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Empirical Investigations of Human Behaviour in Game Theoretic Models of Communication

by

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DEDICATION

This thesis is dedicated to my husband Eric Verbeek for his unending love and support. With him by my side, the good days are great and the bad days are bearable. And to my parents, Sandy and Earl Brown, for being supportive of me no matter what path I choose in life.

ABSTRACT

I present three empirical studies in which humans with conflicting interests play game theoretic models of communication against one another. Two games of varying complexity, a handicap aggressiveness signaling model, and a conventional threat signaling game, are used. Player behaviour in sending and receiving information is compared to the Evolutionarily Stable Strategy (ESS) for each model, and the Evolutionarily Stable Set of strategies for the conventional signaling model. Player success is quantified by comparing their scores to the scores for the equilibrium strategies. Player communication varied with game complexity. Humans did not play the equilibrium strategies for any model used, yet average player scores were not less than scores for the equilibrium strategies, except in the most complicated model of communication. Here, player scores were lower than the ESS vs. ESS, but higher than the ES Set vs. ES Set. These results show that humans play competently but not perfectly.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Overview

The goal of this thesis is to investigate communication between human opponents in two game theoretic models of aggressive interaction. Communication is a fundamental aspect of social behaviour for animals and humans alike. Game theoretic models are particularly useful for investigating communication since they allow for a formal evaluation of interactions between two or more individuals when these interactions are stripped down to the barest essence (Fudenberg & Tirole 1991; Gibbons 1992; Johnstone 1997; Maynard Smith & Harper 2003; Hurd & Enquist 2005).

Although game theoretic models have proven very useful, they do not perfectly represent social interactions in the real world (Osborne 2003). In general, models are too simplistic, having few possible signals or discrete types of individuals, rather than accounting for the fact that states are often continuous, and there are more than just a few possible signals. When observing conflict between animals, it does not appear as though animals are following a simple, discrete, strategy as game theory would predict (Turner & Huntingford 1986) rather, their behaviour is stochastic (Hurd & Enquist 2001). One alternative to the use of current game theoretic models would be to create a truly realistic model of communication; however, accomplishing this lies somewhere between very difficult and impossible. Rather than altering the models we used, I chose to ask the question of how animals would play these simple games, which are used as models of biological communication. As it would be exceedingly difficult (if not impossible) to manipulate animals, such as fish, birds or rodents into playing these games, I chose human participants. All interactions in this thesis are set between individuals with conflicting interests and the three games intentionally vary in degree of complexity. I compared the behaviour of human participants to the equilibrium strategies for three games: a conventional signaling threat game (Enquist 1985), and two versions of Kim's (1995) aggressiveness signaling game. I also asked whether or not subjects were signaling reliably with each other, and if this communication affected their behaviour in the game. As a concrete analysis of their choices, I compared their payoff scores to the equilibrium strategies.

1.2 Communication

Communication has been a topic of interest for ethologists and game theorists for many years. The question of how (or even if) individuals with conflicting interests can communicate meaningfully has been widely debated (Zahavi 1975, 1977; Krebs & Dawkins 1984; Johnstone 1997). Conflict between individuals can occur for many different reasons, such as a fight over a food resource, or access to a mate. Two very good reasons for animals to communicate in such instances are to minimize costs and maximize benefits. For example, communicating intentions can reduce the chance of injury by convincing an opponent not to attack (Geist 1974), or an individual may benefit by convincing their opponent to abandon a resource. The problem with communication in this instance is how to prevent bluffing or cheating from replacing reliable communication when individuals have conflicting interests (Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Game theoretic models have been influential in their use of evolutionarily stable strategies as a way of approaching how reliability is maintained and have done so in a number of ways (Hurd & Enquist 2005).

One attempt to explain how communication can remain reliable between such individuals suggests that a direct innate cost is imposed on sending particular signals, such that the cost incurred is relative to the state of the sender. Only senders of a high enough caliber can afford to send costly signals: this is called handicap signaling (Zahavi 1975, Grafen 1990). The classic example of a handicapped signal is the enormous tail of the peacock. While the handicap hypothesis has been very influential, there are other models which can account for signal reliability that do not require a handicap. It *is* possible to produce reliable communication without having a direct cost to producing signals. This is accomplished by imposing an indirect cost on the sender as a function of the opponent's response. This is termed 'conventional signaling', because if there is any association between the signal sent and the state of the sender, it is established by convention (Enquist 1985; Maynard-Smith & Harper 2003) such that if there are two alternate signals being used to communicate two different conditions, then the signals could conceivably be reversed in meaning. An example of conventional signaling in humans is choosing to display the 'middle finger' or the 'thumbs up'. There is negligible difference in metabolic cost to producing these two signals, but there are costs to using each signal that come from the reaction of the person who receives it.

1.3 Definitions

I will now introduce some technical terms which will be used throughout this thesis. When investigating communication, it is important to have an operational definition to guide research and analysis. Communication occurs when information from a sender causes a receiver to change their behaviour from what it would otherwise have been (Smith 1977, Dawkins & Krebs 1978). It is not uncommon for senders to have an underlying **state** that may or may not be hidden from their opponent. An example of a state is strength, whether a player is strong or weak; another state could be the quality of an individual, whether high or low. To **send information** would be to choose a **signal**, which predicts the sender's future acts, or is indicative of an internal state that is hidden from the receiver. **Receiving**, or **using**, information is demonstrated by a change in the receiver's choice of **behaviour**; this change may also depend on their own internal state, but must always be based on the signal received from another individual.

To operationalize communication in this way allows for a systematic examination of the choices made by players. It enables us to ask questions such as whether the signals being sent are dependent upon the state of the players and whether players take their opponents signal into consideration when choosing which end move behaviour to play.

The amount and type of information made available to players in games will partially determine the best strategy to play. The terms **complete information** and **perfect information** are widely used. Having complete information simply means that that both players know the payoffs for all moves in a given game. To have perfect information would be for players to know the exact state of affairs in the game at all times (Gibbons 1992). Players of the games in this thesis had complete information, as they had the payoff matrix available at all times. However, since these players are making their moves simultaneously, combined with the fact that the E'85 game has a hidden state, our players did not have perfect information.

Throughout the thesis I will be comparing the behaviour of participants to the Evolutionarily Stable Strategy (**ESS**) for each model. An ESS is a strategy which, when adopted by the whole population of players, no player can benefit by deviating from and which cannot be invaded by any other strategy (Maynard Smith & Price 1973). For a strategy to be an ESS, it must be true that the payoff an ESS obtains when playing against itself is more than the payoff that another strategy would obtain when playing against the ESS. The ESS is sometimes thought of as the 'best' strategy to play.

In Chapter 3, I will also compare the behaviour of players to the ES Set for that game. An Evolutionarily Stable Set of strategies (**ES Set**) is a set of strategies that would individually be ESSs if all other members of the set were removed, and that score equally well against each other (Thomas 1985).

1.4 Humans Playing Games

Behavioural game theory, the study of human behaviour in game theoretic interactions, has been largely the purview of economics. Usually games played by humans are of a very simple nature with fairly obvious solutions (Colman 1995;

Camerer 2003). Despite this, there is a huge diversity in the games that are played, ranging from single player games with perfect information, to multi-player games with incomplete information. These simple games often have only one stage of play, and players have only two strategies available. Very few empirical studies have investigated communication in more complicated models as I have done in this thesis. The models used in this thesis have as few as 8 and as many as 324 pure strategies to choose from. All games had two stages with two or more choices at each stage, and one game had an underlying hidden state, which drastically increases game complexity.

Formal game theory tells us how rational self-interested players ought to behave in order to maximize returns against other perfectly rational players. Game theory does not provide realistic predictions about how players will actually behave against any other type of opponent. The assumption of rationality that formal models make has not been empirically supported for humans as they tend to use heuristics and biases in their judgements (Tversky & Kahneman 1974, 1981; Kahneman & Tversky 1982, 1996). One of the many ways that humans are not rational lies in the fact that it is often the subjective value of an outcome that guides people's behaviour, and not the objective value, such as its monetary or payoff value (see Colman 1995). Alternatively, Gigernezer (2000) argues that despite humans being not completely rational, the heuristics that we use help us make decisions which are better than what is considered to be the 'optimal' decision.

In many simple games, humans tend to choose strategies that are non-optimal (Bolton & Zwick 1995; Camerer 2003). This is not to say that humans always play games poorly against one another; humans seem to have a knack for choosing cooperative strategies when playing face to face with each other (Rapoport & Chammah 1966; Blume, DeJong, Kim & Sprinkle 1998). The amount of cooperation seen between individuals, however, depends on the size of the group of players. As the number of players increases, there is a decrease in the amount of cooperation (Marwell & Schmitt 1972). The experiments in this thesis used groups of three players, which should foster cooperation. Humans can be particularly good at coordinating in games with incomplete information when games are couched in locally relevant information and both players have a familiar context, such as players from the same country playing the Rendezvous game (Mehta, Starmer & Sudgen 1994). When this salient and familiar context is removed however, players are forced to rely on mathematical rationality to solve games and fare less than optimally (Colman 1995).

Signaling (sender-receiver) games involve one player of a certain type sending a signal to their opponent, who then chooses an action based on that signal. Results from these games are of particular interest as they are most relevant to this thesis. Brandts & Holt (1992), report that informative signaling was intuitively chosen by senders and that receivers were able to use the payoff matrix to maximize returns and play an intuitive equilibrium. Blume, DeJong, Kim and Sprinkle (1998) present results from a series of sender-receiver games showing that players with convergent interests gradually came to use informative signals over time without a common language base. This set of results shows that it is not unreasonable to expect that players are able to communicate when enough information regarding payoffs and sender type probabilities is made available.

Although humans are not completely rational and do not make optimal decisions in all instances, it is still worthwhile to examine the types of choices that humans make in *these* games as it could enlighten us as to their behaviour choices in real life instances involving a conflict of interests.

1.5 Chapters

In Chapter 2, I will discuss the results from Experiments 1 and 2 involving humans playing Kim's (1995) model of handicap threat signaling as well as a less cognitively taxing version of Kim's game in which signals had no handicapping cost. In Chapter 3, I discuss the results from Experiment 3 which involved humans playing a more complex model of conventional signaling (Enquist 1985).

I assessed playing in terms of communication use and strategy similarity to the Evolutionarily Stable Strategy (and for Enquist's model, to the Evolutionarily Stable Set). Specifically, I asked whether players a) sent information, and whether this information was reliable, and b) received information by using what was provided by their opponent to guide their own behaviour. I predicted that humans would be informative in the signals they sent and would use the information provided by their opponents, though do neither of these things perfectly. I also predicted that human players would not follow equilibrium strategy patterns for either signaling or behaviour, and would obtain fewer points than the ESS for all games played.

REFERENCES

Blume, A., DeJong, D., Kim, Y.-G., & Sprinkle, G. (1998). Experimental evidence on the evolution of meaning in messages in sender-receiver games. *The American Economic Review, 88,* 1323-1340.

Brandts, J. & Holt, C. (1992). An experimental test of equilibrium dominance in signaling games. *The American Economic Review, 82,* 1350-65.

Bolton, G., & Zwick, R. (1995). Anonymity versus punishment in ultimatum bargaining. *Games and Economic Behavior, 10,* 95-21.

Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of animal communication.* Sunderland: Sinauer.

Dawkins, R. (1982). The Extended Phenotype. Oxford: Oxford University Press.

Dawkins, R. & Krebs, J. R. (1978). Animal signals: information or manipulation? In Krebs, J. R. & Davies, N. B. (Eds.), *Behavioural Ecology: an evolutionary approach* (1st ed, pp. 282-309). Oxford: Blackwell.

Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour, 33,* 1152-1161.

Fudenberg, D. & Tirole, J. (1991). *Game Theory.* Cambridge: MIT Press.

Geist, V. (1974). On fighting strategies in animal combat. *Nature, 250,* 354.

Gibbons, R. (1992). *A primer in Game Theory.* Hemel Hempstead: Harvester Wheatsheaf.

Gigerenzer, G. (2000). Adaptive thinking: Rationality in the real world. New York: Oxford University Press.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology, 144,* 517-546.

Hurd, P. & Enquist, M. (2001). Threat display in birds. *Canadian Journal of Zoology,* 79, 931-942.

Hurd, P.L. & Enquist, M. (2005). A strategic taxonomy of biological communication. *Animal Behaviour, 70,* 1155-1170.

