pi}_1 + \hat{\pi}_3} & \frac{P_2^S P_3^O \hat{\pi}_2 + P_4^S P_4^O \hat{\pi}_4}{\hat{\pi}_2 + \hat{\pi}_4} \\ \frac{P_1^S (1 - P_1^O) \hat{\pi}_1 + P_3^S (1 - P_2^O) \hat{\pi}_3}{\hat{\pi}_1 + \hat{\pi}_3} & \frac{P_2^S (1 - P_3^O) \hat{\pi}_2 + P_4^S (1 - P_4^O) \hat{\pi}_4}{\hat{\pi}_2 + \hat{\pi}_4} \\ \frac{(1 - P_1^S) P_1^O \hat{\pi}_1 + (1 - P_3^S) P_2^O \hat{\pi}_3}{\hat{\pi}_1 + \hat{\pi}_3} & \frac{(1 - P_2^S) P_3^O \hat{\pi}_2 + (1 - P_4^S) P_4^O \hat{\pi}_4}{\hat{\pi}_2 + \hat{\pi}_4} \\ \frac{(1 - P_1^S) (1 - P_1^O) \hat{\pi}_1 + (1 - P_3^S) (1 - P_2^O) \hat{\pi}_3}{\hat{\pi}_1 + \hat{\pi}_3} & \frac{(1 - P_2^S) (1 - P_3^O) (\hat{\pi}_2) + (1 - P_4^S) (1 - P_4^O) \hat{\pi}_4}{\hat{\pi}_2 + \hat{\pi}_4} \end{pmatrix}$$
(5.105)

We can also write this transition matrix as:

$$\mathbf{T_{OG}^{\circ}} = \begin{pmatrix} \frac{P_{1}^{S}P_{1}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(1,i)\widetilde{P_{G}^{i}}(i) + P_{3}^{S}P_{2}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{j=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{P_{2}^{S}P_{3}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j) + P_{3}^{S}P_{4}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{j=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{P_{1}^{S}\left(1-P_{1}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(1,i)\widetilde{P_{G}^{i}}(j) + P_{3}^{S}\left(1-P_{2}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{j=1}^{4}\operatorname{Err}_{G}(2,i-1,j)\widetilde{P_{G}^{i}}(j)} \\ \frac{P_{2}^{S}\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j) + P_{3}^{S}\left(1-P_{4}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{j=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{1}^{S}\right)P_{1}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(1,i)\widetilde{P_{G}^{i}}(j) + \left(1-P_{3}^{S}\right)P_{2}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)P_{3}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j) + \left(1-P_{3}^{S}\right)P_{4}^{O}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{j=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{1}^{S}\right)\left(1-P_{1}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(1,i)\widetilde{P_{G}^{i}}(i) + \left(1-P_{3}^{S}\right)\left(1-P_{2}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(3,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{1}^{S}\right)\left(1-P_{1}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)}{\Sigma_{i=1}^{2}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j)} \\ \frac{\left(1-P_{2}^{S}\right)\left(1-P_{3}^{O}\right)\sum_{i=1}^{4}\operatorname{Err}_{G}(2,i)\widetilde{P_{G}^{i}}(j$$

We have:

$$H(G(t+1)) = -\sum_{i=1}^{4} \sum_{j=1}^{2} \hat{\mathbf{T}_{OG}}(\mathbf{i}, \mathbf{j}) A_{O}(j) \log_{2} \left(\sum_{j=1}^{4} \hat{\mathbf{T}_{OG}}(\mathbf{i}, \mathbf{j}) A_{O}(j)\right)$$
(5.107)

The conditional entropy between $A_O(t)$ and G(t+1) is given by:

$$H\left(G\left(t+1\right)|A_{O}\left(t\right)\right) = -\sum_{i\in\{C,D\}} \left\{P_{A_{O}(t)=i}\right\} H\left(G\left(t+1\right)|A_{O}(t)=i\right)$$
$$= -\sum_{i\in\{C,D\}} \sum_{j=1}^{4} \left\{P_{A_{O}(t)=i}\right\} \hat{\mathbf{T}_{OG}}\left(\mathbf{j},\mathbf{i}\right) \log_{2}\left(\hat{\mathbf{T}_{OG}}\left(\mathbf{j},\mathbf{i}\right)\right)$$
(5.108)

Thus, the mutual information between $A_O(t)$ and G(t+1) is:

$$I(G(t+1); A_{O}(t)) = H(G(t+1)) - H(G(t+1)|A_{O}(t))$$

= $-\sum_{i=1}^{4} \sum_{j=1}^{2} \hat{\mathbf{T}_{OG}}(\mathbf{i}, \mathbf{j}) A_{O}(j) \log_{2} \left(\sum_{j=1}^{4} \hat{\mathbf{T}_{OG}}(\mathbf{i}, \mathbf{j}) A_{O}(j)\right)$
+ $\sum_{i \in \{C, D\}} \sum_{j=1}^{4} \left\{ P_{A_{O}(t)=i} \right\} \hat{\mathbf{T}_{OG}}(\mathbf{j}, \mathbf{i}) \log_{2} \left(\hat{\mathbf{T}_{OG}}(\mathbf{j}, \mathbf{i}) \right)$ (5.109)

In the next section, we design an agent based modeling and simulated evolutionary game to check the validity of our hypotheses on necessity of communication, information exchange, and trust raising for evolution of super-reciprocal behavior.

5.4 Experimental Setup

Computational experiments were generally performed as a well mixed population, given the specific mutation rate (varies) and a replacement rate=0.01. However, 1,000,000 updates were performed, and the payoff table was adapted by changing T accordingly. At each update, every player on the torus like 32×32 grid (with wrapping boundary conditions) plays each of its immediate neighbors exactly once. Upon birth, each player begins by consulting its P_C gene for each opponent, and one of the four conditional genes thereafter, depending on its own play and the opponents response. Players are selected for removal randomly with a probability given by the replacement rate r, giving rise to overlapping generations (asynchronous updating) [?, 153, 110]. As long as the player and its opponent are not replaced, they continue to consult their conditional genes to make decisions, so the replacement rate determines the average length of play history between two players (if a players partner is replaced, the partner is greeted by consulting the unconditional gene). To

implement well-mixed populations using our grid structure, we only changed the identity of the pool used for replacing individuals marked for death, thus keeping the rest of the dynamics consistent. The pool is given by all 1,023 remaining strategies in the population (in a Moran process, it is not usual for the individual to be marked for death to be included in the candidates for replication). The chosen player for replacement is selected randomly among all 1,024 players in the population, irrespective of population structure or fitness. After replication, a genotype is mutated with a probability m, which is the mean number of mutations per gene per individual, implemented as a Poisson process. For most of the results in this agent based modeling, the genes probabilities are coarse-grained to 15 bits, which means that the probabilities are chosen from among $2^{15} = 32,768$ possible values, representing the number of possible alleles at that locus. This resolution affects the critical mutation rates. Since the mutation probabilities are thought to represent the decision of entire pathways of perhaps hundreds of genes, they should not be compared to per-nucleotide mutation rates Rather than collecting population averages of plays, we instead study the evolution of strategies by following the line of descent (LoD) of player genotypes for each replicate run. The LoD is obtained by choosing a random player at the end of the run and following its direct ancestors backwards to the first genotype [137]. After reconstruction the LoD, the mean probabilities to cooperate or defect $(P_{CC}, P_{CD}, P_{DC}, P_{DD})$ as well as the fraction of past moves encountered $(\pi_{CC}, \pi_{CD}, \pi_{DC}, \pi_{DD})$ were obtained by taking the average from simulation update 900,000 to 950,000 to exclude any noise in the population that would be different from the LoD. This removes most or all of the transient and also the variance due to picking random genotypes as the originators of the LoD. Since the LoD splits at the most recent common ancestor (MRCA) of the population at the end of the run, the LoD past the MRCA is not necessarily representative of the evolutionary dynamics. Thus, discarding the last 50,000 updates truncates the LoD to genotypes before the MRCA for almost all runs. Using the MRCA genotype instead of the consensus genotype as representative of the fixed point does not change the results.

Additionally, environmental noise was introduced by randomly changing what an agent remembered about it's last move and the opponents move. Depending on the noise probability, what the agent remembered (C or D) was drawn from a uniform random distribution. Mutual information was obtained by either computationally simulating actual agents play the game 1000 times and making 200 moves. Of these 200 moves the first 160 were discarded to eliminate effects from a random first move. Mutual information was calculated from these plays. Alternatively mutual information was directly calculated by using a Markov process that estimated the current and last move probabilities for two interacting agents. These estimates were directly translated into mutual information. Both methods had equivalent results. For all main figures we used the Markov process estimates. Computational experiments required extensive parameter sweeps and many replicates. Accurate assessment of order parameters and mutual information requires a huge amount of replicates. To keep the computational load in a reasonable range (a couple of CPU years) we used a smoothing function (**MatLab** smoothn [154]) instead of increasing the number of replicates, which would have had the same effect.

5.5 Results

In this section, the effect of mutation rate, temptation reward, and environmental noise on evolution of secondary cooperation in our agent based modeling of iterated trust dilemma is investigated. Here, the population is well-mixed, and we change each of the mentioned factors to see how game dynamic changes. We repeat each scenario twenty times. Later, we discuss the effects of these factors together on evolution of cooperation and super cooperation in both IPD and ITD.

5.5.1 Effect of Temptation Payoff

Figure (5.2) shows strategy of players over line of descent. Each subplot represents one gene that corresponds to CC, CD, DC, and DD previous round of game. Each color shows the evolution of strategies for one temptation payoff ($T = 4, \ldots 9$). Figure (5.3)



Figure 5.2: Evolved strategies over line of descent. LoD Genome statistics (P_X) averaged over 20 experiments (1,000,000 generations each) at fixed low mutation rate $\mu = 0.007$, fixed r (1%) and different temptation rewards $T4, \ldots 9$. Each color represents one temptation reward (blue: 4, red: 5, green: 6, black: 7, cyan: 8, and magenta: 9): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.

shows the statistics of interaction over generations. Similar to the previous figure, each

subplot represents one type of played game (CC, CD, DC, and DD). Each color shows the statistics of played games for one temptation payoff ($T = 4, \ldots 9$). Secondary cooperation



Figure 5.3: Game statistics over line of descent. LoD Genome statistics (π_X) averaged over 20 experiments (1,000,000 generations each) at fixed low mutation rate $\mu = 0.007$, fixed r (1%) and different temptation rewards $T4, \ldots 9$. Each color represents one temptation reward (blue: 4, red: 5, green: 6, black: 7, cyan: 8, and magenta: 9): (a) π_1 over line of descent, (b) π_2 over line of descent, (c) π_3 over line of descent, and (d) π_4 over line of descent.

can exist in standard IPD (low temptation payoff); however, this strategy usually has a short life time since it is associated with an initial phase of strategy equilibration that a population undergoes. On the other hand, as we increase the temptation payoff, dominant strategy switches from primary cooperation to secondary cooperation. As we expected, both gene values are very close 0 and 1 in ITD (especially for higher temptation rewards (e.g. 8 or 9)) since secondary cooperation is much more error reluctant than the primary cooperation. Any break in the exchange of CD and DC moves will result in a harsh payoff loss to both players and possibly lengthy periods of error correction.

5.5.2 Effect of mutation rate

Figure (5.4) and (5.5) show statistics of strategies over line of descent for temptation reward 5 and 10 respectively. Each subplot represents one gene $(P_1, P_2, P_3, \text{ and } P_4)$. Each color shows the evolution of strategies for one mutation rate ($\mu = 0.007, \ldots 0.020$). Figure (5.6)



Figure 5.4: Evolved strategies over line of descent. LoD Genome statistics (P_X) averaged over 20 experiments (1,000,000 generations each) at different mutation rate $\mu = 0.007 \dots 0.02$, fixed r (1%) and fixed temptation rewards T = 5. Each color represents one mutation rate (blue: 0.007, red: 0.008, green: 0.009, black: 0.01, cyan: 0.012, magenta: 0.016, and yellow: 0.02): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.

and (5.7) show statistics of interactions between agents over the course of evolution. Similar to the previous figures, each subplot represents one type of played game (*CC*, *CD*, *DC*, and *DD*). Each color shows the statistics of played games for one mutation rate. In these wellmixed populations and for T = 10, it is observed that secondary cooperation only appears at low mutation rates i.e. $\mu \leq 1\%$. For lower values of *T*, i.e., $6 \leq T < 8$, we could not find any



Figure 5.5: Evolved strategies over line of descent. LoD Genome statistics (P_X) averaged over 20 experiments (1,000,000 generations each) at different mutation rate $\mu = 0.007 \dots 0.02$, fixed r (1%) and fixed temptation rewards T = 10. Each color represents one mutation rate (blue: 0.007, red: 0.008, green: 0.009, black: 0.01, cyan: 0.012, magenta: 0.016, and yellow: 0.02): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.



Figure 5.6: Game statistics over line of descent. LoD Genome statistics (π_X) averaged over 20 experiments (1,000,000 generations each) at different mutation rate $\mu = 0.007...0.02$, fixed r (1%) and fixed temptation rewards T = 5. Each color represents one mutation rate (blue: 0.007, red: 0.008, green: 0.009, black: 0.01, cyan: 0.012, magenta: 0.016, and yellow: 0.02): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.



Figure 5.7: Game statistics over line of descent. LoD Genome statistics (π_X) averaged over 20 experiments (1,000,000 generations each) at different mutation rate $\mu = 0.007...0.02$, fixed r (1%) and fixed temptation rewards T = 10. Each color represents one mutation rate (blue: 0.007, red: 0.008, green: 0.009, black: 0.01, cyan: 0.012, magenta: 0.016, and yellow: 0.02): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.

secondary cooperative behavior even in this low mutation rate. Unlike primary cooperation, secondary cooperation is an immensely costly behavior to evolve simply because it relies on the coordination of two genes rather than one. Secondary cooperation is very sensitive to mutation and undergoes a critical transition at $\mu \approx 1.5\%$ for T = 10 to defection (Fig. 5.7 c and d).

5.5.3 Effect of environmental noise

Figure (5.8) and (5.9) show statistics of strategies over line of descent in noisy environments for temptation reward 5 and 10 respectively. Here, we assume both self and opponent noise are identical. Each subplot represents one gene $(P_1, P_2, P_3, \text{ and } P_4)$. Each color shows the evolution of strategies for one noise level ($\epsilon = 0.001, \ldots 0.007$). Figure (5.10) and (5.11) show statistics of interactions between agents over course of evolution in noisy environments. Similar to the previous figures, each subplot represents one type of played game (CC, CD, DC, and DD). Each color shows the statistics of played games for one environmental noise level. According to fig. (5.10) and (5.11), secondary cooperation is more robust to the environmental noise. One reason is the high temptation reward (T = 10). For lower temptation payoffs the sensitivity of secondary cooperation to environmental noise is more obvious. We address this issue later by introducing the order parameter.