Johnstone, R. A. (1997). The evolution of animal signals. In Krebs J. R. & Davies, N. B. (Eds.) *Behavioural Ecology: an Evolutionary Approach* (pp. 155-178). Oxford: Blackwell.

Kahneman, D., & Tversky, A. (1982). Variants of uncertainty. *Cognition, 11,* 143-157.

Kahneman, D., & Tversky, A. (1996). On the reality of cognitive illusions. *Psychological Review, 103,* 582-591.

Kim, Y. G. (1995). Status signaling games in animal contests. *Journal of Theoretical Biology, 176,* 221-231.

Krebs, J. R. & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In Krebs, J. R. & Davies, N. B. (Eds.), *Behavioural Ecology: an Evolutionary Approach* (2nd ed., pp. 380-402). Sunderland: Sinauer.

Marwell, G. & Schmitt, D. (1972). Cooperation in a three-person Prisoner's Dilemma. *Journal of Personality and Social Psychology,* **21,** 376-383.

Maynard Smith, J. & Price, G. (1973). The logic of animal conflict. *Nature, 246,* 15-18.

Maynard Smith, J. & Harper, D. G. (2003). *Animal Signals.* Oxford: Oxford University Press.

Mehta, J., Starmer, C. & Sudgen, R. (1994). Focal points in pure coordination games: An experimental investigation. *Theory and Decision, 36,* 163-185.

Osborne, M. (2003). *An Introduction to Game Theory.* Oxford: Oxford University Press.

Rapoport, A. & Chammah, A. (1966). The Game of Chicken. *American Behavioral Scientist, 10,* 10-14, 23-28.

Smith, W. J. (1977). *The Behavior of Communicating: an Ethological Approach.* Cambridge: Harvard University Press.

Thomas, B. (1985). On evolutionarily stable sets. *Journal of Mathematical Biology, 22,* 105-115.

Turner, G. & Huntingford F. (1986). A problem for game-theory analysis – assessment and intention in male mouthbrooder contests. *Animal Behaviour, 34,* 961-970.

Tversky, A., & Kahneman, D. (1974). Judgement under uncertainty; heuristics and biases. *Science, 185,* 1124-1131.

Tversky, A., & Kahneman, D. (1981). The framing of decisions and the psychology of choice. *Science, 211,* 453-458.

Zahavi, A. (1975). Mate selection – a selection for a handicap. *Journal of Theoretical Biology, 53,* 205-214.

Zahavi, A. (1977). The cost of honesty (Further remarks on the handicap principle). *Journal of Theoretical Biology, 67,* 603-605.

CHAPTER 2

HUMAN BEHAVIOUR IN AN AGGRESSIVENESS SIGNALING GAME

2.1 INTRODUCTION

2.1.1 Communication

Communication is fundamental to social interactions and therefore has been studied by ethologists and game theorists for many years. The question of how (or even if) individuals with conflicting interests can communicate has been widely debated (Zahavi 1975, 1977; Johnstone 1997; Krebs & Dawkins 1984). Individuals with conflicting interests may be expected to bluff or cheat instead of accurately communicate their status or intentions (Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Explaining why individuals do not seem to do this is a central problem of communication. Game theoretic models have been very influential in approaching the problem of signal reliability by conceiving of it as an evolutionarily stable strategy (Hurd & Enquist 2005).

The handicap principle is one explanation of how communication can remain reliable between individuals with conflicting interests. It proposes that an innate cost is imposed on sending particular signals such that only some signalers can afford to use them (Zahavi 1975, Grafen 1990). The classic example of a handicapped signal is the enormous tail of the peacock. Although the tail is a powerful mate attractor, it also attracts predators and slows movement such that when predators are present, and is metabolically expensive to produce.

The model of handicap signaling used in this experiment (Kim 1995) also imposes a handicapping cost to an otherwise more powerful signal. We investigate the ability of human players to communicate despite conflicting interests under two conditions. Experiment one investigates communication with two signals, where one signal has a handicapping cost (as indicated above). Experiment two involves communication with three signals, none of which have a handicapping cost. Comparing communication between a game with a handicapping cost and one without will help determine if handicapping costs are indeed needed for reliable communication between human subjects.

2.1.2 "Hawk-Dove Game" & "Chicken Game"

In biology and behavioural ecology, the game used in our experiments is referred to as the "Hawk-Dove" game, whereas in behavioural game theory and economics the same game is referred to as the game of "Chicken". The game of chicken takes its name from the real-life game in which two individuals drive straight towards each other until one swerves and the other 'wins' the contest. However if both players drive 'straight' and neither player 'swerves', there is the negative consequence of a very costly head-on collision. On the other hand, the Hawk-Dove game posits a population composed of two types of strategists, "Hawks" who escalate and fight, and "Doves" who are pacifists. Individuals in the population are competing over a resource. When Doves meet, they share the resource but when Hawks meet they engage in a costly fight, damaging each other. The temptation is to play Hawk in the hopes that your opponent will play Dove, thus allowing you to obtain the value of the resource; however, this temptation is kept in check by a great cost if your opponent also chooses to play Hawk, in which case the cost of escalating exceeds the value of the resource. The game of chicken is often compared to the Prisoner's Dilemma game which uses the terminology 'cooperate' and 'defect' to refer to similar types of players and this terminology has penetrated much of the research on how humans play the game of Chicken. In the hawk-dove game the move 'hawk' is analogous to driving 'straight' or 'defecting' in Chicken, whereas 'dove' is analogous to 'swerve' or 'cooperate'. For the sake of consistency within this paper, behaviour choices below will be discussed in the terminology of the "Hawk-Dove" game.

2.1.3 How do Humans play the Hawk-Dove game?

The way in which human players behave in the Hawk-Dove game depends greatly on the specific experimental procedures used. Many experiments have deceived subjects into thinking that they are playing against a real opponent when they are instead playing against a fixed computer program. In one such experiment, Sermat (1967a) found that when players with complete information thought they were playing against other human players who were free to change their strategy (but were actually playing against a computer program that played 'Hawk'), they tended to choose 'Hawk' more frequently leading to overall lower payoffs than if they had chosen 'Dove', thus punishing both their opponent and themselves. When subjects knew they were playing against a programmed machine which could not alter its strategy (and was choosing 'Hawk'), they chose 'Dove' more often, thus maximizing their own payoffs. When playing against a tit-for-tat strategy, Sermat (1967b) showed that cooperative behaviour (i.e. choosing 'Dove') increased over time. While using a lower number of trials but still having subjects play against a computer Conrath (1972) found that subjects playing against a program which randomly chose 'Dove' with a probability of 70% and 'Hawk' 30%, were able to fairly accurately describe these percentages, showing that humans are capable of assessing the strategy of their opponent. Despite knowing these probabilities, players still chose 'Dove' over 50% of the time. In the same experiment, Conrath (1972) found that females were slightly more cooperative than males on average, which gives reason to believe that there may be sex differences in the strategies of males and females in the game of chicken. Rapoport & Chammah (1966) report that as they increased the punishment for mutual defection (ie: for both players choosing 'Hawk'), subjects playing against other human subjects were somewhat more likely to choose a cooperative strategy but their proportions of cooperating were only near the equilibrium when the cost of defection was relatively low.

2.1.4 How do humans play signaling games?

Signaling (sender-receiver) games involve one player of a certain type sending a signal to their opponent, who then chooses an action based on that signal. Results from these games are of particular interest as they are most relevant to this experiment. Brandts & Holt (1992) report that informative signaling was intuitively chosen by senders and that receivers were able to use the payoff matrix provided to maximize returns and play an intuitive equilibrium. Blume, DeJong, Kim and Sprinkle (1998) present results from a series of sender-receiver games showing that, over time, players came to use informative signals without a common language base when they had convergent interests. In a set of experiments which varied the preference difference between opponents in a sender-receiver game, Cai & Wang (2006) found that as the difference in preferences increased, the informativeness of signals decreased; however, even when preferences were most different, messages were still somewhat informative and responses were still dependent partially on the message that players received from their opponent. This is especially interesting given that no communication was predicted from their model with divergent preferences. This set of results shows that it is not unreasonable to expect that players are capable of communication in games when enough information is made available.

2.1.5 The Kim (1995) Game

Kim's (1995) model of handicap aggressiveness signaling is a two phase game. In the first phase, two players choose one of two signals to send simultaneously to one another, this is then followed by a play of the hawk-dove game. One of the available signals (which in our experiment we call 'Green') is a costly escalated signal, and the other ('Purple') is not. After the signaling phase, players choose one of two actions: 'Forward', which is our analogue to choosing 'Hawk', or 'Backward', which is analogous to 'Dove'. From this point I will refer to the choices that players made in the language of the game that we used with players. Payoffs to each player are determined by the signals and behaviours of both players. The ESS for the Kim Game is to choose the costly signal 'Green' 3/4, and 'Purple' 1/4, then to play a mixing strategy of 1/3 Dove and 2/3 Hawk when signals coordinate (when players both choose 'Purple' or both choose

'Green'), and when signals discoordinate, the player who chooses the costly signal 'Green' chooses the behaviour 'Forward' and the player who chooses the signal 'Purple' chooses the behaviour 'Backward'. For an extensive form diagram depicting this game and its ESS, see Figure 2-1.

The modified version of the Kim game that we use involves the same basic two-stage game with a signaling phase followed by a behaviour choice in the Hawk-Dove game; however, there are now three signals available, none with a handicapping cost. The ESS for this game is to choose each of the three signals equally frequently. The signals are then used in a rock-paper-scissors fashion, such that when signals discoordinate, one signal predicts Hawk and the other Dove for each discoordinated signal pairing. When signals coordinate, the ESS again is to play the mixing ESS with probabilities 2/3 Hawk and 1/3 Dove.

2.1.6 Purpose

Our study employs empirical techniques to investigate two models of communication between individuals with conflicting interests. We will answer three questions: 1) Do individuals with conflicting interests communicate reliably? That is to say, does the signal that players send predict their future behaviour and does the signal received alter the receiver's behaviour? 2) Do human subjects play a strategy that resembles the ESS? 3) What are the payoff consequences of the human strategy as compared to the ESS?

Experiment 1: Original Kim Game with one of 2 signals handicapped

2.2 EXPERIMENT 1 METHODS

2.2.1 Players and the Kim Game

Participants were 146 undergraduate students (103 female and 43 male), enrolled in an introductory psychology class who received credit for their participation. Students played the Kim game in groups of three. Each player was given a sheet to record their actions and scores, an information sheet explaining the rules of the game and a payoff sheet (See Table 2-1) where they could look up the scores. Experimenters also issued a verbal explanation of the instructions and ensured that all players understood the rules of the game and how to obtain their score from the payoff sheet. For every round there were two active players (player one and player two) and a referee. The students rotated roles such that each player was in each role an equal number of times and completed 20 rounds of the game. The referee served to observe the interaction between the two players, ensure that no cheating occurred and that calculation of scores was accurate. At the end of each round, players wrote the interaction down on their sheet along with their score for that round.

There were two phases of play for each round. First, subjects chose a signal, either 'Purple' (the non-handicapped signal) or 'Green' (the handicapped signal) and (using their hand) covered the wooden chit with the signal word written on it, slid it from behind a concealing screen and upon indication from the researcher, simultaneously showed their opponent. In phase two, players chose their behaviour, either 'Forward' (Hawk) or 'Backward' (Dove) and again covered it with their hand and slid it from behind a screen, and upon instruction from the researcher, simultaneously showed each other their behaviour choice. After choosing their behaviour, players obtained their score, wrote the interaction down and rotated player roles. All 20 rounds of the game took approximately 35 minutes to complete.

2.2.2 Calculating the Expected Payoff for ESS vs. Players

Since there are significant sex differences in both signaling and behaviour (see below), we will look at the ESS vs. males and females separately. To determine the score that the ESS would receive if it played against the human population, we took the behaviour dictated by the ESS for each of the types of signal combinations (Ego Signal Purple & Opponent Signal Purple, G & G, P & G and G & P). For each encounter type we took the probability of the ESS and the opponent each signaling 'Purple' and 'Green' and incorporated the probabilities 'Forward' and 'Backward'.

2.2.3 Calculating the Expected Payoff for ESS vs. ESS

To determine the score that the ESS would receive if it played against itself, we employed the same method as for calculating the expected payoff for the ESS vs. players. As indicated in the original paper by Kim (1995), the ESS would receive a score of zero points per game and thus zero points across 20 games.

2.3 EXPERIMENT 1 RESULTS

2.3.1 Signal Choice

We asked first whether humans would choose signals in ESS proportions, which is to signal 'Purple' (the signal with no handicapping cost) 25% of the time and 'Green' (the signal with a handicapping cost) 75% of the time. There was a significant association between pattern of signaling and the sex of the player ($\chi^2_{(1, N=146)}$=11.33, p=0.001). Females chose 'Purple' 61.11% of the time and 'Green' 38.89% of the time. This is in the opposite direction of the ESS pattern of signaling, and is significantly different as determined by the Chi-Square goodness of fit test ($\chi^2_{(1, N=103)}$=1431.37, p<0.001). Similarly, males chose 'Purple' 67.72% of the time and 'Green' 32.28% of the time. This was also different from the ESS, ($\chi^2_{(1, N=43)}$=832.17, p<0.001). In both cases, players avoided the signal with the cost associated with it (Table 2-2).

2.3.2 Choice of Behaviour

Since the overall pattern of behaviour, when not considering opponent signal, was dependent upon the sex of the players ($\chi^2_{(1, N=146)}$=9.46, p=0.002), we will consider males and females separately when talking about overall behaviour patterns. The behaviour that the players chose was not mediated by the signal of their opponent in either males ($\chi^2_{(1,N=43)}$=0.003, p=0.958) or females ($\chi^2_{(1,N=103)}$=0.001. p=0.978). This is to say, that players were not using the information that their opponent provided to make a decision about their own behaviour. However, ego move was dependent upon ego signal in both females ($\chi^2_{(1,N=103)}$=7.05, p=0.008) and males ($\chi^2_{(1,N=43)}$=4.28, p=0.038), which tells us that players were indicating their future behaviour. Now we will investigate behaviour choices of males and females compared to the behaviour dictated by the ESS (Table 2-3).

When Signals Coordinate (Ego Purple & Opponent Purple; Ego Green & Opponent Green)

We asked whether the behaviour patterns of the players would match the behaviour dictated by the ESS. We will consider each of the four signal match-ups separately, and investigate any sex differences that arise. The ESS end move behaviour when both players chose the signal 'Purple' is to choose 'Forward' 66.66% of the time and 'Backward' 33.33% of the time. Males and females differed in their behaviour choice under this circumstance ($\chi^2_{(1, N=146)}=5.01$, $p=0.03$). Males choose 'Forward' 69.64% of the time and 'Backward' 30.36% of the time. This fits and is not statistically different from the pattern dictated by the ESS ($\chi^2_{(1, N=43)}=1.47$, $p=0.225$). Females chose 'Forward' 62.96% of the time and 'Backward' 37.03% of the time. This did not fit the pattern dictated by the ESS ($\chi^2_{(1, N=103)}=5.11$, $p=0.024$; Table 2-4).

The proportions of 66.66% 'Forward' and 33.33% 'Backward' are also dictated by the ESS when both players choose the signal 'Green'. In this instance there was no association between behaviour and sex ($\chi^2_{(1, N=146)}=1.380$, $p=0.24$). Players chose 'Forward' 59% of the time and 'Backward' 41% of the time, which was significantly different from the proportions of the ESS ($\chi^2_{(1, N=146)}=14.45$, $p<0.001$; Table 2-4).

When Signals Discoordinate (Ego Signals Purple & Opponent Signals Green; Ego Signals Green & Opponent Signals Purple)

When ego chooses 'Purple' and opponent chooses 'Green', the ESS is to choose 'Backward' 100% of the time. As the expected outcome for 'Forward' in this instance is zero, a statistical analysis was not required to determine if players were playing the ESS. There was no difference between males and females ($\chi^2_{(1, N=146)}$=1.38, p=0.240). Players chose 'Forward' 66% of the time and 'Backward' 33% of the time, which is definitely not the same as the ESS (Table 2-5).

Similarly, when ego chooses 'Green' and opponent chooses 'Purple', the ESS is to choose 'Forward' 100% of the time. In this instance, as in the previous, there was no difference between males and females in the behaviour choices ($\chi^2_{(1, N=146)}$=0.725, p=0.394). Players chose 'Forward' 59% of the time and 'Backward' 41% of the time. Again, it is clear that they are not playing the ESS in this instance (Table 2-5).

2.3.3 Scores

Scores ranged from -33 to 52, with a mean of -2.5, and a standard deviation of 13.7. There was no significant difference between males (-3.25 average) and females (-2.19 average) in their average scores (t_{144}=-0.425, p=0.671). Were the ESS to play against itself, it would score 0 points across 20 games, meaning that players did only minimally worse against themselves than the ESS would against itself. If the ESS were to play against the females from our sample it would score -7.89 over 20 games. The same females playing against the

ESS would obtain a score of -11.9 over 20 games. If the ESS were to play against the males from our sample, it would score -12.92 over 20 games. Likewise, the males playing against the ESS would score -16.44 over 20 games. Although the ESS does minimally better than both males and females, it still ends with negative payoff values (Figure 2-2).

Experiment 2: Three Signals and No Handicapping Cost

2.4 EXPERIMENT 2 METHODS

2.4.1 Players and the Modified Kim Game

Participants were 151 undergraduate students (101 female and 50 male), enrolled in an introductory psychology class who received credit for their participation. Students played the modified version of the Kim game in groups of three. The format of the game was identical to that of experiment 1.

There were two phases of play for each round. First, subjects chose one of three signals: 'Purple', 'Green', or 'Blue' and covered the wooden chit with the signal written on it, slid it from behind a concealing screen and upon indication from the researcher, simultaneously showed their opponent. After this, players chose their behaviour, either 'Forward' (Hawk) or 'Backward' (Dove) and again covered it with their hand and slid it from behind a screen and upon instruction from the researcher, simultaneously showed each other their behaviour choice. After choosing their behaviour, players recorded the interaction and rotated player roles. All 20 rounds of the game took approximately 35 minutes to complete.

2.4.2 Calculating the Expected Payoff for ESS vs. Players

Since there are significant sex differences in both signaling and behaviour, we will look at the ESS vs. males and females separately. In order to determine the score that the ESS would receive if it played against the human population, we took the behaviour dictated by the ESS for each of the types of signal match-ups (Ego Signal Purple & Opponent Signal Purple, P & G, P & B, G & P, G & B, G & G, B & B, B & G and B & P). For each encounter type we used the probability of the ESS and the opponent signaling 'Purple', 'Green' and 'Blue' and incorporated the probabilities 'Forward' and 'Backward' used by each.

2.4.3 Calculating the Expected Payoff for ESS vs. ESS

To determine the score that the ESS would receive if it played against itself, we employed the same method as for calculating the expected payoff for the ESS vs. players. Just as with the original Kim game, the ESS would receive a score of zero points per game and thus zero points across 20 games.

2.5 EXPERIMENT 2 RESULTS

2.5.1 Signal Choice

We asked first whether humans would choose signals in the proportions designated by the ESS, which is to choose each signal 1/3 of the time since there is no consequence for choosing either signal. Males and females were significantly different in their pattern of signal choice ($\chi^2_{(1, N=151)}=10.19$, $p=0.006$). Males chose 'Green' 36.5% of the time, 'Purple' 29.6% of the time and

'Blue' 33.9% of the time. Females chose 'Green' 30.9% of the time, 'Purple' 33.5% of the time and 'Blue' 35.6% of the time. In females this is different from the proportions expected by the ESS ($\chi^2_{(2, N=101)}$=6.75, p=0.034). In males, this was also different from the ESS ($\chi^2_{(2, N=50)}$=7.28, p=0.026; Table 2-6).

2.5.2 Choice of Behaviour

Just as in experiment one, again we see that the overall pattern of behaviour was dependent on the sex of players ($\chi^2_{(1, N=151)}$=4.585, p=0.032). The behaviour that players chose was not dependent upon the signal of their opponent in males ($\chi^2_{(2, N=50)}$=0.486, p=0.784) or females ($\chi^2_{(2, N=101)}$=1.36, p=0.507). We also see that behaviour choice was not dependent upon their own signal in males ($\chi^2_{(2, N=50)}$=1.00, p=0.607) or females ($\chi^2_{(2, N=101)}$=3.289, p=0.193; Table 2-7). Rather than separate results for each signal type pairing, we separated results for when signals coordinate or discoordinate.

When signals Coordinate

We will consider the behaviour of males and females separately because of the differences in their signal choices and overall behaviour choices. When signals coordinate, the ESS is to use the Mixing strategy of choosing Forward 66.6% of the time and Backward 33.3% of the time. We found that both males ($\chi^2_{(2, N=50)}$=0.006, p=0.94) and females ($\chi^2_{(1, N=101)}$=1.65, p=0.198) did not choose a pattern of behaviour that differs significantly from the ESS (Table 2-8).

When signals Discoordinate

Again we consider the behaviour of males and females separately. When signals discoordinate, a rock-paper-scissors type of signal dominance should occur so we should see a relationship between a player's signal, their opponent's signal and their behaviour choice. If they were using signals in a rock-paper-scissors fashion, according to the ESS, we would expect to find an equal proportion of plays of Hawk and Dove. This was not the case for females ($\chi^2_{(1, N=101)}$=131.84, p=0.00) or males ($\chi^2_{(2, N=50)}$=110.2, p<0.001; Table 2-8). Females chose Forward 65.8% of the time and Backward 34.2% of the time, just as they did when signals coordinated. Males chose Forward 70.7% of the time and Backward 29.3% of the time.

2.5.3 Scores

Scores ranged from -36 to 44, with a mean of 1.54, and a standard deviation of 13.2. There was no significant difference between males (3.68 average) and females (0.47 average) in the scores obtained (t_{144}=1.41, p=0.161). Were the ESS to play against itself, it would score 0 points across 20 games, meaning that it did minimally worse against itself than players would against themselves. If the ESS were to play against our female subjects, it would score 1.08 points over 20 games, compared to -2.02 points over 20 rounds against the male players. Both males and females playing against the ESS would obtain a score of zero over 20 rounds. Again this shows that the ESS is not the most sensible strategy to employ in all cases. (See Figure 2-3).

2.6 DISCUSSION

This experiment was designed to examine whether human subjects would communicate in an aggressiveness signaling game. In experiment 1, subjects sent, but did not respond to, information. In experiment 2 subjects neither sent information to nor used information from their opponent.

We found that subject's signal predicted their behaviour in the Original Kim Game experiment (experiment 1). However, players did not seem to respond to information by using their opponent's signal to determine which behaviour to use. In no instance was their behaviour dependent upon the signal received from their opponent. It is clear that players did not play the ESS in this game. Their signal choices were in the opposite direction from the ESS signal choices and their behaviour in the Hawk-Dove phase of the game only approximated the ESS behaviour when both players chose the same signal. That players did not respond to signals negated any effect of sending them. Since the point of this game is that by using different signals, players can predict their opponent's behaviour and maximize payoffs to mutual benefit, human players were definitely not playing the ESS. In spite of this, their payoffs were not much lower than the payoff to the ESS playing against itself. This may be due to the fact that players generally chose the costly signal much less frequently, and were thus playing a sensible strategy against other players like themselves. We also saw that if the ESS were to play against the strategy of human players, it would obtain fewer points than the average player score.

In the Modified Kim Game experiment, we found the perplexing result of males and females choosing different proportions of signals from each other and from the ESS. Since there was no cost to any signal, choosing each signal equally was the ESS. Males chose green most frequently and females chose blue most frequently. These differences are most likely simply due to colour preference of the respective genders, rather than a strategic choice, something we did not anticipate in our choice of wording for the signals. Overall though, players chose each of the signals reasonably equally. Players did not send information to their opponents, meaning that there was no association between their signal and their future behaviour. Again we see that players did not use their opponent's signal to choose their own behaviour. When signals coordinated, males and females both chose end move behaviours with the same frequency as the ESS; however, they did not when signals discoordinated. Although players were almost using the ESS signaling proportions and were using the ESS behaviour proportions, they were still not playing the ESS. With three signals available, the ESS is to use a rock-paper-scissors system, where one signal becomes indicative of which behaviour is to follow and for each signal pair, one of the signals predicts Hawk and the other Dove. Since our human players were not sending information or receiving information they were not possibly playing the ESS. Despite not playing the ESS, players still scored relatively well against each other, scoring slightly better on average against themselves than the ESS against itself.

When comparing the results obtained in experiment one to those from experiment two, we see that the game which had the handicapping cost produced more reliable communication. This lends support to the hypothesis that, in humans at least, a handicapping cost may be a necessary start to producing reliable communication between individuals with conflicting interests.