5.6 Discussion

Stochastic strategies which engage in secondary cooperation are evolvable in iterated trust dilemma game (increasing temtation reward to a value greater than "2R - S"). Since these strategies rely on the coordination of two genes, compare to primary cooperation these



Figure 5.8: Evolved strategies over line of descent in noisy environments. LoD Genome statistics (P_X) averaged over 20 experiments (1,000,000 generations each) at different noise rates $\epsilon = 0.001 \dots 0.007$, fixed low mutation rate μ (0.7%), fixed r (1%) and fixed temptation reward T = 5 (IPD). Each color represents one environmental noise level (blue: 0.001, red: 0.002, green: 0.003, black: 0.004, cyan: 0.005, magenta: 0.006, and yellow: 0.007): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.



Figure 5.9: Evolved strategies over line of descent. LoD Genome statistics (P_X) averaged over 20 experiments (1,000,000 generations each) at different noise rates $\epsilon = 0.001 \dots 0.007$, fixed low mutation rate μ (0.7%), fixed r (1%) and fixed temptation reward T = 10 (ITD). Each color represents one environmental noise level (blue: 0.001, red: 0.002, green: 0.003, black: 0.004, cyan: 0.005, magenta: 0.006, and yellow: 0.007): (a) P_1 over line of descent, (b) P_2 over line of descent, (c) P_3 over line of descent, and (d) P_4 over line of descent.



Figure 5.10: Game statistics over line of descent. LoD Genome statistics (π_X) averaged over 20 experiments (1,000,000 generations each) at different noise rates $\epsilon = 0.001 \dots 0.007$, fixed low mutation rate μ (0.7%), fixed r (1%) and fixed temptation reward T = 5 (IPD). Each color represents one environmental noise level (blue: 0.001, red: 0.002, green: 0.003, black: 0.004, cyan: 0.005, magenta: 0.006, and yellow: 0.007): (a) π_1 over line of descent, (b) π_2 over line of descent, (c) π_3 over line of descent, and (d) π_4 over line of descent.


Figure 5.11: Game statistics over line of descent. LoD Genome statistics (π_Y) averaged over 20 experiments (1,000,000 generations each) at different noise rates $\epsilon = 0.001 \dots 0.007$, fixed low mutation rate μ (0.7%), fixed r (1%) and fixed temptation reward T = 10 (ITD). Each color represents one environmental noise level (blue: 0.001, red: 0.002, green: 0.003, black: 0.004, cyan: 0.005, magenta: 0.006, and yellow: 0.007): (a) π_1 over line of descent, (b) π_2 over line of descent, (c) π_3 over line of descent, and (d) π_4 over line of descent.

strategies are more costly, and they are more sensitive to environmental disturbances such as mutation rate and environmental noise that affect the certainty with which agents predict the future states of the environment. Primary cooperation is a strategy that is mostly rely on one gene (P_1) , it is expected that this strategy be more stable than the secondary cooperation under mutational load. Temptation reward 2R - S (with our setup, T = 6) is the critical turning point from primary cooperation to secondary cooperation, and for temptation rewards greater than this critical value primary cooperation is never favored over secondary cooperation; however, for T = 2R - S primary and secondary cooperation as the two dominant attractors of this game will alternate. Since secondary cooperation is more sensitive to mutation rate for small temptation rewards compare to primary cooperation, we expect that for temptation payoff slightly greater than critical value "2R - S" secondary cooperation would not have sufficient payoff advantage to overtake a more robust strategy such as primary cooperation. Nonetheless, by increasing mutation rate or environmental noise both of these strategies switch to defection. This phenomenon happens earlier in ITD for smaller temptation rewards. Using the average play frequencies in each round, we can define two order parameters m_1 and m_2 for IPD and ITD respectively to determine the critical area of this phase transition:

$$m_1 = \frac{\langle \pi_1 \rangle - \langle \pi_4 \rangle}{\langle \pi_1 \rangle + \langle \pi_4 \rangle} \tag{5.110}$$

$$m_2 = \langle \pi_2 \rangle + \langle \pi_3 \rangle - \langle \pi_1 \rangle - \langle \pi_4 \rangle \tag{5.111}$$

These parameters cross zero at a critical mutation rate and environmental noise, indicating the dominant strategies in IPD and ITD. Secondary cooperation is stable at low mutation rate and low environmental noise, and as we increase these parameters it switches to defection. A high temptation reward provides less cost to secondary cooperation and consequently offsets the uncertainty of the environment.

Figures (5.12-5.15) and (5.16-5.19) demonstrate the effect of mutation rate and temptation reward on evolution of strategies and statistics of interactions between agents over course of evolution in noiseless environments for IPD and ITD. Both games depict how strategies switch to defection when we increase the mutation rate. Moreover, these figures show how secondary cooperation becomes more resistant to mutation rate as we increase the temptation reward.



Figure 5.12: Effect of mutation rate and temptation payoff on strategies in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates P_1 over line of descent.

Figure (5.20) and (5.21) present the order parameter one and two and critical turning



Figure 5.13: Effect of mutation rate and temptation payoff on strategies in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...05$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates P_2 over line of descent.



Figure 5.14: Effect of mutation rate and temptation payoff on strategies in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates P_3 over line of descent.



Figure 5.15: Effect of mutation rate and temptation payoff on strategies in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...05$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates P_4 over line of descent.



Figure 5.16: Effect of mutation rate and temptation payoff on statistics of games in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates π_1 over line of descent.



Figure 5.17: Effect of mutation rate and temptation payoff on statistics of games in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates π_2 over line of descent.



Figure 5.18: Effect of mutation rate and temptation payoff on statistics of games in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates π_3 over line of descent.



Figure 5.19: Effect of mutation rate and temptation payoff on statistics of games in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate, and Z-axis indicates π_4 over line of descent.

points of primary and secondary cooperation to defection for IPD and ITD respectively. These figures depict how increasing mutation rate reduces the cooperative behavior in the population and how by increasing temptation reward secondary cooperation becomes more resistant to the mutation rate and uncertainty in the environment.

Figure (5.22) and (5.23) show the effect of environmental noise on the primary and secondaty cooperation for IPD and ITD respectively. Similar to previous figures, these figures exhibit how increasing environmental noise (ϵ_{Self} and ϵ_{Other}) reduces the cooperative behavior in the population and how by increasing temptation reward secondary cooperation becomes more resistant to the environmental noise.

Fig. (5.22) and (5.23) show that although secondary cooperation is more sensitive to mutation rate and it is hard to establish this strategy in population with high mutation rate, it is more robust to environmental noise compare to the primary cooperation. The reason



Figure 5.20: Order parametr one which indictaes critical switching curve from primary cooperation to defection for different temptation reward and mutation rate in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate.



Figure 5.21: Order parametr two which indictaes critical switching curve from secondary cooperation to defection for different temptation reward and mutation rate in noiseless environments averaged over last 50,000 generations of 20 experiments at different mutation rates $\mu = 0.007...0.5$, fixed r (1%) and different temptation rewards T = 5...10. X-axis indicates temptation reward and Y-axis indicates mutation rate.



Figure 5.22: Order parameters for primary and secondary cooperation during IPD and ITD games in noisy environments. Here order parameters indicate how environmental noise causes the phase transition from cooperation to defection in IPD and ITD. Order parameters were averaged over last 50,000 generations of 20 experiments at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r (1%) and different temptation rewards T = 4...10. X-axis indicates environmental noise and Y-axis indicated temptation reward: (a) m_1 for IPD, (b) m_2 for ITD.



Figure 5.23: Effect of self and other noise on primary and secondary cooperation durinf IPD and ITD. Here order parameters indicate how environmental noise causes the phase transition from cooperation to defection in IPD and ITD. Order parameters were averaged over last 50,000 generations of 20 experiments at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r (1%) and T = 5 for IPD and T = 10 for ITD. X-axis indicates environmental noise and Y-axis indicated temptation reward: (a) m_1 for IPD, (b) m_2 for ITD.

for being more robust can be find in the dependency of secondary cooperation to two genes. To establish this strategy, we need to evolve two genes (P_2 and P_3), which will be hard if the mutation rate is high. However, as soon as these genes are evolved, environmental noise has harder time to break the coordination of these two genes compare to the primary cooperation, which relies on just P_1 gene. Moreover, similar to the effect of mutation rate on secondary cooperation, we see that as we increase the temptation reward the robustness of secondary cooperation increases.

Figures (5.24-5.25) and (5.26-5.27) show the effect of environmental noise on mutual information between random variables at two consecutive rounds of IPD and ITD respectively. Similar to previous figures, these figures exhibit how increasing environmental noise (ϵ_{Self} and ϵ_{Other}) reduces the communication between two players and consequently causes switching from cooperative behavior to defection. Interestingly, we see that the phase transition from cooperation to defection occurs at a constant rate of mutual information. Figure (5.28) and (5.29) show the variation of mutual information between game played and action chosen from self player in the next round of game (I_{GS}) vs. the variation of order parameter. Our results show that the minimum rate of information for maintaining primary or secondary cooperation in noisy environment is around 0.18 bits of information for both games. To see how 0.18 bits of information is enough to maintain primary and secondary cooperation in IPD and ITD, we apply the information entropy approximation as:

$$I\left(x\right) = 1 - H\left(x\right)$$

This means that 0.18 bits of information is equivalent to 0.82 entropy in the system. In other words, if the entropy in the system is 0.82, the discrimination rate for such system is



Figure 5.24: Effect of environmental noise on mutual information between random variables during two consecutive rounds of IPD. The phase transition from cooperation to defection (determined by order parameter one) and drop in mutual information have the same pattern. Mutual information between random variables were calculated analytically and estimated from agent based simulation at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r (1%) and fixed temptation rewards T = 5. X-axis indicates environmental noise and Y-axis indicates temptation reward, and Z-axis indicates the mutual information between random variables: (a) I_{GG} , (b) I_{GS} .



Figure 5.25: Effect of environmental noise on mutual information between random variables during two consecutive rounds of IPD. The phase transition from cooperation to defection (determined by order parameter one) and drop in mutual information have the same pattern. Mutual information between random variables were calculated analytically and estimated from agent based simulation at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r (1%) and fixed temptation rewards T = 5. X-axis indicates environmental noise and Y-axis indicates temptation reward, and Z-axis indicates the mutual information between random variables: (a) I_{SG} , (b) I_{SS} .



Figure 5.26: Effect of environmental noise on mutual information between random variables during two consecutive rounds of ITD. The phase transition from cooperation to defection (determined by order parameter two) and drop in mutual information have the same pattern. Mutual information between random variables were calculated analytically and estimated from agent based simulation at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r(1%) and fixed temptation rewards T = 7. X-axis indicates environmental noise and Y-axis indicates temptation reward, and Z-axis indicates the mutual information between random variables: (a) I_{GG} , (b) I_{GS} .



Figure 5.27: Effect of environmental noise on mutual information between random variables during two consecutive rounds of ITD. The phase transition from cooperation to defection (determined by order parameter two) and drop in mutual information have the same pattern. Mutual information between random variables were calculated analytically and estimated from agent based simulation at different environmental noise levels $\epsilon = 0.0...0.5$, fixed r(1%) and fixed temptation rewards T = 7. X-axis indicates environmental noise and Y-axis indicates temptation reward, and Z-axis indicates the mutual information between random variables: (a) I_{SG} , (b) I_{SS} .



Figure 5.28: Mutual information between game played and action selected by player in the next round and order parameter one during rounds of IPD in noisy environments with different noise level. Blue line is the order parameter one and the red line is I_{GS} . The black dashed line indicates the phase transition and critical mutual information during the phase transition.



Figure 5.29: Mutual information between game played and action selected by player in the next round and order parameter one during rounds of ITD in noisy environments with different noise level. Blue line is the order parameter one and the red line is I_{GS} . The black dashed line indicates the phase transition and critical mutual information during the phase transition.



around 0.7445 (this is shown in figure (5.30)), which is a high discrimination rate. In sum,

Figure 5.30: Entropy H(x). The 0.82 entropy is equivalent to 0.7445 discrimination rate.

increasing the mutation rate and environmental noise to higher values leads to a transition into defection. This phase transition for ITD occurs at a much lower genomic mutation rate than what is obsered in IPD. This could be owed to the fragility of secondary cooperation when it comes to mutation, as is imparted to it by its dependence on more genes. The payoff advantage of secondary cooperation needs to be sufficiently high ($T \ge 8$) to allow for this strategy to become the dominant strategy (Fig. (5.31)). A high mutational load reduces the stability of strategies which are dependent to more than one genes (i.e. secondary cooperation). On the other hand, in noisy environments secondary cooperation is more robust to environmental noise in comparison to primary cooperation, since this strategy relies on the coordination of two genes of players, and during rounds of ITD these players comunicate during their interaction. This communication is very robust to environments and compare to primary cooperation it can exists in very noisy environments. For environments that are highly predictable (i.e. low mutation rate), and where there is no payoff advantage to engage in secondary cooperation, primary cooperation remains the dominant strategy.



Figure 5.31: Qualitative phase transition diagram as a function of μ and temptation reward. Black solid lines represent the phase transition cures in noiseless environment and red dashed lines represent the phase transition cures in noisy environments.

5.7 Chapter Summary

In this chapter, we showed that stochastic strategies engaging in secondary cooperation can be evolved by increasing the temptation rewards. Such strategies rely on the synchronization of two genes and are thus much more sensitive to environmental changes that affect the certainty of players in predicting future opponents' moves. Here, we investigated the transitions from secondary cooperation to defection at critical mutation rate, environmental noise, and temptation rewards. A biological or social analogue to secondary cooperation has not yet been formally investigated. It is though not hard to imagine such a behavior existing in the economic markets. In particular, during the emergence of stock price inflations leading to the creation of stock market bubbles, the underlying agreement between investors constantly selling and re-buying the same stock is reminiscent of secondary cooperation. The invloved parties agree to take turns in receiving cost by buying a certain stock, with the promise that they will be able to sell that stock at an increased value in the near future. This game in reality involves more than two parties but the type of observed cooperation is very similar to secondary cooperation.

Chapter 6

Game Theoretic Model for Social Behavior in Animals

The only difference between a taxman and a taxidermist is that the taxidermist leaves the skin.

-Mark Twain

[On filing for tax returns] This is too difficult for a mathematician. It takes a philosopher.

-Albert Einstein

- "Everybody" has to pay taxes! Even businessmen, that rob and steal and cheat from people everyday, even "they" have to pay "taxes"!

-Lennie Pike

It's a Mad, Mad, Mad, Mad World, S. Kramer, 1963

The evolution of altruism has been a fascinating conundrum for evolutionary biologists, and scientists have been trying to discover the mechanisms that maintain cooperation since these behaviors are vulnerable to existence of selfish cheaters [155, 156, 157, 158]. One example of this dilemma is the "tragedy of the commons", where individuals can either contribute to a public good or abstain [114, 116, 158]. Since the public good is distributed to everyone regardless of an investment or not, those individuals who abstain will always fare better, unless the public goods multiplier (the synergy) is unrealistically high [159]. Evolutionary game theory as a quantitative framework for analyzing the rational behavior of species has been used to address how public goods is produced among selfish individuals. Several evolutionary game theoretic mechanisms have been proposed to help us understand the collective behavior of animals [155, 156, 160, 158, 157, 159, 161]. Among the proposed mechanism, punishment (especially altruistic punishment [127]) can explain better how cooperation persists among selfish individuals [162, 127, 163, 164, 165, 166, 167].

While it is possible in principle to enforce cooperation via costly punishment as a signaling mechanism [133], it is shown that even though punishment shifts the cooperation regime to emerge at lower synergy thresholds, individuals evolve to become pure cooperators who do not punish. In other words, punishment loses its communication potential in populations of all cooperators. This means that the *threat* of punishment alone is sufficient to drive cooperation [115], while actual punishment is rare. On the contrary, in natural systems we often observe vigorous punishment [168]. Another difference between the public goods game and (some) natural systems is that in the public goods game the payoff is a linear function of the amount paid in, while in natural systems often a *threshold* determines how much individuals need to contribute in order to obtain a fixed payoff that does not depend on the number of contributors who ultimately trigger it (more wolves hunting in a pack does not increase the size of the moose: you either get the moose or you don't) [169, 157].

To remedy these discrepancies between the public goods game and the game-theoretic dilemma observed for example in collective hunting strategies, in this chapter we introduce the "collective hunting game" as an extension to public goods game where a fixed payoff is distributed equally once enough individuals cooperate (number of contributors \geq threshold). This approach is similar to the proposed models in [169, 157]; however, here instead of a linear fitness function we use a Heaviside step function to make this model applicable to group hunting patterns of hyenas. This alteration changes the game dramatically. Here, if the investment in the public goods exceeds a given threshold, everyone (contributors as well as cheaters) receives an equal share $\frac{r}{n}$, where r and n are the fixed payoff and the number of players in the game respectively, while if the investment does not reach the threshold,

the investment is lost. We find that punishment, as an effective communication mechanism, emerges as a stable strategy in this game, which in return facilitates cooperation. This suggests that the "collective hunting game" is a better model for natural gambles that are "all-or-nothing", and in which the triggered payoff does not depend on a linear fashion in the number of investors.

6.1 Population dynamic of public goods game

Similar to iterated two players game, the population dynamic of such population follows the replicator equation. Here, punishment can be seen as the assortment term "q" in conditional iterated games discussed in chapter 4. In this game, there are two types of players: cooperators or investors and defectors or free riders. Moreover, these players punish free riders with probabilities " α_{pc} " and " α_{pd} ". Cooperators punish free riders with the probability of " α_{pc} ", and defectors punish free riders (their own type) with the probability of " α_{pd} ". Punishment as an aggressive behavior is a costly action. Players accept a cost to punish the free riders and reduce their payoff as a result of punishment. The mean payoff of each type is:

$$\pi_C = \frac{r}{k+1} (k\rho_c + 1) - \gamma \alpha_{pc} (1 - \rho_c)$$

$$\pi_D = \frac{rk\rho_c}{k+1} - \beta \alpha_{pc}\rho_c - \beta \alpha_{pd} (1 - \rho_c) - \gamma \alpha_{pd} (1 - \rho_c)$$
(6.1)

where r is synergy factor, γ is the cost to the punishment, β is the effect of punishment to the free riders, and k is the number of neighbors around the central player in a k + 1 game. Here, r and k are game parameters and constant for a given game. However, β and γ are the strategy parameters. Thus, player has its own α_{pc} (or α_{pd} if the player is defector), β , and γ , which are constant during the player's life time. These parameters can be different from player to player, and they inherit from ancestors to descendant; therefore, these parameters are evolvable during. Having ρ_c , α_{pc} , and α_{pd} is enough to calculate the concentration of each type of players with its known β and γ . We have:

$$\bar{w} = \rho_c \pi_C + \rho_d \pi_D$$

= $\rho_c \pi_C + (1 - \rho_c) \pi_D$
= $\pi_D + \rho_c (\pi_C - \pi_D)$ (6.2)

$$\pi_{C} - \bar{w} = \pi_{C} - \pi_{D} - \rho_{c} (\pi_{C} - \pi_{D})$$

= $(1 - \rho_{c}) (\pi_{C} - \pi_{D})$ (6.3)

$$\pi_D - \bar{w} = \pi_D - \pi_D + \rho_c (\pi_C - \pi_D) = -\rho_c (\pi_C - \pi_D)$$
(6.4)

Thus, the replicator equation for punishing cooperator and defector would be:

$$\dot{\rho_c} = \rho_c (\pi_C - \bar{w}) = \rho_c (1 - \rho_c) (\pi_C - \pi_D) \dot{\rho_d} = \rho_d (\pi_D - \bar{w}) = -\dot{\rho_c} = -\rho_c (1 - \rho_c) (\pi_C - \pi_D)$$
(6.5)

 $\pi_C - \pi_D$ in equation (6.5) can be written as:

$$\pi_C - \pi_D = \frac{r}{k+1} - 1 - \gamma \left(\alpha_{pc} - \alpha_{pd} \right) \left(1 - \rho_c \right) + \beta \rho_c \left(\alpha_{pc} - \alpha_{pd} \right) + \beta \alpha_{pd} \tag{6.6}$$

Therefore, the replicator equation (6.5) can be written as:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 - \gamma \left(\alpha_{pc} - \alpha_{pd}\right) \left(1 - \rho_c\right) + \beta \rho_c \left(\alpha_{pc} - \alpha_{pd}\right) + \beta \alpha_{pd}\right)$$

$$\dot{\rho_d} = -\rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 - \gamma \left(\alpha_{pc} - \alpha_{pd}\right) \left(1 - \rho_c\right) + \beta \rho_c \left(\alpha_{pc} - \alpha_{pd}\right) + \beta \alpha_{pd}\right)$$
(6.7)

If defectors punish equally as cooperators $(\alpha_{pc} = \alpha_{pd})$, the replicator equation (6.7) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 + \alpha_{pc}\beta\right)$$

$$\dot{\rho_d} = \rho_c \left(1 - \rho_c\right) \left(\frac{-r}{k+1} + 1 - \alpha_{pc}\beta\right)$$
(6.8)

Replicator equation (6.8) shows that in the absence of punishment ($\alpha_{pc} = 0$) if synergy factor r is greater than the the group size k + 1, cooperation is evolutionary stable and it is worth to cooperate. Figure (6.1) shows this phase transition for standard public goods game. Here, mixed strategy does not exist, and we have two fixed points as:

$$\rho_c = 0$$
, defection
 $\rho_c = 1$, cooperation
(6.9)



Figure 6.1: Phase transition in standard public goods game as a function of synergy factor.

By taking the derivative of equation (6.8) respect to ρ_c , we can determine the stability of each fixed point. We have:

$$\frac{d\dot{\rho_c}}{d\rho_c} = (1 - \rho_c) \left(\frac{r}{k+1} - 1 + \alpha_{pc}\beta \right)
- \rho_c \left(\frac{r}{k+1} - 1 + \alpha_{pc}\beta \right)$$
(6.10)

According to equation (6.10), cooperation is evolutionary stable if and only if:

$$r \ge \left(1 - \alpha_{pc}\beta\right)(k+1) \tag{6.11}$$

Defection is evolutionary stable if and only if:

$$r < \left(1 - \alpha_{pc}\beta\right)(k+1) \tag{6.12}$$

If $\alpha_{pc} \neq \alpha_{pd}$, we have three fixed points including the mixed strategy:

 $\rho_{c} = 0, \text{ defection}$ $\rho_{c} = 1, \text{ cooperation}$ $\rho_{c} = \frac{1}{(\gamma + \beta) (\alpha_{pc} - \alpha_{pd})} \left(1 + \gamma (\alpha_{pc} - \alpha_{pd}) - \frac{r}{k+1} - \beta \alpha_{pd} \right), \text{ mixed} \quad (6.13)$

Again, by taking the derivative of equation (6.7) respect to ρ_c , we can determine the stability of each fixed point. We have:

$$\frac{d\dot{\rho_c}}{d\rho_c} = (1 - \rho_c) \left(\frac{r}{k+1} - 1 - \gamma \left(\alpha_{pc} - \alpha_{pd} \right) (1 - \rho_c) + \beta \rho_c \left(\alpha_{pc} - \alpha_{pd} \right) + \beta \alpha_{pd} \right)
- \rho_c \left(\frac{r}{k+1} - 1 - \gamma \left(\alpha_{pc} - \alpha_{pd} \right) (1 - \rho_c) + \beta \rho_c \left(\alpha_{pc} - \alpha_{pd} \right) + \beta \alpha_{pd} \right)
+ (\gamma + \beta) \left(\alpha_{pc} - \alpha_{pd} \right) \rho_c (1 - \rho_c)$$
(6.14)

According to equation (6.14), cooperation is evolutionary stable if and only if:

$$r \ge \left(1 - \alpha_{pc}\beta\right)(k+1) \tag{6.15}$$

Defection is evolutionary stable if and only if:

$$r < \left(1 + \gamma \left(\alpha_{pc} - \alpha_{pd}\right) - \alpha_{pd}\beta\right)(k+1)$$
(6.16)

Mixed strategy is evolutionary stable if and only if:

$$\alpha_{pc} < \alpha_{pd} \tag{6.17}$$

which means that defectors should punish their own type more frequent in comparison to cooperators.

If defectors are smart enough to avoid punishing their own type ($\alpha_{pd} = 0$), the replicator equation for punishing cooperator and pure defector is:

$$\dot{\rho_c} = \rho_c \left(\pi_C - \bar{w}\right)$$

$$= \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 + \alpha_{pc} \left(\rho_c \left(\gamma + \beta\right) - \gamma\right)\right)$$

$$\dot{\rho_d} = \rho_d \left(\pi_D - \bar{w}\right) = -\dot{\rho_c}$$

$$= \rho_c \left(1 - \rho_c\right) \left(-\frac{r}{k+1} + 1 - \alpha_{pc} \left(\rho_c \left(\gamma + \beta\right) - \gamma\right)\right)$$
(6.18)

Since $\alpha_{pd} = 0$, mixed strategy fixed point is unstable. Cooperation is evolutionary stable if and only if:

$$r \ge \left(1 - \alpha_{pc}\beta\right)(k+1) \tag{6.19}$$

Defection is evolutionary stable if and only if:

$$r < (1 + \alpha_{pc}\gamma)(k+1) \tag{6.20}$$

6.1.1 Payoff matrix representation of the public goods game

In this section the payoff matrix representation of public goods game is given. Since in this chapter we mostly focus on the matrix representation of the "Collective hunting game" as our model to analyze hyena's hunting patterns, it is good to have the matrix representation of standard public goods game briefly in this section. To do so, we have to calculate the payoff of each strategy against solid population of other types. For more details, please refer to [169, 157, 115]. First, we ignore punishment, and we calculate the payoff matrix for games in which there is no punishment, and in this game defectors or free riders do not receive any negative cost or signal from the cooperative investors. The payoff to a cooperator against a solid population of cooperators is:

$$P_c^c = r - 1$$

The payoff to a cooperator against a solid population of defectors is:

$$P_d^c = \frac{r}{k+1} - 1$$

After repeating the same process for defector, the payoff matrix for public goods game is:

$$E = \begin{array}{cc} C & D \\ C & r - 1 & \frac{r}{k+1} - 1 \\ D & \frac{rk}{k+1} & 0 \end{array} \right)$$
(6.21)

Column wise operations on this payoff matrix gives the following anti-diagonal matrix:

$$E = \begin{array}{cc} C & D \\ C & \left(\begin{array}{cc} 0 & \frac{r}{k+1} - 1 \\ D & \left(\begin{array}{cc} 1 - \frac{r}{k+1} & 0 \end{array} \right) \end{array} \right)$$
(6.22)

This payoff matrix gives the following replicator equation, which is obviously equivalent to equation (6.7), when there is no punishment.

$$\dot{\rho_c} = \rho_c (1 - \rho_c) \left(\frac{r}{k+1} - 1 \right) \dot{\rho_d} = \rho_d (1 - \rho_d) \left(-\frac{r}{k+1} + 1 \right)$$
(6.23)

By introducing punishment to the game, cooperators and defectors act as moralists and immoralists [133] with probability of punishment α_{pc} and α_{pd} . Moralists are cooperators that punish and receive an additional cost for punishment [115, 170, 171, 172]. On the other hands, immoralists are foolish defectors that punish their own type. By using payoffs (6.1), we can write the payoff matrix of the standard public goods game of punishing cooperators and defectors as:

$$E = \begin{pmatrix} C & D \\ r - 1 & \frac{r}{k+1} - 1 - \alpha_{pc}\gamma \\ D \begin{pmatrix} \frac{rk}{k+1} - \alpha_{pc}\beta & -\alpha_{pd}(\beta + \gamma) \end{pmatrix}$$
(6.24)

Column wise operation on this payoff matrix gives the following anti-diagonal matrix:

$$E = \begin{pmatrix} C & D \\ 0 & \frac{r}{k+1} + \alpha_{pd} \left(\beta + \gamma\right) - \alpha_{pc} \gamma - 1 \\ D \begin{pmatrix} 1 - \frac{r}{k+1} - \alpha_{pc} \beta & 0 \end{pmatrix}$$
(6.25)

By analyzing this anti-diagonal payoff matrix, we see that the stability conditions for punishing cooperator and defector are identical to (6.15) and (6.16). By ignoring insane immoralists in this game, the payoff matrix for this new game would be:

$$E = \begin{pmatrix} C & D \\ r - 1 & \frac{r}{k+1} - 1 - \alpha_{pc}\gamma \\ D \begin{pmatrix} \frac{rk}{k+1} - \alpha_{pc}\beta & 0 \end{pmatrix}$$
(6.26)

Column wise operation on this payoff matrix gives the following anti-diagonal matrix:

$$E = \begin{array}{cc} C & D \\ C & 0 \\ D \\ \left(\begin{array}{c} 0 & \frac{r}{k+1} - \alpha_{pc}\gamma - 1 \\ 1 - \frac{r}{k+1} - \alpha_{pc}\beta & 0 \end{array} \right) \end{array}$$
(6.27)

By analyzing this anti-diagonal payoff matrix, we see that the stability conditions for punishing cooperator and pure defector are identical to (6.19) and (6.20).