Although our design included a signaling phase of play before the Hawk-Dove game, the results we obtained in the Hawk-Dove portion of the game were similar to Sermat's (1967a) findings. Our players, who were playing against other human subjects, chose a distinctively aggressive strategy (choosing Hawk upwards of 70% of the time), which is what Sermat (1967a) found when players thought they were playing against opponents who were free to change their actions at any moment. Just like Conrath (1972), we found differences between males and females in the way they played the Hawk-Dove portion of the game for the modified version of the Kim Game, where females chose a more 'cooperative' strategy (i.e. choosing Dove) than their male counterparts. An interesting future study with this model would involve manipulating the gender of groups of players to see if strategies for either sex change with the sex of their opponent.

With regards to the sender-receiver literature, sending information in our game, which essentially acts as a promise of future behaviour, is slightly different from sending in sender-receiver games where senders are sharing information about a particular state of the world. In previous cases where interests between individuals differed, information was still sent and used (Cai & Wang 2006). Our players sometimes sent information but did not use the information provided by their opponent to help decide which behaviour to choose. A possible reason for the divergence of results could be because of the degree to which interests were divergent. The amount of time that players played for could also account for why we did not see much communication. Most sender-receiver games have many more trials and thus more time to develop communication between players. Future experiments with our model should have players engaged in play for a longer period of time to see if communication will occur given enough plays of the game.

My Signal = Purple & Opponent Signal = Purple

		My Move: Forward	My Move: Backward
Opponent's Move	Forward	-2	0
	Backwards	4	0

My Signal = Green & Opponent Signal = Purple

		My Move: Forward	My Move: Backward
Opponent's Move	Forward	-3	-1
	Backwards	3	-1

My Signal = Purple & Opponent Signal = Green

		My Move: Forward	My Move: Backward
Opponent's Move	Forward	-2	0
	Backwards	4	0

My Signal = Green & Opponent Signal = Green

		My Move: Forward	My Move: Backward
Opponent's Move	Forward	-3	-1
	Backwards	3	-1

Table 2-1: Payoff matrix given to players in Experiment 1. Each table is labeled with one of the four possible signal match-ups.

Sex difference in Signal Choice					
		Ego Signal			
		Purple	Green	Total	
Sex	Male	579	276	855	χ^2=11.33
	Female	1257	800	2057	p=0.001
	Total	1836	1076	2912	

Female Signal Choice Different from ESS					
		Ego Signal			
		Purple	Green	Total	
	Observed	1257	800	2057	χ^2=1430.37
	Expected	514	1543	2057	p<0.001
	Total	1771	2343	4114	

Male Signal Choice Different from ESS					
		Ego Signal			
		Purple	Green	Total	
	Observed	579	276	855	χ^2=832.17
	Expected	214	641	855	p<0.001
	Total	793	917	1710	

Table 2-2: Signal use as a function of Sex for Experiment 1. Also, 'Obtained from players' vs. 'Expected by ESS' cell counts for Signal Choice, separated by sex.

Overall Sex difference in Behaviour Choice

		Ego Move			
		Forward	Backward	Total	
Sex	Male	577	278	855	χ^2=9.46
	Female	1264	793	2057	p=0.002
	Total	1841	1071	2912	

Opponent Signal Does NOT Mediate Ego Move in Males

		Ego Move			
		Forward	Backward	Total	
Opponent Signal	Purple	356	171	527	χ^2=0.003
	Green	221	107	328	p=0.958
	Total	577	278	855	

Opponent Signal Does NOT Mediate Ego Move in Females

		Ego Move			
		Forward	Backward	Total	
Opponent Signal	Purple	802	503	1305	χ^2=0.001
	Green	462	289	751	p=0.978
	Total	1264	792	2056	

Ego Signal DOES Mediate Ego Move in Males

		Ego Move			
		Forward	Backward	Total	
Ego Signal	Purple	404	175	579	χ^2=4.28
	Green	173	103	276	p=0.038
	Total	577	278	855	

Ego Signal DOES Mediate Ego Move in Females

		Ego Move			
		Forward	Backward	Total	
Ego Signal	Purple	801	456	1257	χ^2=7.058
	Green	463	337	800	p=0.008
	Total	1264	793	2057	

Table 2-3: Overall behaviour choice in Experiment 1 as a function of sex, ego signal and opponent signal. Cell counts, X^2 and p-values reported.

Ego and Opponent Signal PURPLE, Sex Difference in Behaviour					
		Ego Move			
		Forward	Backward	Total	
Sex	Male	257	112	369	χ^2=5.01
	Female	522	307	829	p=0.025
	Total	779	419	1198	
Ego and Opponent Signal PURPLE, Males do NOT Differ from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	257	112	369	χ^2=1.472
	Expected	246	123	369	p=0.225
	Total	503	235	738	
Ego and Opponent Signal PURPLE, Females Differ from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	522	307	829	χ^2=5.114
	Expected	553	276	829	p=0.024
	Total	1075	583	1658	
Ego and Opponent Signal GREEN, NO Sex Difference in Behaviour					
		Ego Move			
		Forward	Backward	Total	
Sex	Male	74	44	118	χ^2=1.380
	Female	183	141	324	p=0.240
	Total	257	185	442	
Ego and Opponent Signal GREEN, Behaviour Different from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	257	185	442	χ^2=14.45
	Expected	294	147	442	p<0.001
	Total	552	332	884	

Table 2-4: Behaviour Choice when signals coordinate in Experiment 1. Also, 'Obtained from players' vs. 'Expected by ESS' cell counts for ego move. Cell counts, X^2 and p-values reported.

Ego Signal PURPLE and Opponent Signal GREEN NO Sex Difference in Behaviour					
		Ego Move			
		Forward	Backward	Total	
Sex	Male	147	63	210	χ^2=1.380
	Female	279	148	427	p=0.240
	Total	426	211	637	

Ego Signal GREEN and Opponent Signal PURPLE NO Sex Difference in Behaviour					
		Ego Move			
		Forward	Backward	Total	
Sex	Male	99	59	158	χ^2=0.725
	Female	280	196	476	p=0.394
	Total	379	255	634	

Table 2-5: Sex Differences in Behaviour Choice when Signals Discoordinate for Experiment 1. Cell counts, X^2 and p-values reported.

Sex Difference in Ego Signal						
		Ego Signal				
		Purple	Green	Blue	Total	
Sex	Male	296	365	339	1000	χ^2=10.19
	Female	676	623	719	2018	p=0.006
	Total	972	988	1058	3018	
Female Signal Choice Different from ESS						
		Ego Signal				
		Purple	Green	Blue	Total	
	Observed	676	623	719	2018	χ^2=6.75
	Expected	672	673	673	2018	p=0.034
	Total	1348	1296	1392	4036	
Male Signal Choice Different from ESS						
		Ego Signal				
		Purple	Green	Blue	Total	
	Observed	296	365	339	1000	χ^2=7.28
	Expected	333	333	334	1000	p=0.026
	Total	629	698	673	2000	

Table 2-6: Signal use as a function of Sex for Experiment 2. Also, 'Obtained from players' vs. 'Expected by ESS' cell counts for Signal Choice, separated by sex.

Overall Sex difference in Behaviour Choice					
		Ego Move			
		Forward	Backward	Total	
Sex	Male	692	308	1000	χ^2=4.585
	Female	1315	699	2014	p=0.032
	Total	2007	1007	3014	

Opponent Signal Does NOT Mediate Ego Move in Males					
		Ego Move			
		Forward	Backward	Total	
Opponent Signal	Purple	212	101	313	χ^2=0.486
	Green	242	103	345	p=0.784
	Blue	238	104	342	
	Total	692	308	1000	

Opponent Signal Does NOT Mediate Ego Move in Females					
		Ego Move			
		Forward	Backward	Total	
Opponent Signal	Purple	433	217	650	χ^2=1.360
	Green	417	216	633	p=0.507
	Blue	465	266	731	
	Total	1315	699	2014	

Ego Signal Does NOT Mediate Ego Move in Males					
		Ego Move			
		Forward	Backward	Total	
Ego Signal	Purple	445	220	675	χ^2=3.289
	Green	389	232	621	p=0.193
	Blue	471	247	718	
	Total	1315	699	2014	

Ego Signal Does NOT Mediate Ego Move in Females					
		Ego Move			
		Forward	Backward	Total	
Ego Signal	Purple	206	90	296	χ^2=1.00
	Green	258	107	365	p=0.607
	Blue	228	111	339	
	Total	692	308	1000	

Table 2-7: Overall behaviour choice in Experiment 2 as a function of sex, ego signal and opponent signal. Cell counts, X^2 and p-values reported.

When Signals Coordinate, Females DO NOT Deviate from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	448	248	696	χ^2=1.65
	Expected	464	232	696	p=0.198
	Total	912	480	1392	
When Signals Coordinate, Males DO NOT Deviate from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	238	120	358	χ^2=0.006
	Expected	239	119	358	p=0.94
	Total	477	239	716	
When Signals Discoordinate, Females Deviate from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	868	451	1319	χ^2=131.83
	Expected	659	660	1319	$p<0.001$
	Total	1527	1111	2638	
When Signals Discoordinate, Males Deviate from ESS					
		Ego Move			
		Forward	Backward	Total	
	Observed	454	188	642	χ^2=110.21
	Expected	321	321	642	$p<0.001$
	Total	775	509	1284	

Table 2-8: Ego Move when Signals Coordinate & Discoordinate for Experiment 2. 'Obtained from players' vs. 'Expected by ESS' cell counts for ego Move.

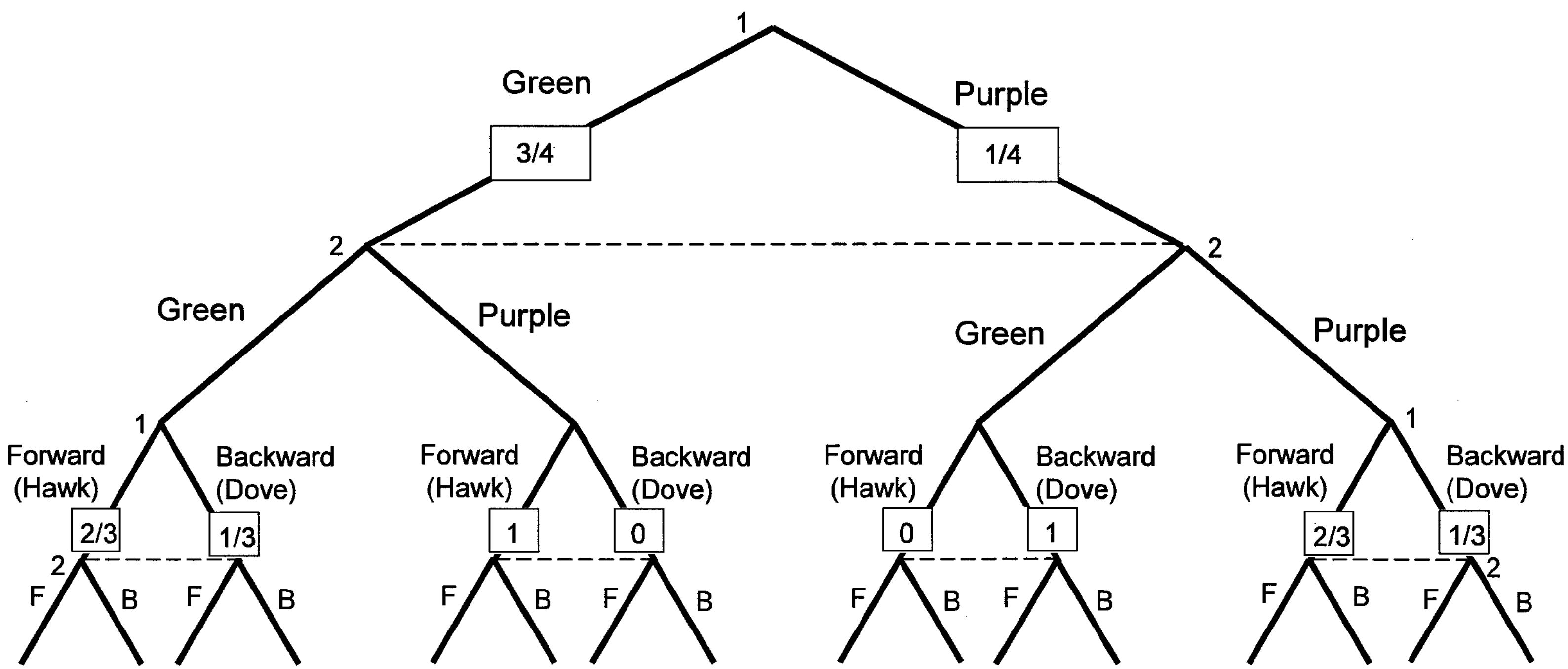

Figure 2-1: Extensive Form Diagram for Experiment 1. ESS proportions for signal choice and behaviour choice indicated in boxes.

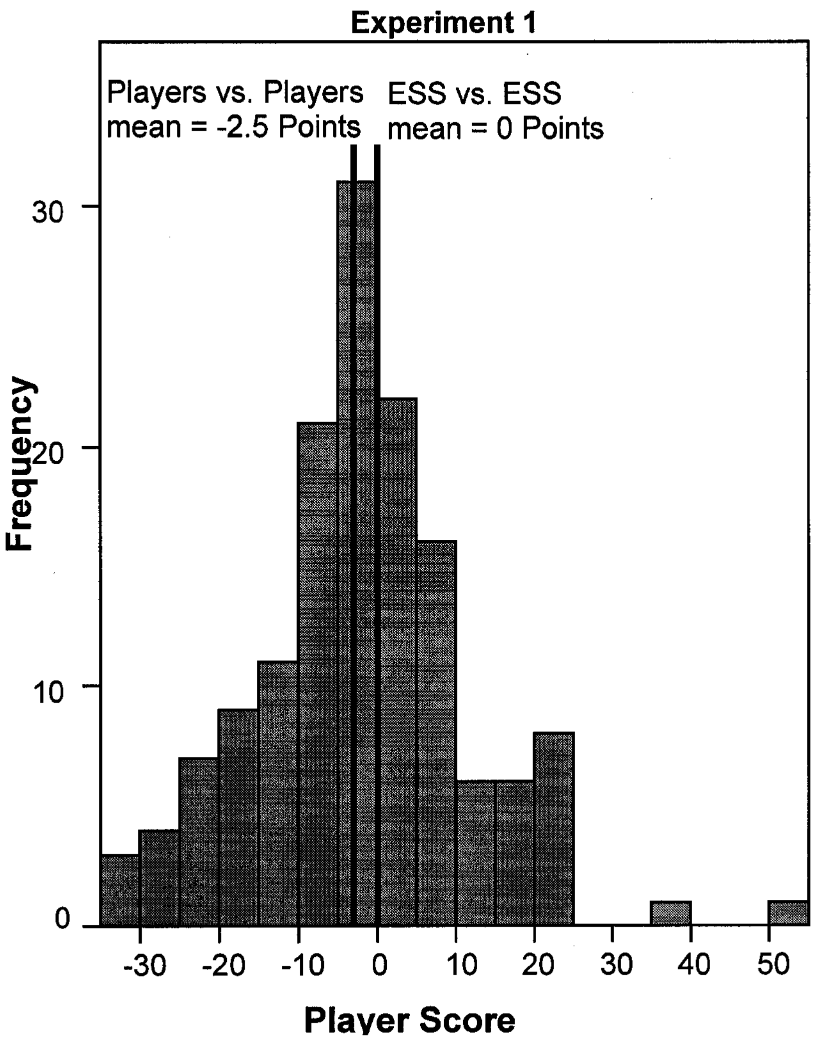

Figure 2-2: Distribution of player scores from Experiment 1 with the average score for the players and the ESS vs. ESS.

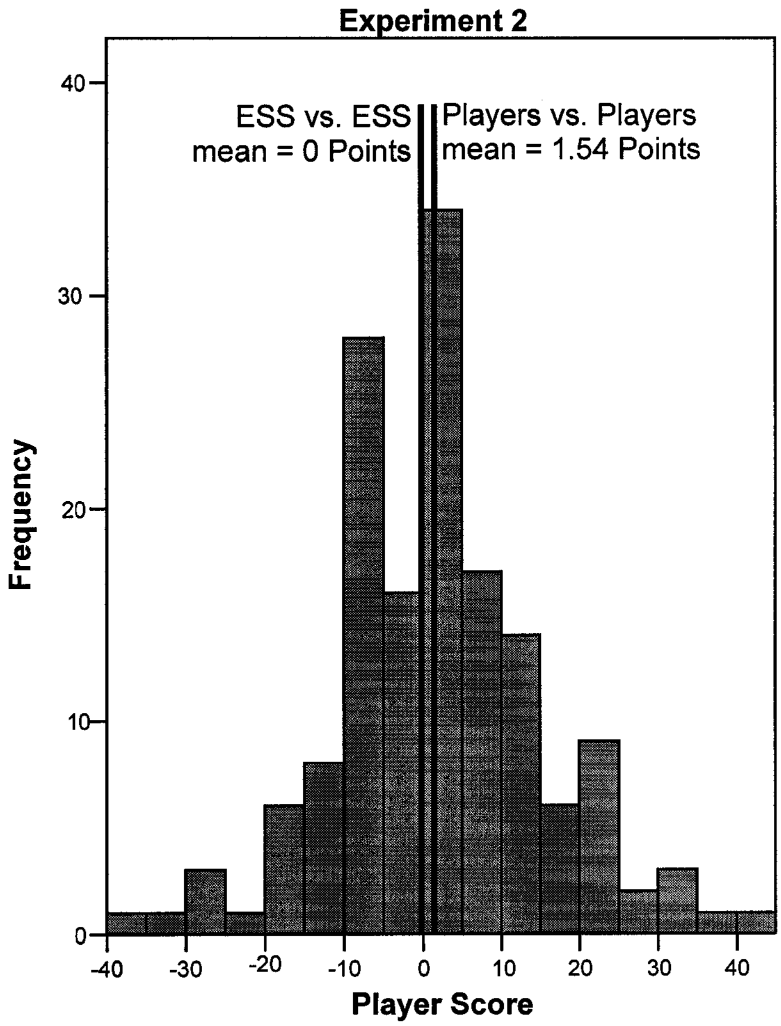

Figure 2-3: Distribution of player scores from Experiment 2 with the average score for the players and the ESS vs. ESS.

REFERENCES

Blume, A., DeJong, D., Kim, Y.-G., & Sprinkle, G. (1998). Experimental evidence on the evolution of meaning in messages in sender-receiver games. *The American Economic Review, 88,* 1323-1340.

Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of animal communication.* Sunderland: Sinauer.

Brandts, J. & Holt, C. (1992). An experimental test of equilibrium dominance in signaling games. *The American Economic Review, 82,* 1350-65.

Cai, H., & Wang, J. (2006). Overcommunication in strategic information transmission games. *Games and Economic Behavior, 56,* 7-36.

Conrath, D. (1972). Sex Role and "Cooperation" in the Game of Chicken. *The Journal of Conflict Resolution, 16,* 433-443.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology, 144,* 517-546.

Hurd, P.L. & Enquist, M. (2005). A strategic taxonomy of biological communication. *Animal Behaviour 70,* 1155-1170.

Johnstone, R. A. (1997). The evolution of animal signals. In Krebs J. R. & Davies, N. B. (Eds.) *Behavioural Ecology: an evolutionary approach* (pp. 155-178). Oxford: Blackwell.

Kim, Y-G. (1995). Status Signaling Games in Animal Contests. *Journal of Theoretical Biology, 176,* 221-231.

Krebs, J. R. & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In Krebs, J. R. & Davies, N. B. (Eds.), *Behavioural Ecology: an evolutionary approach* (2nd ed., pp. 380-402). Sunderland: Sinauer.

Maynard Smith, J. & Harper, D. G. (2003). *Animal Signals.* Oxford: Oxford University Press.

Sermat, V. (1967a). The possibility of influencing the other's behaviour and cooperation: chicken versus prisoner's dilemma. *Canadian Journal of Psychology, 21*, 204-219.

Sermat, V. (1967b). The effect of initial cooperative or competitive treatment upon a subject's response to conditional cooperation. *Behavioral Science, 12,* 301-313.

Rapoport, A. & Chammah, A. (1966). The game of chicken. *American Behavioral Scientist, 10,* 10-14, 23-28.

Zahavi, A. (1975). Mate selection – a selection for a handicap. *Journal of Theoretical Biology, 53,* 205-214.

Zahavi, A. (1977). The cost of honesty (Further remarks on the handicap principle). *Journal of Theoretical Biology, 67,* 603-605.

CHAPTER 3

HUMAN BEHAVIOUR IN A CONVENTIONAL THREAT SIGNALING GAME

3.1 INTRODUCTION

3.1.1 What is Communication?

Communication lies at the heart of most social interactions, and consumes a significant part of any social creature's time. Communication is one of the most important and most studied topics within ethology (e.g. Darwin 1872; Tinbergen 1948; Zahavi 1975, 1977; Dawkins & Krebs 1978; Krebs & Dawkins 1984). Despite this and a considerable amount of attention, theoretical understanding of communication remains poor (e.g. Caryl 1979; Hinde 1981; Markl 1985; Johnstone 1997; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2004). Game theory has advanced understanding through the use of formal models of communication in animals (reviews in Johnstone 1997; Hurd & Enquist 2005) and remains an active area of research into this topic.

Communication has traditionally been operationally defined as a stimulus (signal) from a sender causing a receiver to change its behaviour (Smith 1977; Dawkins & Krebs 1978). This operational definition can be broken down into two parts: sending information and receiving information. In the former, the signaler must choose a signal based on some state or condition of relevance which is hidden from the receiver (Smith 1977). The second part of communication takes place when the receiver chooses to respond differently after receiving different signals, presumably in the belief that the signals indicate the hidden state (Hurd 1995). It is easily understood how communication evolves between individuals with common interests (Krebs & Dawkins 1984); however, we will be looking specifically at interactions between individuals with conflicting interests since this aspect still requires explanation (Adams 2001; Hurd & Enquist 2005).

We will frame examples in the language of threat displays, since this example clearly involves conflicting interest and is one of the traditional centers of the ethological study of communication (Tinbergen 1948; Morris 1957; Cullen 1966; Blurton-Jones 1968; Caryl 1979; Hinde 1981).

3.1.2 Why Communicate?

One theory which has often been proposed to explain how communication can exist between individuals with conflicting interests was to appeal to the "good of the species" (Dawkins & Krebs 1978). Such group selection arguments have been long discredited among evolutionary biologists (Williams 1966; Dawkins 1990), yet live on in textbooks (e.g. Carlson et. al. 2002) and other less rigorous forms of scientific discourse. Communication must be beneficial to the individual in order for natural selection to produce individuals that communicate. Communication (e.g. threat display) has a clear potential to benefit the individual: it may allow individuals to avoid injury during aggressive interactions (Geist 1974). On the other hand, individuals may also benefit by manipulating others through threat displays that are mere "bluffs" (Dawkins & Krebs 1978; Caryl 1979; Adams & Caldwell 1990). The question of how evolution deters bluffing has been difficult to explain (Johnstone 1997; Bradbury & Vehrencamp 1998; Admas 2001; Hurd & Enquist 2005; Maynard Smith & Harper 2004).

One theoretical attempt to reconcile the existence of threat displays in the face of such temptation to cheat was to deny that threat displays communicated any information at all (Caryl 1979). The idea that threat displays do not impart information has since been refuted by demonstrations that different displays do predict future acts (Hinde 1981;

Enquist et al 1985, Popp 1987ab; Senar 1990; Waas 1991; Molles & Vehrencamp 2001; Hurd & Enquist 2001).

The study of the evolution of communication has been greatly influenced by game theoretical models and thinking (reviews in Johnstone 1997; Johnstone 1998; Hurd & Enquist 2005). Communication has been described theoretically as an arms race between senders and receivers. Senders are continually evolving adaptations to manipulate receivers into believing generated claims, while receivers are in turn evolve counter-adaptations and sales resistance (Dawkins & Krebs 1979). However, an arms race can never reach an evolutionarily stable endpoint (Fudenberg & Tirole 1991), making it difficult to describe and interpret communication formally as an arms race. Much game theory debate has centered on whether handicaps or other costs are required in order for communication to be stable (Zahavi 1975, 1977; Grafen 1990; Maynard Smith 1991, 1994; Adams & Mesterton-Gibbons 1995; Hurd 1995; Kim 1995; Hurd & Enquist 1998).