6.1.2 Punishment as a signaling mechanism between cooperators and defectors in PGG

Here, we try to quantify the amount of information that punishing cooperator gains about the population by punishing free riders over rounds of standard public goods game. The main purpose of this section is to show that punishment on top of its direct effects on the fitness of players, similar to assortment in conditional games, is a communication mechanism that helps cooperators gain information from the environment. This mechanism convey information to the game by discriminating between defectors and cooperators. In other words, punishment is a conditional strategy on the opponent's type. Without punishment it is impossible for players with unconditional strategies to exchange information and distinguish between free riders and investors in the group. Similar to assortment, a perfect punishment strategy protects cooperators against any invasion of free riders. The more effective cooperators punish the free riders, the more information they gain about the population and their opponents' type, and consequently the more immune they will be against defectors. By adding error into this communication channel, we try to analyze the effect of noise on punishment and consequently on fate of the public goods game. Similar to previous section, we consider two punishing scenarios: first, both cooperators and defectors punish free riders, and second, only cooperators punish free riders. Although the punishing defector (immoralist) reduces the payoff to the defector in one interaction, it might gain more payoff in long run by fooling vigilant/punishing cooperators.

6.1.2.1 Communication between punishing cooperator and pure defector over rounds of public goods game in noiseless environment

Since defectors do not punish their own type and they play unconditionally, we just consider the behavior or strategy of cooperators against their opponents. Here, action is not to cooperate or to defect. In this section, we are interested how punishment provides a communication channel during rounds of public goods game; thus, here, strategy is to punish (P) or to forgive (F). It is obvious that cooperators do not punish cooperators. They just punish defectors with probability α_{pc} , and this bring discrimination into the game. The strategy matrix of punishing cooperator and pure defector can be written as:

$$S_C = \begin{pmatrix} C & D & C & D \\ p_{P|C} & p_{P|D} \\ p_{F|C} & p_{F|D} \end{pmatrix} = \begin{pmatrix} P \\ 0 & \alpha_{pc} \\ 1 & 1 - \alpha_{pc} \end{pmatrix}$$
(6.28)

$$S_{D} = \begin{array}{ccc} C & D & PC & D \\ F \begin{pmatrix} p_{P|C} & p_{P|D} \\ p_{F|C} & p_{F|D} \end{pmatrix} &= \begin{array}{ccc} P \begin{pmatrix} 0 & 0 \\ 1 & 1 \end{pmatrix}$$
(6.29)

where $p_{P|X}$ is the probability of punishment if the opponent's type is "X", and $p_{F|X}$ is the probability of forgiveness if the opponent's type is "X". Based on these strategy matrices, the probability of punishment (P) and forgiveness (F) for punishing cooperator is:

$$P_C^F = \rho_c + (1 - \alpha_{pc}) (1 - \rho_c)$$

$$P_C^P = \alpha_{pc} (1 - \rho_c)$$
(6.30)

Consequently, by using equation (6.30) the entropy in the action of punishing cooperator (A_C) is:

$$H(A_C) = -\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) - \alpha_{pc}(1 - \rho_c) \log\left(\alpha_{pc}(1 - \rho_c)\right)$$
(6.31)

Similarly, the conditional entropy of punishing cooperator's action given the opponent's type is:

$$H\left(A_{C}|O\right) = \sum_{j\in\{C,D\}} \rho_{j}H\left(A_{C}|O=j\right)$$
$$= -(1-\rho_{c})\left(\alpha_{pc}\log\alpha_{pc} + (1-\alpha_{pc})\log(1-\alpha_{pc})\right)$$
(6.32)



Figure 6.2: Effect of punishment probability on mutual information between action of punishing cooperator and opponent's type. X-axis is punishment probability (α_{pc}), Y-axis is the concentration of punishing cooperation in population, and Z-axis is mutual information between action of punishing cooperator and opponent type.

Therefore, the mutual information between the action of punishing cooperator and opponent's type is:

$$I(A_C; O) = H(A_C) - H\left(A_C | O\right)$$

= $-\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right)$
- $\alpha_{pc}(1 - \rho_c) \log\left(\alpha_{pc}(1 - \rho_c)\right)$
+ $(1 - \rho_c)\left(\alpha_{pc}\log\alpha_{pc} + (1 - \alpha_{pc})\log(1 - \alpha_{pc})\right)$ (6.33)

Figure (6.2) shows this mutual information for different α_{pc} and different concentration of punishing cooperator. According to figure (6.2), it is obvious that the mutual information between punishing probability of cooperator and available information for punishing cooperator, which is the mutual information between punishing parameter α_{pc} and concentration of players, increases as we increase the punishing probability α_{pc} . The mutual information is maximum when population is divided equally to cooperators and defectors. If players play unconditionally ($\alpha_{pc} = 0$), there is no information to gain, and as a result, if synergy factor "r" is low, cooperator is vulnerable to existence of defectors in the population.

6.1.2.2 Communication between punishing cooperator and pure defector over rounds of public goods game in noisy environment

To model the effect of environmental noise on the action of punishing cooperator, we define the following error matrix:

$$\Xi = \begin{array}{cc} C & D \\ \Xi = \begin{array}{c} C \\ D \\ \epsilon \\ \epsilon \end{array} \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon \\ \epsilon \\ 1 - \epsilon \end{pmatrix}$$
(6.34)

Error matrix Ξ shows how punishing cooperator estimates the frequency of interacting with each type over rounds of PGG. By applying this error matrix to the actual concentration of players, the estimated frequencies would be:

$$\begin{pmatrix} \hat{\rho_c} \\ \hat{\rho_d} \end{pmatrix} = \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon & 1 - \epsilon \end{pmatrix} \begin{pmatrix} \rho_c \\ 1 - \rho_c \end{pmatrix}$$

$$= \begin{pmatrix} \epsilon + \rho_c - 2\epsilon\rho_c \\ 1 - \epsilon - \rho_c + 2\epsilon\rho_c \end{pmatrix}$$

$$(6.35)$$

By plugging estimated concentrations (6.35) into equation (6.2), we can calculate the mutual information between action of punishing cooperator and opponent's type. Figure (6.3) shows this mutual information for different α_p and concentration of punishing cooperator in environments with different level of noise.

6.1.2.3 Communication between punishing cooperator and defector in public goods game

In this section, we are interested how players with punishing attitude communicate and exchange information over rounds of public goods game. In this section, both cooperators and defectors punish free riders. Punishing defectors by defectors seems to be a foolish strategy; however, if the effect of punishment for defectors is not that high, defectors can fool vigilant cooperators by punishing their own type (especially in noisy environments in which players make mistake in recognizing the type of their opponent) and accept a small penalty to the hope of receiving long term benefit from cooperators. Similar to previous section, here strategy is to punish (P) or to forgive (F). It is obvious that cooperators do not receive punishment from both type. On the other hand, defectors are penalized with the probability α_{pc} and α_{pd} by cooperators and defectors respectively, and this bring discrimination into the game. The strategy matrix of punishing cooperator and defector can be written as:

$$S_C = \frac{P}{F} \begin{pmatrix} p_{P|C} & p_{P|D} \\ p_{F|C} & p_{F|D} \end{pmatrix} = \frac{P}{F} \begin{pmatrix} 0 & \alpha_{pc} \\ 1 & 1 - \alpha_{pc} \end{pmatrix}$$
(6.36)



Figure 6.3: Effect of assortment and environmental noise on mutual information between action of conditional cooperator and opponent type. X-axis is punishment probability $(\alpha_p c)$, Y-axis is the concentration of punishing cooperation in population, and Z-axis is mutual information between action of punishing cooperator and opponent's type: (a) one percent noise, (b) two percent noise, (c) five percent noise, (d) ten percent noise, (e) twenty five percent noise, and (f) fifty percent noise.
$$S_D = \frac{P}{F} \begin{pmatrix} p_{P|C} & p_{P|D} \\ p_{F|C} & p_{F|D} \end{pmatrix} = \frac{P}{F} \begin{pmatrix} 0 & \alpha_{pd} \\ 1 & 1 - \alpha_{pd} \end{pmatrix}$$
(6.37)

Based on these strategy matrices, the probability of punishment (P) and forgiveness (F) for punishing cooperator is:

$$P_C^F = \rho_c + (1 - \alpha_{pc}) (1 - \rho_c)$$

$$P_C^P = \alpha_{pc} (1 - \rho_c)$$
(6.38)

$$P_D^F = \rho_c + (1 - \alpha_{pd}) (1 - \rho_c)$$

$$P_D^P = \alpha_{pd} (1 - \rho_c)$$
(6.39)

Consequently, by using equations (6.38) and (6.39), we can calculate the entropy of players' actions as:

$$H(A_C) = -\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) - \alpha_{pc}(1 - \rho_c) \log\left(\alpha_{pc}(1 - \rho_c)\right)$$
(6.40)

$$H(A_D) = -\left(\rho_c + (1 - \alpha_{pd})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pd})(1 - \rho_c)\right) - \alpha_{pd}(1 - \rho_c) \log\left(\alpha_{pd}(1 - \rho_c)\right)$$
(6.41)

Similarly, the conditional entropy of action given type of opponents for each player is:

$$H\left(A_{C}|O\right) = \sum_{j\in\{C,D\}} \rho_{j}H\left(A_{C}|O=j\right)$$
$$= -(1-\rho_{c})\left(\alpha_{pc}\log\alpha_{pc} + (1-\alpha_{pc})\log(1-\alpha_{pc})\right)$$
(6.42)

$$H\left(A_{D}|O\right) = \sum_{j \in \{C,D\}} \rho_{j} H\left(A_{D}|O=j\right)$$
$$= -(1-\rho_{c})\left(\alpha_{pd}\log\alpha_{pd} + (1-\alpha_{pd})\log(1-\alpha_{pd})\right)$$
(6.43)

Therefore, the mutual information between action of punishing players and opponent's type is:

$$I(A_C; O) = H(A_C) - H\left(A_C | O\right)$$

= $-\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pc})(1 - \rho_c)\right)$
 $- \alpha_{pc}(1 - \rho_c) \log\left(\alpha_{pc}(1 - \rho_c)\right)$
 $+ (1 - \rho_c)\left(\alpha_{pc} \log \alpha_{pc} + (1 - \alpha_{pc})\log(1 - \alpha_{pc})\right)$ (6.44)

$$I(A_D; O) = H(A_D) - H\left(A_D | O\right)$$

= $-\left(\rho_c + (1 - \alpha_{pd})(1 - \rho_c)\right) \log\left(\rho_c + (1 - \alpha_{pd})(1 - \rho_c)\right)$
 $-\alpha_{pd}(1 - \rho_c) \log\left(\alpha_{pd}(1 - \rho_c)\right)$
 $+ (1 - \rho_c)\left(\alpha_{pd}\log\alpha_{pd} + (1 - \alpha_{pd})\log(1 - \alpha_{pd})\right)$ (6.45)

Figure (6.4) shows this mutual information for different α_{pc} , α_{pd} , and concentration of punishing cooperator. Similar to previous section, we can apply the error matrix Ξ to estimate the concentration of players, and by plugging these estimated values into equations (6.44) and (6.45), we can calculate the mutual information between action of vigilant/punishing players and type of opponent.

6.2 Collective hunting game

One example of ubiquitous yet vulnerable cooperative behavior among selfish cheater is group hunting of mammals such as spotted hyenas in their despotic societies, where the highest ranking individuals obtain the largest share of the kill [173]. The hunting patterns of spotted hyenas is very interesting. These mammals hunt most locally abundant ungulate species, and their hunting group size varies with prey type. Approximately, only one-third of hunting attempts result in prey capture. The success rate is a function of the hyenas' age, experience, and the group size [174]. They mostly prefer to do solitary hunting; however, they show some opportunistic behavior in attending easy hunts. The kill size is more than what hyen needs, and this is beneficial to the clan. After they kill the prey (1-3 hyen per wildebeest, up to 11 for zebra), the kill is distributed to the entire clan (20-50 animals), with the highest ranks obtaining the largest share [174]. Now, the question is what makes such "unjust" societies stable? We know that female hyenas rule in hyena society. They are about ten percent larger than males and also show aggressive behavior frequently toward lower rank females and males. Therefore, this aggressive behavior and punishment attitude might be the signaling force which rules as a communication mechanism to maintain cooperation among hyenas. To address this question, we introduce collective hunting game



Figure 6.4: Effect of punishment probability on mutual information between action of punishing players and opponent type. X-axis is punishment probability (α), Y-axis is the concentration of punishing cooperator in population, and Z-axis is mutual information between action of punishing players and opponent's type: (a) mutual information between action of vigilant/punishing cooperator and opponent's type (b) mutual information between action of vigilant/punishing defector and opponent's type



Figure 6.5: Using Heaviside step function to model all or nothing situations in group hunting behavior of animals.

as a new game-theoretic formulation by extending the standard public goods game to model the social behavior of hyenas in their "unjust" society and study how a despotic group structure can be robust, evolutionary stable, and enforced by punishment. In standard public goods game one cooperator is enough for defector to receive a payoff greater than zero (6.1); however, in mammals with group hunting behavior this is not true. If the group size is not greater than a threshold, which is a function of the prey size, the hunt will be unsuccessful and nobody receives anything; therefore the payoffs to the strategies should be modified for hunting behavior. The easiest way to modify this behavior is to use a Heaviside step function as it is shown in figure (6.5). This approach is similar to the proposed models [169, 157]; however, Pacheco et al. applied a linear fitness function in their model. inHere, we instead apply a Heaviside step function to have a better model of group hunting behavior of hyenas. Heaviside step function is the simplest modification to PGG. Since we don't apply the calculus of variation to this game, we don't need to worry about the break point in Heaviside function. If we want to apply optimization techniques to this problem, it is better to use smooth and differentiable nonlinear functions (e.g. logistic or tangent hyperbolic functions) for collective hunting game. Using the step function yields to the following payoffs for different strategies in the clan:

$$\pi_C = \frac{r}{k+1} \theta \left(k\rho_c + 1 - \zeta \right) - 1 - \gamma \alpha_{pc} \left(1 - \rho_c \right)$$

$$\pi_D = \frac{r}{k+1} \theta \left(k\rho_c \right) - \beta \alpha_{pc} \rho_c - \beta \alpha_{pd} \left(1 - \rho_c \right) - \gamma \alpha_{pd} \left(1 - \rho_c \right)$$
(6.46)

By Comparing equations (6.1) and (6.46), we see that the important parameter in the collective hunting game is the threshold of the contributed hunters. Based on this parameter we can have completely different properties that we could not find in the standard public goods game.