3.1.3 Handicap or Not?

The idea that there must be a handicapping cost in order for stable communication to occur between individuals with conflicting interests has proven to be very persuasive to evolutionary biologists (e.g. Zahavi 1975, 1977; Grafen 1990; Iwasa et al. 1991; Godfray 1991, 1995; Maynard Smith 1991, 1994; Johnstone & Grafen 1992, 1993; Adams & Mesterton-Gibbons 1995; Hurd 1995; Kim 1995; Yachi 1995; Iwasa, and Pomiankiwski 1999). A handicap in this case is an inherent cost (such as energy expenditure) to using a particular signal. According to this model it is the cost of the handicap which constrains the ability of the signaler to choose a signal and forces signal reliability.

3.1.4 Humans Playing Games

The empirical investigation of human behaviour in game theoretic interactions has been largely dominated by economics and economic theory and has been given the name of 'behavioral game theory'. Usually, the games that are played in these empirical studies are of a simple nature, and have fairly simple solutions (eg. Colman 1995; Camerer 2003). Humans have shown a limited capacity for playing in a way that game theory would predict rational agents to play. Even simple games require an extensive amount of time (more than two hours) being played for human behaviour to have a pattern resembling equilibrium (Camerer 2003). To the best of our knowledge, no study so far has examined human performance in a game as complex as Enquist's 1985 model of conventional signaling (see below).

3.1.5 The E'85 Game

Enquist (1985) presents a conventional signalling game (which we shall call the E'85 game) in which signals without inherent costs were chosen by senders such that they signaled their fighting ability to each other. This game demonstrates that signals do not need to be handicapped for reliable signalling to be evolutionarily stable. The cost that deters bluffing comes in the form of the provoked response of the opponent. This E'85 conventional signaling game models two players with conflicting interests. Each player is assigned a state (either strong or weak) in a move by nature (Hurd & Enquist

2005) which is hidden from their opponent. The players then signal to each other simultaneously using one of two signals, either 'I am Strong' or 'I am Weak'. The choice of signal has no inherent effect on payoffs, and if there is an association between signal and hidden state, it is entirely by convention. After the signalling phase, players choose one of three behaviours (Full-attack, Pause-attack or Flee), after which payoffs are determined. The individual playing the game is referred to as "Ego" and their opponent is referred to as "Opponent". The payoffs are functions of the players' states, their behaviours and their opponent's behaviours (Table 3-1).

3.1.6 ESS

In the field of formal game theory, an Evolutionarily Stable Strategy (ESS) is defined as a strategy which, when played by a population, cannot be invaded by any other strategy (Maynard Smith 1982). An ESS can be thought of as the mathematically ideal strategy to play in a game. The E'85 game has one ESS. This ESS is to signal state accurately (e.g. signal "I am Strong" if strong, and signal "I am Weak" if weak), then Full-attack when Ego state is strong and Opponent has signaled strong, and when Ego state is weak and Opponent has signaled weak. When Ego state is strong and Opponent has signaled weak, the ESS is to Pause-attack (if the Opponent is also playing the ESS, this allows the Opponent to flee). When Ego state is weak, and the Opponent has signaled strong, the ESS is to Flee (Table 3-2).

3.1.7 ES Set

Recently, Hamblin & Hurd (2007) demonstrated that an Evolutionarily Stable Set (ES Set) exists for the E'85 game. An Evolutionarily Stable Set of strategies (ES Set), is a set of strategies that score equally well against each other but would individually be ESSs if all other members of the set were removed (Thomas 1985). The ES Set solution is non-communicative and consists of four strategies with any signal choice followed by "Full-attack" as the end-move behaviour regardless of ego's state and the opponent's signal. Additionally, Hamblin and Hurd (2007) found that a simulation using a genetic algorithm found that the ES Set had much greater attractive power in the strategy space than the ESS, to the extent that random populations almost always evolved to the ES Set and would not evolve to the ESS without a strong predisposition towards communication. It is reasonable to expect that our human players would be more likely to play the non-communicative ES Set than the ESS, as it is simpler to understand and employ and has greater attractive power than the ESS.

3.1.8 Purpose

Historically, the question has been posed as to whether individuals with competing interests can communicate reliably (Johnstone 1997). As noted above, many game theoretic models involve individuals in such conflicts. For an ESS to exist there must be mutual anticipation of strategies, meaning that signals must reliably predict behaviours in a way that is anticipated by the receiver (Hurd & Enquist 2005). Game theoretic models are useful tools for predicting the behaviour of organisms in a perfect system but, to determine how humans, or any other animal behaves, we must first observe them empirically. Animals make use of threat displays in a very 'noisy' way;

signals, though informative, are very imprecise (Hurd & Enquist 2001). Such imprecision is markedly different from game theoretical equilibria.

Our study will answer three questions. 1) Do individuals with competing interests communicate reliably with each other? That is to say, do subjects send reliable information to each other, and do they change their behaviour in response to information provided by their opponent. 2) Do players use the ESS or ES Set? 3) What are the consequences of players' choices? Specifically we compared the average payoff that players obtained to the expected payoff for both the ESS and ES Set.

3.2 METHODS

3.2.1 Players & the E85 Game

Participants were 187 students (114 females and 73 males) enrolled in introductory psychology classes who received course credit for their participation. Students played the E'85 game in groups of 3 in which there were 2 active players (player 1 and player 2) and one referee playing a total of 20 rounds. Positions were rotated each round such that every participant was player 1, player 2 and the referee an equal number of times. The role of the referee was to deal a card to each player, ensure that no cheating took place, and to verify that scores were calculated accurately. Each player was given a set of materials including a score sheet on which they recorded the information from each round, an instruction sheet which explained the details of the game, and a payoff sheet that contained a score value for each type of encounter. Players were given verbal instructions on how to play the game and care was taken to ensure that players understood how to use the payoff table to obtain their score for each round. The scores were determined using the payoffs specified in the payoff matrix. (See Table 3-1).

Each round had three phases. In the first phase each player is assigned a strength state (either "strong" or "weak") according to a card randomly dealt by the referee. This card was only revealed at the end of the round. If the player received a red card, they were strong; if the player received a black card, they were weak. The deck was shuffled between each round. In the second phase each player chose one of two possible signals to display to their opponent (either "I am strong" or "I am weak"). The signals were written on wooden chits and players showed their signal at the same time, so that each player had the same amount of information about their opponent at all times. In the third phase, each player chose one of three behaviours ("Full-attack", "Pause-attack" or "Flee"). Just as in phase two, these behaviours were written on wooden chits and players showed their behaviour to their opponent simultaneously. Following the third phase of play, each player looked up their score for that round on the payoff sheet. Scores were determined as a function of their strength, their opponent's strength, their choice of behaviour and their opponent's choice of behaviour. After 20 rounds of the game, players added up their scores for each round to obtain their total number of points. The entire game took approximately one hour to complete.

3.2.2 Calculating Expected Payoff for ESS and ES Set vs. Players

In order to determine the score that the ESS would receive if it played against the human population, we calculated the ESS's score against the weighted average of all human moves under all four possible match-ups between states (S vs. S, S vs. W, W vs. S and W vs. W). For each encounter type we used the ESS behaviour and incorporated the probability of the opponent signalling strong and weak (based on signalling probabilities of our subjects) as well as the probability that the subjects engaged in each of the three behaviours, following which we multiplied these probabilities by the payoffs for each situation. For the ES Set we averaged over the four strategies in the ES Set such that they signaled strong and weak equally often and then used only Full-attack. We then incorporated the probabilities of the human signals and behaviours.

3.2.3 Calculating Expected Payoff for ESS vs. ESS and ES Set vs. ES Set

To determine the score that the ESS would receive if it played against itself, we took the average of the payoffs received much like for the ESS vs. Players but since one of the defining aspects of the ESS is to always signal accurately, we only needed to look at cases where signal indicated state for both players. We then took the average payoff, as determined by the behaviours of the ESS in the introduction (Table 3-2). For the ES Set vs. ES Set, we used the same procedure except that the signal was chosen randomly, and the behaviour was always Full-attack.

3.3 RESULTS

3.3.1 Signal Choice

Our first question was whether players would provide accurate information to their opponent. Players' signals were not independent of their states ($\chi^2_{(1, N=187),}$= 122.21, $p<0.001$). They signaled 'strong' more often when their state was strong (62%) than when their state was weak (44%). They also signaled 'weak' more often when their state was weak (56%) than when their state was strong (38%). There was a significant difference between males and females in their choice of signals when their Ego state was strong ($\chi^2_{(1, N=187)}$ = 6.26 p=0.014). This difference was not present when Ego state was weak ($\chi^2_{(1, N=187)}$ = 0.547, p=0.46; Table 3-3).

3.3.2 Signal Reliability

We determined the reliability of a player's signal by looking at the probability that they are of a certain state when they give one signal rather than the other. This will be calculated using Bayes' Theorem, $p(A|B) = [p(B|A)p(A)] / p(B)$, where p(A) is the probability that players are of state A, and p(B) is the probability that players used signal B. In our sample, the probability that a player's state was strong, given that they signaled strong, is 0.58 (about 58% of the time that they signal strong, they actually are strong). The probability that a player's state was weak, given that they signaled weak is 0.60 (about 60% of the time that a player signals weak, they actually are weak). This shows the ambiguous nature of the signals being sent which in part explains why their behaviour should not be expected to match the ESS, as the ESS is to always signal reliably.

3.3.3 Choice of Behaviour

When considering behaviour, we will look at behaviour when Ego state is strong and weak separately and further separate investigation by Opponent display. We will also consider the role of Ego Signal in influencing behaviour choice; for example, if a player is weak but signals strong, would they be more likely to use a behaviour congruent with a strong state? To do this we will hold Ego State and Opponent Signal constant and see how Ego display changes behaviour choice. The most common behaviours, regardless of Opponent display were Full-attack when Ego state was strong and Pause-attack when Ego state was weak.

When Ego's State is Strong

When Ego state is strong and Opponent displays strong, subjects were more likely to Full-attack (73.0%) than Pause-attack (23.8%) and the incidence of Fleeing was very low (3.2%) (Table 3-4). We found no difference between the sexes in their behaviour when their state was strong and Opponent displayed strong ($\chi^2_{(2, N=187)} = 1.100$, p=0.577; Table 3-4). There was also no significant effect of Ego signal on Ego behaviour ($\chi^2_{(2, N=187)} = 5.59$, p=0.061; Table 3-5), meaning that the subjects' signal did not predict their behaviour under this condition.

The same pattern is apparent when Ego state is strong and the Opponent displays weak. Players are most likely to Full-attack (78.4%) than Pause-attack (18.4%) and again Fleeing is low (3.2%). There was no effect of sex in this situation either ($\chi^2_{(2, N=187)} = 2.49$, p=0.287; Table 3-4). There was an effect of Ego Signal on Ego behaviour when Ego state was strong and the Opponent displayed weak ($\chi^2_{(2, N=187)} = 43.53$, p<0.001; Table 3-5). In this case, when Ego signal was strong, there was an increased likelihood of choosing Pause-attack, rather than Full-attack. This is in the direction predicted by the ESS.

Opponent display did not mediate Ego behaviour when Ego state was strong ($\chi^2_{(1, N=187)} = 2.089$, p=0.352; Table 3-4); i.e. Ego behaviour was not different depending on the opponent's display when Ego state was strong, collapsing across ego signals.

When Ego's State is Weak

When Ego state was weak and Opponent displayed strong, Pause-Attack was the most frequent behaviour (43.1%), Fleeing was second highest (37.3%) and Full-Attack was the lowest (19.5%). There was a significant difference between males and females in their behaviour choice under this circumstance, ($\chi^2_{(2, N=187)} = 9.93$, p=0.007; Table 3-4) with males more likely than females to flee and females more likely to Pause-attack. There was a significant effect of Ego display on Ego behaviour ($\chi^2_{(2, N=187)} = 12.83$, p=0.002; Table 3-5). When Ego signal was weak, subjects were more likely to flee, than when they signaled strong.

When Ego state is weak and Opponent displayed weak, players were most likely to Pause-attack (49.6% of the time), less likely to Flee (25.8%) and least likely to Full-attack (24.6%). There was a significant sex difference ($\chi^2_{(2, N=187)} = 12.87$, p=0.002) with males more likely Full-attack, and females more likely to Pause-attack (Table 3-4). There was no effect of Ego signal on Ego behaviour in this case ($\chi^2_{(2, N=187)} = 4.44$, p=0.108; Table 3-5).

Opponent signal did mediate Ego behaviour when Ego state was weak ($\chi^2_{(2,N=187)}$=28.67, p<0.001; Table 3-4). That is to say that when we collapse across ego signal, players' behaviour was changed by the signal from their opponent when their state was weak.

3.3.4 Scores

The average player's score was 486.25±296.32 (range -335 to 1240). We did not find a significant difference between males (485.9) and females (486.4) in their final scores (t_{185} = -0.11, p=0.991). Against the ESS, players score an expected 485 points, which is just as well as against each other. When we set the player strategy against the ES Set, players obtained a very low score of only 288 points over 20 games (Figure 3-1).

If the ESS were to play against the population of players from our sample, it would score 502 points across 20 rounds, assuming that each of the four state combinations occurred an equal number of times. If the ESS were playing against itself, the score over 20 games would be 850 points (Figure 3-1). Both of those scores are much better than the ESS would score against the ES Set, which is 275 points.

Were the ES Set to play against our population of human players, it would score 559 points over 20 rounds. Against the ESS, it would score 600 points and against itself it would score 425 points (Figure 3-2). When we compared the average score for humans to the predicted score for the ES Set against itself, we found that humans scored significantly higher (t_{186}=2.827, p=0.005).

3.4 DISCUSSION

This experiment was designed to answer three questions about how individuals with competing interests behave within the framework of the E'85 game. We first asked whether individuals would communicate reliably. Communication requires that two conditions be met. The first part of communication involves sending information. We found that players' signals were dependent on their state. Players did use the strong signal more when they actually were strong. But by no means were players sending perfect information. They had a 58% chance of being strong when they used the strong signal, and a 60% chance of being weak when they used the weak signal. It is surprising that there is not a larger discrepancy between reliability of signals based on Ego strength considering that weak players have more to gain by communicating than strong players because weak individuals are more sensitive to costs (Hurd 1997). It would have been beneficial to signal reliably when weak as a strong Opponent playing the ESS would Pause-attack, allowing the weak player to Flee, thereby reducing costs to the self.

The signal that players sent to their opponents also affected their own behaviour in the cases when Ego state was the opposite of Opponent display. So, when Ego state was strong, and Opponent signaled weak, players chose Pause-attack more when they signaled weak than when they signaled strong. When Ego state was weak and Opponent displayed strong, players were more likely to Flee when they signaled weak, than when they signaled strong. This shows some sort of commitment to their signal choice when Ego state and Opponent signal are opposing. No such effects were found when Ego state and Opponent signal were the same.

The second part of communication involves receiving signals, which is demonstrated by a change in behaviour based on the signal received. We found that only when players were weak did their opponent's signal alter their behaviour. Players were 1.4 times more likely to flee when their state was weak and their Opponent displayed strong than when their Opponent displayed weak.

We also directly asked whether players would be able to find and use either equilibrium strategy. Players did not use the same strategy as the ESS. First, they signaled state only ambiguously. Second, their behaviour did not match the ESS. The

ESS when Ego state is strong is to Full-Attack when the Opponent signals strong, and Pause-Attack when the Opponent signals weak. When strong, players chose to Full-Attack most, often regardless of Opponent signal. The ESS when Ego state is weak is to Full-Attack when Opponent signals weak and Flee when Opponent signals strong. When Ego state was weak and Opponent signaled weak, players chose Pause-Attack most frequently, and Full-Attack least frequently. The incidence of Fleeing increased when Opponent signaled strong but Pause-Attack remained most frequent – this increase in Fleeing is a change towards ESS, but falls short of matching it.

It was reasonable to expect that humans may play the ES Set since it is less cognitively demanding and has a greater basin of attraction than the ESS in simulations. The ES Set is a set of strategies with absolutely no communication between players. Human players go above and beyond the ES Set, by both sending signals to their opponent and even sometimes changing their behaviour based on signals received. While it is difficult to compare the behavior of humans to the ESS and ES Set because there is some overlap in both equilibrium strategies, it is fair to say that they did not play either strategy, if only because of the large amount of variability in their behaviour choice.

Finally, our last question was about the consequences of these behavioural choices in terms of payoffs. Players playing against each other scored an average of 486 points per game, which is substantially less than that achieved by the ESS playing against itself (850), and the ESS against the player strategy (502). Against the ESS, they would score 485 points, whereas against the ES Set, they would score 288 points. The ES Set playing against the player strategy would score 559 points, against itself would score 425 and against the ESS would score 600 points. Although the ES Set is more of a reasonable expectation for human players, they are not playing the ES Set and when playing against themselves, they score significantly better than the ES Set does against itself. This result demonstrates that the noisy behaviour seen in real animal contests may not reflect an ESS solution to a very complicated game, but may be an adaptive non-equilibrium outcome of a simpler game.

Other explanations for our results include the possibility that our experiment is modeling different interactions than the game theoretical models do. For example, our subjects played repeated games in small groups where reputation effects could influence strategies. We do not know what the effect of having players play the game multiple times in this way is, but it seems highly unlikely that repeated play explains all of our results. We also do not know how hard it is for players to find the ESS, given the payoffs we provide. It is possible that without formal game theory training, players would be unable to find either of the equilibrium solutions. Future directions for research on this topic include: testing subjects who have had some game theory training, having subjects play in larger groups to reduce reputation effects, pitting subjects against a computer program which plays one of the equilibrium solutions.

I am Strong & Opponent is Strong

Opponent's Move

		Full Attack	Pause Attack	Flee
My	Full Attack	35	35	95
Move	Pause Attack	30	35	100
Is	Flee	-15	0	50

I am Strong & Opponent is Weak

Opponent's Move

		Full Attack	Pause Attack	Flee
My	Full Attack	85	85	95
Move	Pause Attack	80	85	100
Is	Flee	-15	0	50

I am Weak & Opponent is Weak

Opponent's Move

		Full Attack	Pause Attack	Flee
My	Full Attack	35	35	95
Move	Pause Attack	30	35	100
Is	Flee	-15	0	50

I am Weak & Opponent is Strong

Opponent's Move

		Full Attack	Pause Attack	Flee
My	Full Attack	-70	-70	95
Move	Pause Attack	-75	-70	100
Is	Flee	-70	0	50

Table 3-1: Payoff matrix given to each subject. Each table is labeled with one of the four possible encounter types. This is the exhaustive set of all possible payoffs in the E'85 game.

Ego State	Ego Signal	Opponent Signal	Opponent Behaviour	Full Attack	Pause Attack	Flee
S	S	S	Full Attack	**35**	30	0
		W	Flee	95	**100**	50
	W	S	Pause Attack	35	**35**	0
		W	Full Attack	**35**	30	-15
W	S	S	Full Attack	**-70**	-75	-70
		W	Flee	95	**100**	50
	W	S	Pause Attack	-70	-70	**0**
		W	Full Attack	**35**	30	-15

Table 3-2: Payoffs to signals and behaviours when the Opponent is playing the ESS. Ego signals and behaviours which correspond to the ESS are in black, while those that are not, are in grey. Payoffs which are bolded and in boxes correspond to the ESS. It is easily seen that higher payoffs cannot be achieved by changing behaviour from the ESS. S=Strong, W=Weak.

Relationship between Ego State and Ego Signal					
		Ego Signal			
		S	W	Total	
Ego State	S	1152	698	1850	$X^2 = 122.97$
	W	831	1051	1882	$p < 0.001$
	Total	1983	1749	3732	
Sex Difference in Signal choice when Ego state STRONG					
		Sex			
		F	M	Total	
Ego Signal	S	722	422	1144	$X^2 = 6.26$
	W	399	298	697	$p = 0.014$
	Total	1121	720	1841	
No Sex Difference in Signal choice when Ego state WEAK					
		Sex			
		F	M	Total	
Ego Signal	S	508	323	831	$X^2 = 0.54$
	W	658	388	1046	$p = 0.460$
	Total	1166	711	1877	

Table 3-3: Signal use as a function of strength state and sex of signaler. Cell counts, X^2 and p-values for tests regarding signalling. S=Strong, W=Weak, M=Male, F=Female.

Mediation of Ego Behaviour Based on Opponent Signal						
		Ego Behaviour				
		A	P	F	Total	
Ego State Strong	Opp Sig S	689	225	30	994	$X^2 = 2.08$
	Opp Sig W	679	206	20	905	p = 0.352
	Total	1368	431	50	1849	
		A	P	F	Total	
Ego State Weak	Opp Sig S	205	455	393	1053	$X^2 = 28.67$
	Opp Sig W	203	412	214	829	p <0.001
	Total	408	867	607	1882	
NO Sex Difference when Ego State STRONG and Opponent Signal STRONG						
		Ego Behaviour				
		A	P	F	Total	
Sex	F	428	131	18	577	$X^2 = 1.10$
	M	261	94	12	367	p = 0.577
	Total	689	225	30	944	
NO Sex Difference when Ego State STRONG and Opponent Signal WEAK						
		Ego Behaviour				
		A	P	F	Total	
Sex	F	435	91	18	544	$X^2 = 2.49$
	M	269	74	11	354	p = 0.287
	Total	704	165	29	898	
Sex Difference when Ego State WEAK and Opponent Signal STRONG						
		Ego Behaviour				
		A	P	F	Total	
Sex	F	116	302	225	643	$X^2 = 9.93$
	M	89	151	167	407	p = 0.007
	Total	205	453	392	1050	
Sex Difference when Ego State WEAK and Opponent Signal WEAK						
		Ego Behaviour				
		A	P	F	Total	
Sex	F	108	279	135	522	$X^2 = 12.87$
	M	95	131	78	304	p = 0.002
	Total	203	410	213	826	

Table 3-4: Behaviour choice as a function of Ego state, Opponent state and Ego sex. Cell counts, X^2 and p-values for tests regarding signalling. Opp Sig = Opponent Signal, S=Strong, W=Weak, M=Male, F=Female, A=Full-Attack, P=Pause-Attack, F=Flee.

Ego Signal does NOT Mediate Ego Behaviour when Ego State STRONG and Opponent Signal STRONG						
		Ego Behaviour				
		A	P	F	Total	
Ego Signal	S	411	154	18	583	
	W	278	71	12	361	$X^2 = 5.59$
	Total	689	225	30	994	$p = 0.061$

Ego Signal DOES Mediate Ego Behaviour when Ego State STRONG and Opponent Signal WEAK						
		Ego Behaviour				
		A	P	F	Total	
Ego Signal	S	416	136	9	561	
	W	287	29	20	336	$X^2 = 43.53$
	Total	703	165	29	897	$p < 0.001$

Ego Signal DOES Mediate Ego Behaviour when Ego State WEAK and Opponent Signal STRONG						
		Ego Behaviour				
		A	P	F	Total	
Ego Signal	S	111	214	154	479	
	W	94	239	238	571	$X^2 = 12.83$
	Total	205	453	392	1050	$p = 0.002$

Ego Signal Does NOT Mediate Ego Behaviour when Ego State WEAK and Opponent Signal WEAK						
		Ego Behaviour				
		A	P	F	Total	
Ego Signal	S	97	175	80	352	$X^2 = 4.44$
	W	106	235	133	474	$p = 0.108$
	Total	203	410	213	826	

Table 3-5: Behaviour choice as a function of Ego state, Opponent signal and Ego signal. Cell counts, X^2 and p-values for tests regarding behaviour. S=Strong, W=Weak, A=Full-attack, P=Pause-attack, F=Flee.

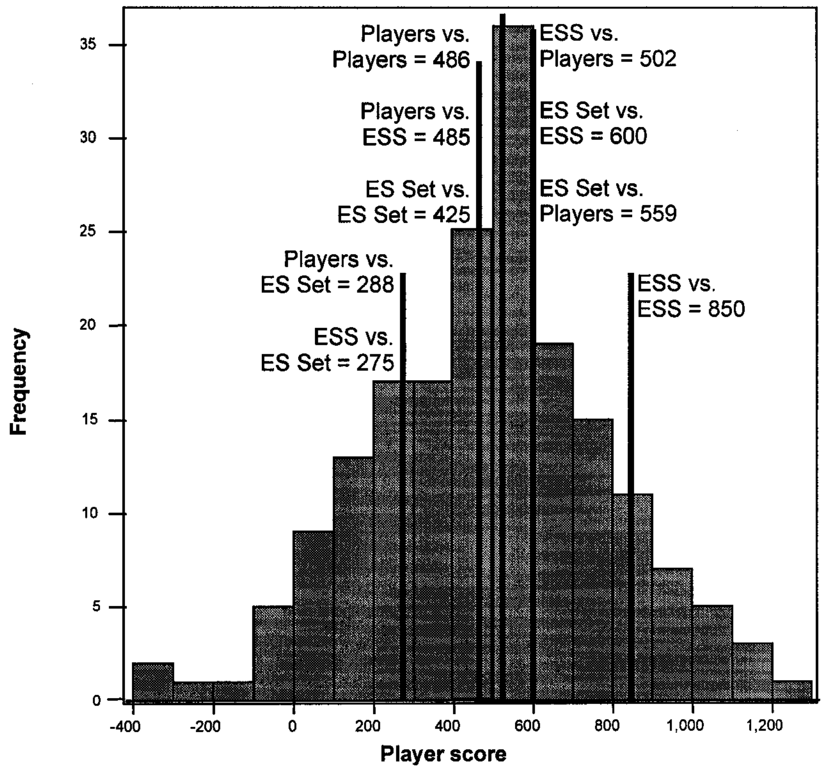

Figure 3-1: Distribution of player scores with the average score for the players in our group and the score for all strategies against each other showing that although the ESS does best against itself, it does not do well against the player strategy and that the average human strategy scores higher than the ES Set against itself.