6.2.1 Collective hunting game with no punishment

Similar to the standard game, first we ignore punishment and we analyze collective hunting games between pure cooperators and defectors. The payoffs to the cooperators and defectors for this game is:

$$\pi_C = \frac{r}{k+1} \theta \left(k\rho_c + 1 - \zeta \right) - 1$$

$$\pi_D = \frac{r}{k+1} \theta \left(k\rho_c \right)$$
(6.47)

Therefore, the payoff matrix for this game is:

$$E = \begin{array}{c} C & D \\ C & k+1 \\ D \\ \left(\begin{array}{c} \frac{r}{k+1}\theta \left(k+1-\zeta\right)-1 & \frac{r}{k+1}\theta \left(1-\zeta\right)-1 \\ \frac{r}{k+1}\theta \left(k-\zeta\right) & 0 \end{array} \right) \end{array}$$
(6.48)

6.2.1.1 Solitary hunting $(\zeta = 1)$

In solitary hunting, the payoff matrix is:

$$E_{\zeta=1} = \begin{array}{cc} C & D \\ C & \frac{r}{k+1} - 1 & \frac{r}{k+1} - 1 \\ D & \frac{r}{k+1} & 0 \end{array} \right)$$
(6.49)

which is equivalent to:

$$E_{\zeta=1} = \begin{array}{cc} C & D \\ C & \left(\begin{array}{cc} 0 & \frac{r}{k+1} - 1 \\ D & 1 & 0 \end{array} \right) \end{array}$$
(6.50)

According to payoff matrix (6.50), when kill-size r is small (r < k + 1), it is not worth to cooperate; however, if the kill-size is big, the collective hunting game becomes a coexistence game, in which both strategies are evolutionary unstable, and the mixed strategy is stable. The fraction of cooperation in the mixed strategy is:

$$\rho_c = 1 - \frac{k+1}{r} \tag{6.51}$$

and it becomes larger as the kill-size increases. Figures (6.6-6.9) show this phenomenon. Figure (6.10) shows the fraction of cooperation in the mixed strategy as a function of killsize.



Figure 6.6: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = 1$ (solitary hunting) and kill size (r) is 1. Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to one and is less than group size; therefore, defector is ESS.



Figure 6.7: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = 1$ (solitary hunting) and kill size (r) is 4 (less than the group size). Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to four and is less than group size; therefore, defector is ESS.



Figure 6.8: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = 1$ (solitary hunting) and kill size (r) is 10. Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to 10 and is greater than group size; therefore, mixed strategy is ESS.



Figure 6.9: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = 1$ (solitary hunting) and kill size (r) is 4 (less than the group size). Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to 20 and is greater than group size; therefore, mixed strategy is ESS.

Figure 6.10: Effect of kill-size on the fraction of cooperation in the mixed strategy. Dashed dot red line is the fraction of defection and solid blue line is the fraction of cooperation in the mixed strategy. X-axis is kill size, and Y-axis indicates the fraction of cooperation and defection in the mixed strategy.

6.2.1.2 All or nothing $(\zeta = k + 1)$

In all or nothing game, the payoff matrix is:

$$E_{\zeta=k+1} = \begin{array}{cc} C & D \\ C & \frac{r}{k+1} - 1 & -1 \\ D & 0 \end{array}$$
(6.52)

which is equivalent to:

$$E_{\zeta=k+1} = \begin{pmatrix} C & D \\ 0 & -1 \\ D & 1 - \frac{r}{k+1} & 0 \end{pmatrix}$$
(6.53)

According to payoff matrix (6.53), defector is always evolutionary stable. If kill-size r is small (r < k + 1), cooperation is not evolutionary stable and cooperation does not pay; however, if the kill-size is big enough, both strategies are stable, and all or nothing game becomes a coordination game, in which both strategies or stable. In this game initial frequency of the strategies indicates the winner of the game, and it is not possible to have mixture of cooperators and defectors in the final population. In this game the mixed strategy is unstable and it determines the domain of attraction of both stable strategies. Figures (6.11-6.14) show this phenomena.



Figure 6.11: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = k + 1$ (all or nothing) and kill size (r) is 1. Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to one and is less than group size; therefore, defector is ESS.



Figure 6.12: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = k + 1$ (all or nothing) and kill size (r) is 4 (less than the group size). Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to four and is less than group size; therefore, defector is ESS.



Figure 6.13: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = k + 1$ (all or nothing) and kill size (r) is 10. Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to 10 and is greater than group size; therefore, both strategies are ESS.



Figure 6.14: Effect of kill-size on the dynamic of collective hunting game, when $\zeta = k + 1$ (all or nothing) and kill size (r) is 4 (less than the group size). Different initial concentration were considered. Red solid lines are the concentration of defectors and blue solid lines are the concentration of cooperators. Here, kill-size is equal to 20 and is greater than group size; therefore, both strategies are ESS.

6.2.1.3 Small group hunting $(1 < \zeta < k)$

In small group hunting, the payoff matrix is:

$$E_{1<\zeta< k} = \begin{array}{cc} C & D \\ C & \frac{r}{k+1} - 1 & -1 \\ D & \frac{r}{k+1} & 0 \end{array}$$
(6.54)

which is equivalent to:

$$E_{1<\zeta< k} = \begin{array}{c} C & D \\ C \begin{pmatrix} 0 & -1 \\ D \end{pmatrix} \\ 1 & 0 \end{array}$$
(6.55)

According to payoff matrix (6.55), in small group hunting the only evolutionary stable strategy is defection, and cooperation does not pay; therefore, this game seems to be a boring case since we are just interested in cases in which cooperation emerges and is maintained among selfish genes. Now, the question is if unequal sharing of resources (similar to what we have in despotic societies of hyenas) stabilize "small group hunting" game without punishment? To answer this question, we introduce two types of players: rich and poor. Rich players are generally rear in the group. These players have more access to the resources. To involve these rich and poor types into our model, we define despotic distribution "D" to the game. If a cooperator is rich, they will receive more share of the kill in comparison to the poor cooperator which receive less ($\frac{1}{D}$ of the kill). The same rule applies to the poor and rich defectors. The payoffs to these players is:

$$\pi_{C}^{R} = \frac{r}{\nu_{R} + \frac{\nu_{p}}{D}} \theta \left(\sum_{i=1}^{k} n_{i} + 1 - \zeta \right) - 1$$

$$\pi_{C}^{P} = \frac{r}{D\nu_{R} + \nu_{p}} \theta \left(\sum_{i=1}^{k} n_{i} + 1 - \zeta \right) - 1$$

$$\pi_{D}^{R} = \frac{r}{\nu_{R} + \frac{\nu_{p}}{D}} \theta \left(\sum_{i=1}^{k} n_{i} - \zeta \right)$$

$$\pi_{D}^{P} = \frac{r}{D\nu_{R} + \nu_{p}} \theta \left(\sum_{i=1}^{k} n_{i} - \zeta \right)$$
(6.56)

where $n_i \in \{0, 1\}$ indicates the strategy type (0: defection, 1: cooperation), ν_R and ν_P are the number of rich and poor in the group respectively. By using these payoffs we can write the payoff matrix of this game as:

$$E = \begin{cases} C^{R} & C^{P} & D^{R} & D^{P} \\ C^{R} & \left(\frac{r}{k+1} - 1 & \frac{rD}{D+k} - 1 & -1 & -1 \\ \frac{r}{Dk+1} - 1 & \frac{r}{k+1} - 1 & -1 & -1 \\ \frac{r}{Dk+1} & \frac{rD}{D+k} & 0 & 0 \\ \frac{r}{Dk+1} & \frac{r}{k+1} & 0 & 0 \\ \end{cases}$$
(6.57)

$$E = \begin{cases} C^{R} & C^{P} & D^{R} & D^{P} \\ C^{R} & 0 & \frac{rk(D-1)}{(k+1)(D+k)} & -1 & -1 \\ \frac{rk(1-D)}{(Dk+1)(k+1)} & 0 & -1 & -1 \\ \frac{rk(1-D)}{(Dk+1)(k+1)} & 0 & -1 & -1 \\ 1 & \frac{rk(D-1)}{(k+1)(D+k)} + 1 & 0 & 0 \\ \frac{rk(1-D)}{(Dk+1)(k+1)} + 1 & 1 & 0 & 0 \end{pmatrix}$$
(6.58)

Payoff matrix (6.58) shows that both types of defection strategies are evolutionary stable. Moreover, we see that rich cooperator loses the competition against a rich defector and poor cooperator loses the game to the poor defector. If despotic parameter D is greater than one, rich cooperator can win the game against a poor defector if:

$$r > \frac{(Dk+1)(k+1)}{k(D-1)} \approx \frac{Dk+1}{D-1}$$
 for big group size

If despotic parameter D is less than one which is advantageous to the poor players, poor cooperator can win the game against a rich defector if and only if:

$$r > \frac{(D+k)(k+1)}{k(1-D)} \approx \frac{D+k}{1-D}$$
 for big group size

This shows that it is possible to have cooperation as evolutionary stable strategy among poor or rich defectors; however, having poor or rich strategies does not yield to coexistence of defectors and cooperators. Next, we show that how punishers use punishment as a signaling mechanism to maintain cooperation in the clan. These punishers accept a punishing cost to reduce payoff of the free riders by punishing them. Table (6.1) summarize the stability of fixed points for collective hunting game with no punishment.

Game	cooperation	defection	mixed strategy
Solitary hunting	unstable	stable if	stable if
$(\zeta = 1)$		r < k + 1	r > k+1
All or Nothing	stable if	stable	unstable
$(\zeta = K + 1)$	r > k+1		
Small group hunting	unstable	stable	unstable
Small group hunting	C_R wins against D_P	C_P wins against D_R	unstable
between rich and poor	if $r > \frac{Dk+1}{D-1}$	if $r > \frac{D+k}{1-D}$	

Table 6.1: Stability of collective hunting game's fixed points while players don't punish free riders.

6.2.2 Effect of punishment on collective hunting game

By introducing punishment probabilities (α_{pc} and α_{pd}), the payoff matrix of such collective hunting game would be:

$$E = \begin{pmatrix} C & D \\ \frac{r}{k+1}\theta \left(k+1-\zeta\right) - 1 & \frac{r}{k+1}\theta \left(1-\zeta\right) - 1 - \gamma \alpha_{pc} \\ \frac{r}{k+1}\theta \left(k-\zeta\right) - \beta \alpha_{pc} & -(\beta+\gamma) \alpha_{pd} \end{pmatrix}$$
(6.59)

or:

$$E = \frac{C}{D} \begin{pmatrix} 0 & \frac{r}{k+1}\theta (1-\zeta) - 1 - \gamma \alpha_{pc} + (\beta+\gamma) \alpha_{pd} \\ \frac{r}{k+1}\theta (k-\zeta) - \frac{r}{k+1}\theta (k+1-\zeta) + 1 - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.60)

Here, besides hunting threshold " ζ ", there are four punishing parameters that can affect fate of the game.

6.2.2.1 Solitary hunting $(\zeta = 1)$

The payoff matrix for solitary hunting game is:

$$E = \begin{pmatrix} C & D \\ 0 & \frac{r}{k+1} - 1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} \\ 0 & 1 - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.61)

According to payoff matrix (6.61), we can have all sort iterated games. For example if effect of punishment is high and cooperators punish more frequently, cooperation can be evolutionary stable. On the other hand, if cost of punishment is high, and defectors do not punish more frequently, even if kill size is greater than hunting group size (if there is no punishment, defection cannot be ESS in this case) defection can be evolutionary stable as well. To find the stability conditions of fixed points, we have to derive the replicator equation for this game. We have:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 - \gamma \alpha_{pc} + \left(\beta + \gamma\right) \alpha_{pd} - \left(\frac{r}{k+1} - \left(\beta + \gamma\right) \left(\alpha_{pc} - \alpha_{pd}\right)\right) \rho_c\right)$$
(6.62)

The fixed points for this game are:

$$\rho_{c} = 0, \text{ defector}$$

$$\rho_{c} = 1, \text{ cooperator}$$

$$\rho_{c} = \frac{r - (k+1) \left(1 + \gamma \alpha_{pc} - (\beta + \gamma) \alpha_{pd}\right)}{r - (k+1) \left(\beta + \gamma\right) \left(\alpha_{pc} - \alpha_{pd}\right)}, \text{ mixed}$$
(6.63)

By taking the derivative of this replicator equation respect to the fraction of cooperators in the population, we can identify the evolutionary stable fixed points. We have:

$$\frac{d\dot{\rho}_{c}}{d\rho_{c}} = (1 - \rho_{c}) \left(\frac{r}{k+1} - 1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} - \left(\frac{r}{k+1} - (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} \right)
- \rho_{c} \left(\frac{r}{k+1} - 1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} - \left(\frac{r}{k+1} - (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} \right) \quad (6.64)
- \left(\frac{r}{k+1} - (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} (1 - \rho_{c})$$

Cooperation is robust against the invasion of defectors if and only if:

$$\beta \alpha_{pc} > 1 \tag{6.65}$$

Cooperation can invade a population of pure defectors if and only if:

$$\frac{r}{k+1} - 1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} > 0$$
(6.66)

If mixed strategy exists, it will be evolutionary stable if and only if:

$$\frac{r}{k+1} - (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) > 0 \tag{6.67}$$

If cooperators and defectors equally punish free riders, payoff matrix (6.61) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & \frac{r}{k+1} - 1 - \beta \alpha_{pc} \\ D \begin{pmatrix} 1 - \beta \alpha_{pc} & 0 \end{pmatrix} \end{pmatrix}$$
(6.68)

Replicator equation (6.62) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 + \beta \alpha_{pc} - \frac{r}{k+1} \rho_c\right)$$
(6.69)

The fixed point of this equation are:

$$\rho_{c} = 0 , \text{ defector}$$

$$\rho_{c} = 1 , \text{ cooperator}$$

$$\rho_{c} = \frac{r - (k+1) (1 - \beta \alpha_{pc})}{r} , \text{ mixed}$$
(6.70)

Mixed strategy if exists, is stable if and only if:

$$\alpha_{pc} < \frac{1}{\beta} \min\left(1, \frac{r}{k+1} - 1\right) \tag{6.71}$$

Cooperation is robust against the invasion of defectors if and only if:

$$\alpha_{pc} > \frac{1}{\beta} \tag{6.72}$$

Cooperation can invade a population of pure defectors if and only if:

$$\alpha_{pc} < \frac{1}{\beta} \left(\frac{r}{k+1} - 1 \right) \tag{6.73}$$

If defectors are smart enough to stop punishing their own type, the payoff matrix (6.61) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & \frac{r}{k+1} - 1 - \gamma \alpha_{pc} \\ D \begin{pmatrix} 1 - \beta \alpha_{pc} & 0 \end{pmatrix} \end{pmatrix}$$
(6.74)

Replicator equation (6.62) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(\frac{r}{k+1} - 1 - \gamma \alpha_{pc} - \left(\frac{r}{k+1} - (\beta + \gamma) \alpha_{pc}\right) \rho_c\right)$$
(6.75)

Considering this replicator equation, the fixed point of this game would be:

$$\rho_{c} = 0, \text{ defector}$$

$$\rho_{c} = 1, \text{ cooperator}$$

$$\rho_{c} = \frac{r - (k+1) (1 + \gamma \alpha_{pc})}{r - \alpha_{pc} (k+1) (\beta + \gamma)}, \text{ mixed}$$
(6.76)

Cooperation is evolutionary stable if and only if:

$$\alpha_{pc} > \frac{1}{\beta} \tag{6.77}$$

Defection is evolutionary stable if and only if:

$$\alpha_{pc} > \frac{r - (k+1)}{\gamma \left(k+1\right)} \tag{6.78}$$

Mixed strategy is stable if and only if:

$$\alpha_{pc} < \min\left(\frac{r - (k+1)}{\gamma (k+1)}, \frac{1}{\beta}\right) \tag{6.79}$$

6.2.2.2 All or nothing $(\zeta = k + 1)$

The payoff matrix for all or nothing game is:

$$E = \begin{pmatrix} C & D \\ 0 & -1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} \\ D \begin{pmatrix} 1 - \frac{r}{k+1} - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.80)

Similar to solitary hunting game, we can infer by checking the payoff matrix (6.80) that all or nothing game can be take the form of all sort of iterated two players game. For example, if effect of punishment is high and cooperators punish more frequently, even if kill size is small, cooperation can be evolutionary stable. On the other hand, if cost of punishment is high, and defectors do not punish often compare to cooperators, even if kill size is greater than hunting group size, defection can be evolutionary stable as well. To find the stability conditions of fixed points, we have to derive the replicator equation for this game. We have:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} + \left(\frac{r}{k+1} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd}\right)\right) \rho_c\right)$$
(6.81)

The fixed points for this game are:

$$\rho_{c} = 0 , \text{ defector}$$

$$\rho_{c} = 1 , \text{ cooperator}$$

$$\rho_{c} = \frac{(k+1)\left(1 + \gamma\alpha_{pc} - (\beta + \gamma)\alpha_{pd}\right)}{r + (k+1)\left(\beta + \gamma\right)\left(\alpha_{pc} - \alpha_{pd}\right)} , \text{ mixed}$$
(6.82)

By taking the derivative of this replicator equation respect to the fraction of cooperators in the population, we can identify the evolutionary stable fixed points. We have:

$$\frac{d\dot{\rho}_{c}}{d\rho_{c}} = (1 - \rho_{c}) \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} + \left(\frac{r}{k+1} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} \right)
- \rho_{c} \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} + \left(\frac{r}{k+1} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} \right)
+ \left(\frac{r}{k+1} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \right) \rho_{c} (1 - \rho_{c})$$
(6.83)

Cooperation is robust against the invasion of defectors if and only if:

$$\beta \alpha_{pc} + \frac{r}{k+1} > 1 \tag{6.84}$$

Cooperation can invade a population of pure defectors if and only if:

$$(\beta + \gamma) \alpha_{pd} - \gamma \alpha_{pc} > 1 \tag{6.85}$$

Mixed strategy is evolutionary stable if and only if:

$$\alpha_{pd} - \alpha_{pc} > \frac{r}{(k+1)\left(\beta + \gamma\right)} \tag{6.86}$$

If cooperators and defectors equally punish free riders, payoff matrix (6.80) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & -1 + \beta \alpha_{pc} \\ D \begin{pmatrix} 1 - \beta \alpha_{pc} - \frac{r}{k+1} & 0 \end{pmatrix}$$
(6.87)

Replicator equation (6.81) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(-1 + \beta \alpha_{pc} + \frac{r}{k+1}\rho_c\right)$$
(6.88)

The fixed point of this equation are:

$$\rho_c = 0 , \text{ defector}$$

$$\rho_c = 1 , \text{ cooperator}$$

$$\rho_c = \frac{(k+1)(1-\beta\alpha_{pc})}{r} , \text{ mixed}$$
(6.89)

Mixed strategy exists if and only if:

$$1 - \frac{r}{k+1} < \beta \alpha_{pc} < 1 \tag{6.90}$$

This fixed point is always unstable. Cooperation is robust against the invasion of defectors if and only if:

$$\beta \alpha_{pc} + \frac{r}{k+1} > 1 \tag{6.91}$$

Cooperation can invade a population of pure defectors if and only if:

$$\beta \alpha_{pc} > 1 \tag{6.92}$$

If defectors are smart enough to stop punishing their own type, the payoff matrix (6.80) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & -1 - \gamma \alpha_{pc} \\ D \begin{pmatrix} 1 - \frac{r}{k+1} - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.93)

Replicator equation (6.62) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(-1 - \gamma \alpha_{pc} + \left(\frac{r}{k+1} + \left(\beta + \gamma\right) \alpha_{pc}\right) \rho_c\right)$$
(6.94)

Considering this replicator equation, the fixed point of this game would be:

$$\rho_{c} = 0 , \text{ defector}$$

$$\rho_{c} = 1 , \text{ cooperator}$$

$$\rho_{c} = \frac{(k+1)(1+\gamma\alpha_{pc})}{r+\alpha_{pc}(k+1)(\beta+\gamma)} , \text{ mixed}$$
(6.95)

Cooperation is evolutionary stable if and only if:

$$\beta \alpha_{pc} + \frac{r}{k+1} > 1 \tag{6.96}$$

Defection is always evolutionary stable; thus, mixed strategy cannot be evolutionary stable. Thus, this game can only be coordination game, and we cannot have cooperation and defection simultaneously in the population.

6.2.2.3 Small group hunting $(1 < \zeta < k)$

The payoff matrix for small group hunting game is:

$$E = \begin{pmatrix} C & D \\ 0 & -1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} \\ D \begin{pmatrix} 0 & -1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} \\ 1 - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.97)

Similar to the previous games, according to payoff matrix (6.97), we can have all sort of iterated two players games. To find the stability conditions of fixed points, we have to derive the replicator equation for this game. We have:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd}\right) \rho_c\right)$$
(6.98)

The fixed points for this game are:

$$\rho_{c} = 0 , \text{ defector}$$

$$\rho_{c} = 1 , \text{ cooperator}$$

$$\rho_{c} = \frac{1 + \gamma \alpha_{pc} - (\beta + \gamma) \alpha_{pd}}{(\beta + \gamma) (\alpha_{pc} - \alpha_{pd})} , \text{ mixed}$$
(6.99)

By taking the derivative of this replicator equation respect to the fraction of cooperators in the population, we can identify the evolutionary stable fixed points. We have:

$$\frac{d\dot{\rho}_c}{d\rho_c} = (1 - \rho_c) \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \rho_c \right)$$
$$- \rho_c \left(-1 - \gamma \alpha_{pc} + (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \rho_c \right)$$
$$+ (\beta + \gamma) \left(\alpha_{pc} - \alpha_{pd} \right) \rho_c \left(1 - \rho_c \right)$$

Cooperation is robust against the invasion of defectors if and only if:

$$\alpha_{pc} > \frac{1}{\beta} \tag{6.100}$$

Cooperation can invade a population of pure defectors if and only if:

$$-1 - \gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} > 0 \tag{6.101}$$

If mixed strategy exists, it will be evolutionary stable if and only if:

$$\alpha_{pc} < \alpha_{pd} \tag{6.102}$$

If cooperators and defectors equally punish free riders, payoff matrix (6.61) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & -1 + \beta \alpha_{pc} \\ D \begin{pmatrix} 0 & -1 + \beta \alpha_{pc} \\ 1 - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.103)

Replicator equation (6.98) is simplified to:

$$\dot{\rho_c} = \left(-1 + \beta \alpha_{pc}\right) \rho_c \left(1 - \rho_c\right) \tag{6.104}$$

Here, mixed strategy does not exist. Cooperation is robust against the invasion of defectors if and only if:

$$\beta \alpha_{pc} > 1 \tag{6.105}$$

Cooperation can invade a population of pure defectors if and only if:

$$\beta \alpha_{pc} > 1 \tag{6.106}$$

If defectors are smart enough to stop punishing their own type, the payoff matrix (6.97) is simplified to:

$$E = \begin{pmatrix} C & D \\ 0 & -1 - \gamma \alpha_{pc} \\ D \begin{pmatrix} 0 & -1 - \gamma \alpha_{pc} \\ 1 - \beta \alpha_{pc} & 0 \end{pmatrix}$$
(6.107)

Replicator equation (6.98) is simplified to:

$$\dot{\rho_c} = \rho_c \left(1 - \rho_c\right) \left(-1 - \gamma \alpha_{pc} + \left(\beta + \gamma\right) \alpha_{pc} \rho_c\right)$$
(6.108)

Considering this replicator equation, the fixed point of this game would be:

$$\rho_{c} = 0 , \text{ defector}$$

$$\rho_{c} = 1 , \text{ cooperator}$$

$$\rho_{c} = \frac{1 + \gamma \alpha_{pc}}{\alpha_{pc} (\beta + \gamma)} , \text{ mixed}$$
(6.109)

Cooperation is evolutionary stable if and only if:

$$\alpha_{pc} > \frac{1}{\beta} \tag{6.110}$$

Here, defector is always evolutionary stable; thus, mixed strategy cannot be evolutionary stable. Tables (6.2-6.10) summarize the stability of fixed points for collective hunting game with no punishment.

Table 6.2: Stability of collective hunting game's fixed points, while players punish free riders, and one hunter is enough to kill the prey (general rule).

Strategy	Solitary hunting $(\zeta = 1)$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	$\gamma \alpha_{pc} - (\beta + \gamma) \alpha_{pd} > \frac{1}{k+1} - 1$
Mixed strategy	$\alpha_{pd} - \alpha_{pc} < \frac{r}{(\beta + \gamma)(k+1)}$

Table 6.3: Stability of collective hunting game's fixed points, while players punish equally free riders, and one hunter is enough to kill the prey.

Strategy	Solitary hunting $(\zeta = 1 \text{ and } \alpha_{pc} = \alpha_{pd})$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	$\alpha_{pc} > \frac{r - (k+1)}{\beta(k+1)}$
Mixed strategy	$\alpha_{pc} < \frac{1}{\beta} \min\left(1, \frac{r}{k+1} - 1\right)$

Table 6.4: Stability of collective hunting game's fixed points, while only cooperators punish free riders, and one hunter is enough to kill the prey.

Strategy	Solitary hunting $(\zeta = 1 \text{ and } \alpha_{pd} = 0)$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	$\alpha_{pc} > \frac{r - (k+1)}{\gamma(k+1)}$
Mixed strategy	$\alpha_{pc} < \min\left(\frac{r - (k+1)}{\gamma(k+1)}, \frac{1}{\beta}\right)$

Strategy	All or nothing $(\zeta = k + 1)$
Cooperation	$\beta \alpha_{pc} + \frac{r}{k+1} > 1$
Defection	$(\beta + \gamma) \alpha_{pd} - \gamma \alpha_{pc} < 1$
Mixed strategy	$\alpha_{pd} - \alpha_{pc} > \frac{r}{(\beta + \gamma)(k+1)}$

Table 6.5: Stability of collective hunting game's fixed points, while players punish free riders, and cooperation of all group is necessary to kill the prey (general rule).

Table 6.6: Stability of collective hunting game's fixed points, while players punish equally free riders, and cooperation of all group is necessary to kill the prey.

Strategy	All or nothing $(\zeta = k + 1 \text{ and } \alpha_{pc} = \alpha_{pd})$
Cooperation	$\beta \alpha_{pc} > 1 - \frac{r}{k+1}$
Defection	$\alpha_{pc} < \frac{1}{\beta}$
Mixed strategy	Unstable

Table 6.7: Stability of collective hunting game's fixed points, while only cooperators punish free riders, and cooperation of all group is necessary to kill the prey.

Strategy	All or nothing $(\zeta = k + 1 \text{ and } \alpha_{pd} = 0)$
Cooperation	$\beta \alpha_{pc} > 1 - \frac{r}{k+1}$
Defection	Stable
Mixed strategy	Unstable

Table 6.8: Stability of collective hunting game's fixed points, while players punish free riders, and cooperation of small group (game of hyenas) is necessary to kill the prey (general rule).

Strategy	Small group hunting $(1 < \zeta \leq k)$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	$-\gamma \alpha_{pc} + (\beta + \gamma) \alpha_{pd} < 1$
Mixed strategy	$\alpha_{pd} > \alpha_{pc}$ and $\alpha_{pc} < \frac{1}{\beta}$

6.3 Discussion

Hyena live in "clans where the high-ranking females enjoy better access to food, are protected from aggression, and have more offspring than lower ranked females [175, 173, 176, 177]. This despotic societal structure is blatantly unjust, yet it appears that it is an evolutionarily

Strategy	Small group hunting $(1 < \zeta \leq k \text{ and } \alpha_{pc} = \alpha_{pd})$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	$\alpha_{pc} < \frac{1}{\beta}$
Mixed strategy	Does not exist

Table 6.9: Stability of collective hunting game's fixed points, while players punish equally free riders, and cooperation of small group (game of hyenas) is necessary to kill the prey.

Table 6.10: Stability of collective hunting game's fixed points, while only cooperators punish free riders, and cooperation of small group (game of hyenas) is necessary to kill the prey.

Strategy	Small group hunting $(1 < \zeta \leq k \text{ and } \alpha_{pd} = 0)$
Cooperation	$\alpha_{pc} > \frac{1}{\beta}$
Defection	Stable
Mixed strategy	Unstable

stable adaptation. In this chapter, we tried to analyze hyenas group hunting pattern to find what ecological factors favor such despotic societal structure and what are the selective pressures that make such an unjust society possible. To do so, we applied evolutionary game theory since it has been used successfully to study a number of different behaviors that at first appeared paradoxical in the light of evolution [16, 36, 48]. Among well-established game theoretic model, we chose the standard Public Goods game (PGG) to model and study societal structure of hyenas since this game describes the dilemma of cooperation from the point of view of a group. Considering the aggression of higher rank females towards the lower ranks in the clan, we also introduced "punishment to the game as a possible mechanism that can maintain cooperation and protect investors against the free riders in the group. Our results depict that while punishment establishes cooperation among a well-mixed group of defectors and cooperators, it is not an effective strategy since in the standard public goods game cooperators and defectors do not coexist. Coexistence of defectors and cooperators is an assumption to the unjust societal structure of hyenas that cannot be avoided since in hyenas clan cooperators and defectors coexist.

Thus, we had to modify the standard public goods game to make it applicable to group hunting behavior of hyenas. One problem with the standard public goods game is that the payoffs are linear functions of the kill size; however, in reality the payoff does not increase as number of hunters increases. Hyena can take down medium to large prey that they alone could not kill [174]. Participating in the hunt can be costly, but the payoff is worth it. However, the size of the kill (the total payoff) does not depend linearly on the number of hunters: either there are enough hunters or not. And if there are enough to take down the prey, adding more hunters does not increase the size of the kill (if we assume that the hyena always hunt the same size animal).

In this chapter, we introduced the "Collective Hunting Game (CTG) as a modification to the standard public goods game by substituting the linear payoff of the game with a threshold dependence payoff. This modification changes the dynamics of the game dramatically. In collective hunting game the threshold parameter is very critical and based on this parameter we can have three different game regimes: (1) The solitary hunting ($\zeta = 1$): a single hunter is sufficient to take down the prey). This game is somewhat uninteresting as it is not a collective game. We see that, without punishment, it is possible to have coexistence of cooperators and defectors when the kill size is big. Moreover, if cooperators punish free riders and the rate of their punishment is greater than $\frac{1}{\beta}$, they are evolutionary stable. On the other hand, if punishment rate of cooperators is less than a critical value (please refer to table (6.2-6.10) for more details), cooperators and defectors coexist, and punishment becomes an effective strategy. (2) The All-or-nothing game: (($\zeta = k + 1$, where k is the size of the group.) In this game, a single defector is sufficient to doom the hunting success: all must participate. This game is interesting mathematically, because the evolutionary fixed

point (the optimal rational strategy) is frequency dependent in the absence of punishment. If more than a critical number of agents participate, the evolutionary dynamics drive the population towards the "all-cooperate fixed point, while if fewer than the critical number participate, evolutionary dynamics drive the population towards all-defection. Moreover, if defectors punishment rate is greater than cooperators punishment rate ($\alpha_{pd} - \alpha_{pc} >$ $\frac{r}{(\beta+\gamma)(k+1)}$), they can coexist, and again punishment becomes an effective strategy. (3) The Hyena game $(1 < \zeta < k + 1)$, where k is the size of the group.) This is arguably the most interesting case when it comes to hyena, as the clan size can be $k \approx 40 - 130$ [174], but it is very unlikely that they will all participate in the hunt. Here, we showed that in the absence of punishment it is impossible to maintain cooperation in a well-mixed population of cooperators and defectors. However, if players punish and defectors punishment rate is greater than cooperators punishment rate, cooperators and defectors can coexist. This is exactly what we see among hyperas since usually higher rank punish lower ranks. Despite its promising performance, the collective hunting game still misses the most obvious and defining characteristic of hyena society: its despotic structure. It is possible to modify the collective hunting game so that each agent that participates has a genetically inherited rank, and individuals with higher rank obtain a larger part of the kill. A simple mathematical model of only two classes predicts the spontaneous evolutionary emergence of an unjust society where the higher ranked class (which we dubbed "the one percent) cooperates, and receives most of the profit. The lower class defects, but still receives a small payoff for free (the "food stamps). Although expanding the model to more than two classes is tedious mathematically speaking, it can easily be done in agent-based simulations.
6.4 Chapter summary

In this chapter, first we analyzed the standard public goods game to investigate necessary conditions for maintaining cooperation. Then by extending the standard game to collective hunting game, we discovered properties that we could not find in the standard game. These properties are abundant among social animals, and collective hunting game seems to be a good ground work to study social behavior in animals. While public goods game does not describe complex societal structure of hyena clans, collective hunting game has rich structure describing collaborative strategies considering the necessary threshold parameter for all or nothing situations and allowing punishment. In collective hunting game, without punishment the intermediate game (game with few hunters) did not exhibit interesting properties (defection is the only evolutionary stable strategy). To maintain cooperation in this game, we have to modify our assumptions and include unequally distribution of the resources to stabilize this game with few collective hunters.

Chapter 7

Summary and Concluding Remarks

The world is so empty if one think only of mountains, rivers, and cities; but to know someone here and there who thinks and feels with us, and though distant, it close to us in spirit - this makes the earth feel like an inhabited garden.

-Johan Wolfgang von Goethe

Butch Cassidy: Well, the way I figure it, we can either fight or give. If we give, we go to jail. Sundance Kid: I've been there already. Butch Cassidy: We could fight - they'll stay right where they are and starve us out. Or go for position, shoot us. Might even get a rock slide started, get us that way. What else can they do? Sundance Kid They could surrender to us, but I wouldn't count on that.

Butch Cassidy and the Sundance Kid, G. Roy Hill, 1969

In this research, I investigated different mechanisms that could yield to cooperation among species. Since Hamilton's "*relatedness*" idea, different mechanisms (e.g. assortment and spatial structure, direct and indirect reciprocity, group selection, and inclusive fitness) have been proposed to address the existence of cooperation among selfish individuals. All of the published mechanisms show levels of communication and information flow about the state of population between individuals; however, there is no theory that quantify the minimum amount of information for maintaining cooperation in the population. Here, to quantify the role of information on the evolution of altruism, I studied above mentioned mechanisms on different stochastic evolutionary games and explored conditions that each mechanism needs to have to maintain cooperation among selfish individuals. Moreover, to quantify the effects of communication and information flow on evolution of altruistic behavior, first we designed and run different experiments on Avida to see if information can be a selective trait or not. To do so, we applied the "Price equation" to track the variation of information content over the course of evolution. Then, we set up different stochastic iterated games to check how communication enforces cooperation in noiseless and noisy environments. Our ultimate goal in this research was to answer the following question:

"How much information an species should have about each other to show cooperative behavior?"

7.1 On the selectability of information content

Here, two different experimental evolutionary designs were applied in Avida to study if information content is a selectable trait. To track the evolution of information content and other highly correlated traits to information content such as number of performed logic tasks and some uncorrelated traits to information content and fitness (e.g. difference between frequency of two instructions (NopA and NopB)), the Price equation was used to track the variation of these traits in the first experiment. Furthermore, in the second experiment the Price equation was applied to track the genome length as a weakly correlated trait to fitness and information content. These experiments depict a strong correlation between the left hand side and the right hand side of the Price equation for all of the features examined. This shows that the Price equation is a good linear estimator for features that are highly or weakly correlated or completely uncorrelated to fitness. For highly correlated characters, the distribution of the right hand side of this equation is normally distributed around a positive value. On the other hand, if character is uncorrelated to fitness, the distribution of the right hand side and its terms will be very narrow and normally distributed around zero. In addition, for genome length as a feature that is weakly correlated to fitness, the distribution of the right hand side and the left hand side of the equation around the identity line is more scattered. Finally, these experiments demonstrate the role of selection and mutation on different levels of feature-fitness correlation. If the feature is highly correlated to fitness, the mean of first term (selection) and the second term (mutation) of the right hand side are highly separated, since the trait is positively selected and mutations are mostly deleterious. On the other hand, if the character is not correlated to fitness, the mean of first and the second term are around zero, and if the character has a weak correlation to fitness, the mean of the first and second term of right hand side is again around zero; however, the variance of these terms is going to be greater than the variance of first and the second term of an uncorrelated character to fitness.

Moreover, to probe the forces acting on features in different evolutionary states, the Price equation was applied to different states of population from highly unstable take-over events in which the change in mean fitness and mean character is high to a stable state in which the average of fitness and character remain constant. The results show that whenever there is a major variation in population and the fitness of population increases, the variance of the first term and the second term is low (especially for the features highly correlated to fitness) since advantageous mutation cancel the effect of deleterious mutation. On the other hand, if population is in a stable state, the variance of the first term and the second term is high (especially for the features highly correlated to fitness) since these traits are highly selected (the covariance is very strong) and mutation are all lethal or deleterious (highly negative). Moreover, average of first term and second term are almost equal and they cancel out each other in the right hand side of the equation. It is obvious that at the beginning of the experiments, the mutation term has significant effects on the evolution of character. This pattern is repeated whenever we have major variation in the population. On the other hand, when the population becomes stable, the effect of the mutation term reduces and first term and the second term cancel out each other.

7.2 Inclusive fitness theory in stochastic games

In this research, I studied the evolution of cooperation in a well-mixed population by doing infinitely large iterated stochastic games. I investigated the interaction of cooperators and defectors in these conditional games and tracked the evolution of cooperation and defection over the course of evolution. Here, cooperators cooperate with defectors conditionally and cooperate with cooperators unconditionally. I obtained a precise necessity condition for natural selection to favor cooperation over defection in these stochastic games. Cooperation is favored when the assortment "q" (one other interpretation of this parameter is having blind faith to defectors) is small. By repeating these iterated games, I observed that the the conditional parameter evolves to a small positive value. This means that cooperators evolve to an opportunistic or vigilant cooperator. They cooperate with the same type, yet hardly cooperate with the defectors. In other words, cooperators maximize their information about the game over the course of evolution. Interestingly, the conditional cooperation "q" for the evolved cooperator is not zero, as we expected. I assume the reason is that after the invasion of opportunistic cooperation, this parameter loses its potential carried information about the population since cooperators are playing unconditionally to each other and as a result, it is possible that drift brings this stable population to a critical state in which this cooperative strategy is an evolutionary unstable strategy; therefore, it is important to have a non-zero q for cooperators to avoid this critical state and become vulnerable to the invasion of defectors.

Moreover, I tracked the change of population's entropy over the course of evolution, and we observed that as population evolves, cooperators decrease their conditional parameter and become more vigilant. After a while, defection goes extinct, and the entropy of population decreases to a small value. The entropy does not go to zero because as soon as the defectors are wiped out, there is no difference between the pure and vigilant cooperators, and drift causes small variations in the population.

7.3 Iterated trust dilemma and the evolution of cooperation

In chapter 5, we investigated the emergence of secondary cooperation as possible stable altruistic strategy when the cooperation reward is less than or equal to the summation of temptation and sucker payoff in IPD. We observed that stochastic strategies engaging in secondary cooperation can be evolved by increasing the temptation payoff. These strategies depend on the synchronization of two genes and are thus much more sensitive to environmental changes that affect the certainty of players in forecasting future states of the game. Secondary cooperation is vulnerable to the invasion of defectors at critical mutation rate and temptation payoff values. Our results show that secondary cooperation is much more unstable in both genetic and phenotypic level when mutation rate is high due to the high degree of coordination required by this strategy; however, if these strategies are established in the population they are more robust to environmental noise in comparison to primary cooperation. This strategy needs higher level of certainty among players or a very high fitness benefit derived from alternating T and S payoffs to establish in the population. For environments that are highly predictable, i.e. at low mutation rate, and where there is no payoff advantage to engage in secondary cooperation, primary cooperation still is the strategy of choice.

7.4 Public goods game and altruism in despotic societies

In chapter 6, we investigated the properties of standard public goods game and extended it to collective hunting game to address the social behavior of animals. This extension yielded to properties that we could not find in the standard game. These properties are abundant among social animals, and this new game seems to be a potential model to study social behavior in animals. While public goods game does not describe complex societal structure of hyena clans, collective hunting game has rich structure describing collaborative strategies considering the necessary threshold parameter for all or nothing situations and allowing punishment. In collective hunting game, if the investment in the public good exceeds a given threshold, everyone (contributors as well as free riders) receives an equal share, and if the investment does not reach the threshold, the investment is lost. We find that effective punishment emerges as a stable strategy in this game, which in return facilitates cooperation. This suggests that the "collective hunting" is a better model for natural gambles that are "allor-nothing", and in which the triggered payoff does not depend on the number of investors in a linear fashion.

7.5 Future works

To further investigate the role of information and communication on the evolution of cooperation in stochastic game, the first step would be the extension of conditional strategies. Here, instead of having cooperators playing conditionally with defectors, we can have general players who play conditionally based on their previous payoff. Therefore, instead of having two types of players, we will have general players and we can track the entropy of these conditional strategies in the population over the course of evolution to investigate necessity conditions for maintaining cooperation in these stochastic games.

In collective hunting game, cooperation could not emerge for the case of few hunters. To maintain cooperation in this case, we have to think of a modification to our assumptions and include unequally distribution of the resources to stabilize this case with few collective hunters. Moreover, we have to apply this game to real data of hyena clans to see if this new game can predict the hyenas' sophisticated social behavior. Furthermore, in hyenas the punishers are usually the cheaters, and the size of the rich defectors is one; therefore, matrix representation of this game seems to be problematic, and we have to think of another approach to analyze the clan of hyenas.

For the iterated trust dilemma game, although it is not hard to imagine such a behavior existing in the economic markets, we still need to find a biological or social analogue to secondary cooperation. Particularly, when stock price inflation leads to the creation of stock market bubbles, the underlying agreement between investors constantly selling and re-buying the same stock is reminiscent of secondary cooperation. In this situation, parties agree to take turns in receiving a cost i.e. buying a certain stock, with the promise that they will be able to sell that stock at an increased value in the near future. This game in reality involves more than two parties but the type of cooperation observed is very much close to secondary cooperation. A future study into the implications of this could possibly help to predict the circumstances that cause the emergence and bursting of such bubbles.

APPENDICES

Appendix A

On the Validity of the Price Equation

Price Equation provides a fundamental insight into the relationship between characters' variation and fitness of organisms in consecutive generations [178]. This equation has been the groundwork of multiple theories in evolutionary biology and population dynamics, and its fame as a simple equation which describes the evolution of characters ($\bar{w}\Delta z = cov(w_i, z_i)$) is similar to the $E = mc^2$ in physics [49, 178, 179]. The Price equation, presented in equation (A.1), provides a genuine and realistic way to discuss arduous problems in population genetics by making a few simple rearrangements and changes in notation of relationship between individuals' fitness and characters in different populations [178]:

$$\bar{w}\Delta\bar{z} = cov(w_i, z_i) + E(w_i\Delta z_i)$$
(A.1)

where $w_i = \frac{n'_i}{n_i}$ is the fitness of type *i* in the ancestral population. n_i and n'_i are the total number of entities in two consecutive ancestral and descendant populations. $\Delta z_i = z'_i - z_i$ is the amount of change in character in type *i*. z_i and z'_i are the quantitative character of entities in ancestral and descendant population respectively. $\bar{w} = \frac{\sum_{j=1}^{i_a} n_j w_j}{\sum_{j=1}^{i_a} n_j}$ is the mean fitness in the ancestral population. $\Delta \bar{z} = z' - z$ is the variation of the character's mean in two consecutive generations. z and z' are the average of quantitative character in ancestral and descendant population respectively and given by:

$$z = \frac{\sum_{j=1}^{i_a} n_j z_j}{\sum_{j=1}^{i_a} n_j}$$
$$z' = \frac{\sum_{j=1}^{i_a} n'_j z'_j}{\sum_{j=1}^{i_a} n'_j}$$
(A.2)

Price equation asserts that the direction of change in a character's mean, $\Delta \bar{z}$, is related to the covariance between that character and the fitness plus expectation of random change in character value caused by mutation. In other words, if a character has positive correlation with fitness and is positively selected, this character increases through generations; however, if the mutation rate is high the random effect of the second term in the Price equation wipes out the effect of natural selection, and character's mean changes randomly.

The Price equation adds substantial insight into many problems of evolutionary biology as well as other fields such as chemistry, sociology, and economy by partitioning selection into meaningful components. Price himself believed that this theory was an important step toward a general theory of selection, which unifies all types of selection [180]. Although this equation presents a simple and general mechanism for the evolution of characters, it has a flip side which could easily induce imprecise or even improper results [179]. It has been argued that Price in his proof assumed that:

$$Cov(w_i, z_i) = \sum_{i=1}^{n^a} \frac{n^i}{n^a} (w^i - \bar{w})(z^i - \bar{z})$$
(A.3)

However, as we know, a covariance is a property of a joint distribution of two random variables and equation A.3 is just a linear estimation of this function, and if the random variables are non-linearly correlated, using this equation could be misleading [181]. Moreover, existence of certain limiting assumptions about the casual connectivity between the entities in ancestral and descendant population in this equation, makes it impossible to address some processes such as migration; thus to address these problems some generalizations to this equation has been proposed, and by having less restrictive assumption on the populations, new form of Price equation has the capacity to represent phenomena that was not possible to include in the original form of the equation [182].

The Price equation has another limitation in ancestral descendant relationship. If we apply this equation to an evolving population, in which the ancestral-descendant relationship is one to one, meaning that an ancestor generates just one type of descendant, Price equation becomes a tautology. However, if the ancestral-descendant relationship is one to many, and an ancestor have variety of descendant types and fitness values, the Price equation (both in its original and generalized form) with a linear estimation can be misleading. In our experiments, we examined this problem using both the original and generalized form of the Price equation. Table (A.1) and (A.2) show the variation of the left hand side, right hand side, avidians' information content and fitness over the first five generations. It is obvious that the left hand side and right hand side of Price equation are equal when there is a one to one relationship between the ancestral entity and descendants (generation 2 in table (A.1)). If we have one to many relationship between two consecutive generations, we have to use a linear estimation of the information content (which is addressed in generalized form of the Price equation). Now, if we have many to many relationships, it is uncertain what would be the correct relationship between ancestral and descendant entities, due to the fact that there are many connection matrices. The straight forward approach would be using the most probable or the simplest solution to this problem. Figure (A.1) shows one possible ancestral-descendant relationship of many other possibilities for the first five generations of our experiment.

Generation	LHS	$HS RHS cov(w_i, z_i) E(w_i \times \Delta z_i)$		$E(w_i \times \Delta z_i)$	$egin{array}{c} { m Ancestral} \\ { m Entities} \\ ({ m and} & { m their} \\ { m frequency}) \end{array}$	Descendant Entities (and their frequency)	\bar{z}_a	$ar{z}^d$	$ar{w}_a$	$ar{w}^d$
2	-0.0033	-0.0033	0	-0.0033	1(1)	2(2)	17.8483	17.8352	0.2494	0.2494
3	0.1681	0.0475	0	0.0475	1(2), 2(2)	2(3), 3(1), 4(1)	17.8417	18.5160	0.2494	0.1496
4	8498	9575	-0.0941	8634	$ \begin{array}{ccc} 1(1), & 2(3), \\ 3(1), & 4(1) \end{array} $	$\begin{array}{ccc} 2(4), & 3(2), \\ 4(1), & 5(1), \\ 6(2), & 7(4), \\ 8(2), & 9(1) \end{array}$	18.4047	13.2929	0.1425	0.1343

Table A.1: Variation of Price equation's left hand side, right hand side, and digital organisms' information content and fitness during the first four generations.

Table A.2: Variation of original and generalized Price equation's left hand side, right hand side, and digital organisms' information content and fitness during the first four generations.

Gen.	LHS	RHS_O	RHS_G	$cov(C^a_*,$	$z^a) {E(C^a_* imes \Delta z^a) \over \Delta z^a)}$	$\begin{array}{c} -{}^n d / {}_n a \times \\ cov(C_d^*, z_d) \end{array}$	Ancestral Entities (and their fre- quency)	Descendant Entities (and their fre- quency)	\bar{z}_a	\bar{z}^d	\bar{w}_a	\bar{w}^d
2	0	-0.003	-0.006	0.003	-0.006	-0.003	1(1), 2(1)	1(2), 2(2)	17.84	17.84	0.12	0.17
3	0.422	0.695	0.788	0.003	0.692	0.093	$ 1(2), \\ 2(2) $	1(1), 2(3), 3(1), 4(1)	17.84	18.40	0.17	0.17
4	-4.918	-8.116	-9.095	-0.755	-7.361	-0.979	1(1), 2(3), 3(1) , 4(1)	$\begin{array}{c} 1(5),\\ 2(4),\\ 3(1),\\ 4(1),\\ 5(1),\\ 6(1),\\ 7(1),\\ 8(1),\\ 9(1) \end{array}$	18.40	14.72	0.17	0.16
5	-2.416	-6.489	5.628	13.331	-6.842	-0.861	1(5), 2(4), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(1)	$\begin{array}{c} 1(5),\\ 2(6),\\ 4(1),\\ 5(1),\\ 6(2),\\ 7(1),\\ 8(1),\\ 9(1),\\ 10(1),\\ 11(1),\\ 12(1),\\ 13(1),\\ 14(1),\\ 15(1),\\ 14(1),\\ 15(1),\\ 18(1),\\ 17(1),\\ 18(1),\\ 19(1),\\ 20(1),\\ 21(1) \end{array}$	14.72	12.68	0.17	0.12

In addition, the generalized form of the equation has been introduced to address the situations that were not included in the original form such as emmigration, immigration, or having sexual reproduction by introducing a connectivity relationship (connection matrix).



Figure A.1: One possible ancestral-descendant relationship for the first five generations.

However, if we lose the track of this relationship (which is common in nature), or we have many to many relationships, we will have many possible scenarios, and each of them could be true. Figure (A.2) shows two possible connectivity out of many possible connectivity in our experiment. If ancestral/descendant entities are identical, there is no problem in using



Figure A.2: Two possible connection relationships in generation three: (a) symmetric form, (b) nonsymmetric form.

generalized form of the equation. However, if these entities are not identical, we can have multiple solutions. In this case, it is suggested to use the most probable structure. To do so, we need to have a distribution of the possible solutions, then we need to use the expected values of characters in descendant and ancestor populations in the "Price equation." Finally, in our experiments, especially in those with highly selectable traits, we noticed that the right hand side of Price equation over estimates the left hand side of the equation. To address this issue, we checked the variation of parameters of Price equation over different states of population fr two highly selectable tratis (information content and number of performed tasks), and we found out that this bias occurs over the stable states (Fig. (A.3)). Thus, after an exhaustive search among the generation in which the maximum bias occurs



Figure A.3: Over estimation of RHS (xlabel) of LHS (ylabel) for two highly selected traits (information content and number of different performed tasks): (a) LHS vs. RHS of Price equation applied to number of different performed task during a take over event (generations 101 to 1100), (b) LHS vs. RHS of Price equation applied to number of different performed task during a stable (generations 3001 to 4000), (c) LHS vs. RHS of Price equation applied to information content during a take over event (generations 101 to 1100), (d) LHS vs. RHS of Price equation applied to information content during a stable (generations 3001 to 4000), (c) LHS vs. RHS of Price equation applied to 1100), (d) LHS vs. RHS of Price equation applied to information content during a stable (generations 3001 to 4000).

(generation 9086), we selected an organism that could reproduce and survived on its own as the ancestral organism. We ran another experiment with this new head-default organism for 90 generations with the same experimental set up, and the result of analysis for four logic tasks, "and", "nand", "not", "nor", and "number of different performed tasks" were considered to find the source of over estimation. The results are presented in fig. (A.4-A.8). This new head-default avidian performs "Not" and "Nand", and since it does not perform "And" or "Nor" during this new experiment, the order of error for these traits are 10^{-3} and 10^{-7} respectively. The fitness of new head-default organism in the original experiment was 32514; however, in this new experiment, its fitness dropped to 110.206. Luckily in this new experiment, we had an early lethal mutation over the second generation, which caused a change in covariance part of the right hand side. At the third generation, this avidian reproduced 11 of its type (the frequency increases from 3/4 to 11/12), and its mutant did not go extinct over this generation; thus there no mutation happened over the transition between the second and the third generation and the second term is zero. It is obvious to see that there is also no change on average on trait trait, and thus, the left hand side is zero as well. However, since there is a covariance after emergence of this lethal mutation, the covariance term is positive, which causes this over estimation phenomenon. Over the forth generation, the number of original avidian increases to 13 (its frequency increases from 11/12 to 13/14); therefore, the difference from LHS and RHS is not that much (it is still distinguishable in fig. (A.4).) At fifth generation, the mutant dies, and LHS and RHS become identical. Since the rate of lethal mutation increases with population size, and it is more probable over stable states, we expect to see this bias more often over stasis and also if we increase the population size.



Figure A.4: Price equation left hand side and right hand side when applied to "and" logic task over 90 generations of new Avida run with new head-default organism: (a) LHS vs. RHS of Price equation for "and" logic task, (b) error between LHS and RHS of Price equation for "and" logic task.



Figure A.5: Price equation left hand side and right hand side when applied to "nand" logic task over 90 generations of new Avida run with new head-default organism: (a) LHS vs. RHS of Price equation for "nand" logic task, (b) error between LHS and RHS of Price equation for "nand" logic task.



Figure A.6: Price equation left hand side and right hand side when applied to "nor" logic task over 90 generations of new Avida run with new head-default organism: (a) LHS vs. RHS of Price equation for "nor" logic task, (b) error between LHS and RHS of Price equation for "nor" logic task.



Figure A.7: Price equation left hand side and right hand side when applied to "not" logic task over 90 generations of new Avida run with new head-default organism: (a) LHS vs. RHS of Price equation for "not" logic task, (b) error between LHS and RHS of Price equation for "not" logic task.



Figure A.8: Price equation left hand side and right hand side when applied to "number of different performed logic tasks" logic task over 90 generations of new Avida run with new head-default organism: (a) LHS vs. RHS of Price equation for "number of different performed logic tasks" logic task, (b) error between LHS and RHS of Price equation for "number of different performed logic tasks".

Appendix B

Avida, a Virtual Environment for Digital Organisms

Avida is a virtual environment/software in which self-replicating computer programs (or digital organisms) evolve by the basic forces of population-genetic operations, in particular mutation [34, 138, 183]. Each digital organism is represented by a sequence of assembly language like instructions (such as pop, add, if-less etc.). These instructions are interpreted by Avida and confer fitness to the organism depending on how well the executed instructions perform in a given environment. In particular, each organism is responsible for copying itself into the next generation, and an Avida organism usually begins with a genome, an instruction sequence, that can copy the organism. During this replicating process "errors", such as point mutations, insertions and deletions could occur [183].

Avida maintains a *population* of digital organisms and they compete for limited sources in the environment. Gaining resources affects an organism's growth rate, how quickly that can run their instructions to copy themselves (and perform other operations in the environment). Thus a gain in resources, an increase in *fitness* affects an organism's ability to create progeny. An Avida experiment allows the researcher to set:

- Structural parameters such as the instructions available for the organisms.
- Environmental parameters such as the availability and distribution of resources.

• Runtime parameters such as the mutation rate.

Having done so, the researcher can run an experiment on a population of organisms, observe the evolutionary results, and inspect in detail the organisms and their evolutionary trajectories.

In a classic experiment [137], Avida's environment incorporated a set of mathematical tests that allowed an increase in fitness for any organism that can perform various mathematical logic functions (AND, NAND, EQU). Initial organisms had no ability to perform such functions, only copy themselves, but over time were able to incorporate increasingly complicated logic functions as part of their genome. These operations conferred fitness to those organisms and allowed them to garner extra CPU cycles which can be used to accelerate organisms' replication [137, 183, 184].

The evolution of Avida organisms in the logic environment resulted in a kind of punctuated equilibrium, where the discovery of a new (and more fruitful) logic function by an organism granted a evolutionary advantage so great that the particular organisms and its progeny quickly "took over" the population, a so called *take over* event. Take over was typically followed a time of stasis as organisms evolved and drifted, until again a new function was discovered and the process repeated.

Appendix C

Queller's Derivation of Inclusive Fitness Theory

Here, frist we show:

$$cov(g,zz') = cov(g',zz')$$

To do so, we define "q" as:

q = zz'

The statistical properties of this new random variable is:

$$\mathbf{E}\left(q\right) = p_i^2 \tag{C.1}$$

$$\delta_q^2 = p_i^2 \left(1 - p_i\right) \left(1 + p_i\right) \tag{C.2}$$

Therefore, the left hand side of the "Price equation" can be written as:

$$cov(g, zz') = cov(g, q) = \mathbf{E} \left[(g - \bar{g})(q - \bar{q}) \right]$$

= $\mathbf{E} (gq) - \bar{g}\bar{q} = \mathbf{E} (gq) - p_i^3 = p_i^2 - p_i^3 = p_i^2 (1 - p_i)$ (C.3)

The right hand side of the equation C.1 can be written as:

$$cov(g', zz') = \mathbf{E}(gq) - \bar{g}\bar{q} = \mathbf{E}(gq) - p_i^3 = p_i^2(1 - p_i)$$
 (C.4)

Therefore, we have:

$$cov(g, zz') = cov(g', zz')$$

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