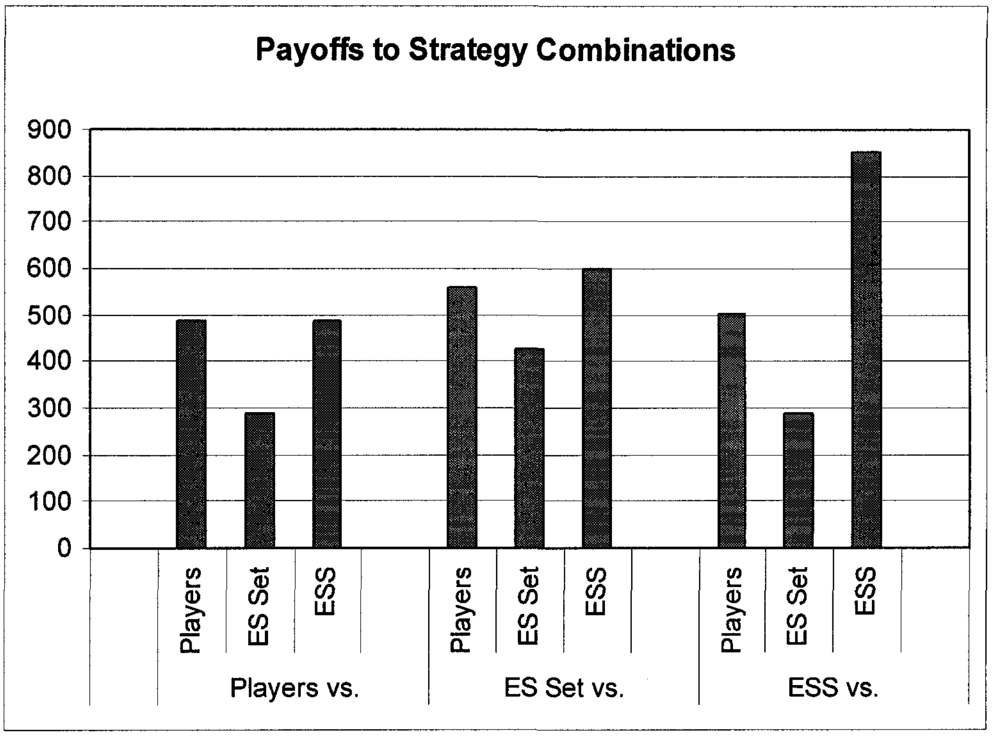

Figure 3-2: Scores obtained by each strategy (Player, ES Set & ESS) when played against each other strategy.

REFERENCES

Adams, E. S. (2001). Threat displays in animal communication: handicaps, reputation, and commitment. In Neese, R. (Ed.), *Evolution and the Capacity for Commitment* (pp. 99-119). New York: Russell Sage Foundation

Adams, E. S., & Caldwell, R. L. (1990). Deceptive communication in asymmetric fights for the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour, 39*, 706-716.

Adams, E. S., & Mesterton-Gibbons, M. (1995). The cost of threat displays and the stability of deceptive communication. *Journal of Theoretical Biology, 175*, 405-421.

Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of Animal Communication.* Sunderland: Sinauer.

Carlson, N. R., & Buskist, W., & Enzle, M., & Heth, D. (2002). *Psychology: The Science of Behaviour.* Needham Heights: Allyn & Bacon.

Camerer, C. F. (2003). *Behavioral Game Theory*. Princeton: Princeton University Press.

Caryl, P. G. (1979). Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour, 68,* 136-169.

Colman, A. M. (1995). *Game Theory & its Applications* (2 ed.; W. P. Robinson, Ed.). Oxford: Butterworth-Heinemann.

Darwin, C. (1872). *The Expression of Emotion in Man and Animals.* London: Appleton.

Dawkins, R. (1976). *The Selfish Gene.* Oxford: Oxford University Press.

Dawkins, R. & Krebs, J. R. (1978). Animal signals: information or manipulation? In Krebs, J. R. & Davies, N. B. (Eds.), *Behavioural Ecology: an Evolutionary Approach* (1st ed, pp. 282-309). Oxford: Blackwell.

Dawkins, R. & Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London B, 205,* 489-511.

Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour, 33,* 1152-1161.

Enquist, M., Plane, E. & Roed, J. (1985). Aggressive communication in fulmars *Fulmaris glacialis*. *Animal Behaviour, 33,* 1007-1020.

Fudenberg, D. & Tirole, J. (1991). *Game Theory.* Cambridge: MIT Press.

Geist, V. (1974). On fighting strategies in animal combat. *Nature, 250,* 354.

Godfray, H. C. (1991). Signalling of need by offspring to their parents. *Nature, 352,* 328-330.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology, 144,* 517-546.

Hamblin, S. & Hurd, P. L. (in press). Genetic algorithms and non-ESS solutions to game theory models.. *Animal Behaviour.*

Hinde, R. A. (1981). Animal signals: ethological and games-theory approaches are not incompatible. *Animal Behaviour, 29,* 535-542.

Hurd, P. L. (1995). Communication in discrete action--response games. *Journal of Theoretical Biology, 174,* 217-222.

Hurd, P. L. (1997). Cooperative signalling between opponents in fish fights. *Animal Behaviour, 54,* 1309-1315.

Hurd, P. L. & Enquist M. (1998). Conventional signalling in aggressive interactions: the importance of temporal structure. *Journal of Theoretical Biology, 192,* 197-211.

Hurd, P. & Enquist, M. (2001). Threat display in birds. *Canadian Journal of Zoology,* 79, 931-942.

Hurd, P.L. & Enquist, M. (2005). A strategic taxonomy of biological communication. *Animal Behaviour, 70,* 1155-1170.

Iwasa, Y., Pomiankiwski, A. & Nee, S. (1991). The evolution of costly mate preferences II. The "handicap" principle. *Evolution, 45,* 1431-1442.

Iwasa, Y. & Pomiankiwski, A. (1999). Good parent and good genes models of handicap selection. *Journal of Theoretical Biology, 200,* 97-109.

Johnstone, R. A. & Grafen, A. (1992). Error-prone signaling. *Proceedings of the Royal Society of London B, 248,* 229-233.

Johnstone, R. A. & Grafen, A. (1993). Dishonesty and the handicap principle. *Animal Behaviour, 46,* 759-764.

Johnstone, R. A. (1997). The evolution of animal signals. In Krebs J. R. & Davies, N. B. (Eds.) *Behavioural Ecology: an Evolutionary Approach* (pp. 155-178). Oxford: Blackwell.

Johnstone, R. A. (1998). Game theory and communication. In Dugatkin, L. A. & Reeve, H. K (Eds.), *Game Theory and Animal Behavior* (pp. 64-93). New York: Oxford.

Kim, Y. G. (1995). Status signalling games in animal contests. *Journal of Theoretical Biology, 176,* 221-231.

Krebs, J. R. & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In Krebs, J. R. & Davies, N. B. (Eds.), *Behavioural Ecology: an Evolutionary Approach* (2nd ed., pp. 380-402). Sunderland: Sinauer.

Markl, H. (1985). Manipulation, moldulation, information, cognition: some of the riddles of communication. In Holldobler, B. & Lindauer, M. (Eds.), *Experimental Behavioral Ecology and Sociobiology* (pp. 163-194).

Maynard Smith, J. & Harper, D. G. (2003). *Animal Signals.* Oxford: Oxford University Press.

Maynard Smith, J. (1982). *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.

Maynard Smith, J. (1991). Honest signaling: the Philip Sidney game. *Animal Behaviour, 42,* 1034-1035.

Maynard Smith, J. (1994). Must reliable signals always be costly? *Animal Behaviour, 47,* 1115-1120.

Molles, L. E. & Vehrencamp, S. L. (2001). Songbird cheaters pay a retaliation cost: Evidence for auditory conventional signals. *Proceedings of the Royal Society of London B, 268,* 2013-2019.

Popp, J. W. (1987a). Agonistic communication among wintering Purple Finches. *Wilson Bulletin, 99,* 97-100.

Popp, J. W. (1987b). Risk and effectiveness in the use of agonistic displays by American Goldfinches. *Behaviour, 103,* 141-156.

Senar, J.C. (1990) Agonistic communication in social species: what is communicated?. *Behaviour, 112,* 270-283.

Smith, W. J. (1977). *The Behavior of Communicating: an Ethological Approach.* Cambridge: Harvard University Press.

Thomas, B. (1985). On evolutionarily stable sets. *Journal of Mathematical Biology, 22,* 105-115.

Tinbergen, N. (1948). Social releasers and the experimental method required for their study. *Wilson Bulletin, 60,* 6-52.

Williams, G.C. (1966). *Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought.* Princeton: Princeton University Press.

Waas, J. R. (1991). Do little blue penguins signal their intentions during aggressive interactions with strangers. *Animal Behaviour, 41,* 375-382.

Yachi, S. (1995). How can honest signalling evolve? The role of the handicap principle. *Proceedings of the Royal Society of London B, 262,* 283-288.

Zahavi, A, (1975). Mate selection – a selection for a handicap. *Journal of Theoretical Biology, 53,* 205-214.

Zahavi, A. (1977). The cost of honesty (Further remarks on the handicap principle). *Journal of Theoretical Biology, 67,* 603-605.

CHAPTER 4

CONCLUSIONS

4.1 Summary

Much interest has been focused on whether meaningful communication can occur between individuals with conflicting interests. While the games used in this thesis are far from perfect models of biological communication, they still offer a framework which we can apply to human subjects in an effort to formally and empirically study communication. The predictions that models make (in general) do not match how individuals behave in nature, where vast complexity and diversity result in behaviours that are highly variable (Hurd & Enquist 2001).

In Chapter two, using two games from Kim's (1995) paper on handicapped threat signaling, we see that humans are more likely to send information in a game with a handicapping cost to choosing a particular signal, than in a game where there is no cost to signal choice. When players did send information to their opponent, the information was not completely reliable, in that it did not perfectly predict their future behaviour. In neither of the games played did humans use the signal provided by their opponent to help make decisions regarding their own choice of behaviour. Given that the signals they sent were either weakly reliable (original game) or not reliable at all (modified game), it is not surprising that humans did not use their opponent's signal. Human strategy did not resemble the ESS for either game, but players sometimes chose equilibrium proportions in the end move behaviour phase. Despite not playing the ESS, their scores did not suffer.

The results from Chapter three, where humans played Enquist's (1985) model of conventional threat signaling, indicate that human subjects are capable of somewhat reliably sending information which reveals private in-game information. They do not, however, always use the information provided to them, only doing so when their strength state is weak. Somewhat in line with the ESS, their behaviour choices differed depending on their underlying state; however, humans were not clearly playing either equilibrium solution. Their average score, although lower than the expected score for the ESS against itself, was higher than the expected score for the ES Set against itself. Recall that it was reasonable to expect that humans would play the non-communicative ES Set because it is simpler and has more attracting power than the ESS in simulations. Despite this, humans did communicate and their average score was higher than the ES Set would score against itself.

Overall we found that humans sometimes sent information, though by no means did they do this perfectly. The phrase 'sending information' means both that they are sending signals which predict their future behaviour and that they are sending signals which are indicative of a hidden underlying state. Strategies chose by players differed from the equilibrium solutions for all games, which is in agreement with both Tversky & Kahneman (1974) in that humans were not cognitively capable of determining the optimal behaviour, and Gigerenzer (2000) in that humans chose heuristic solutions that were superior to an analytic optimum. The fact that our subjects' strategy choices did not result in a lower score than what the equilibria would obtain (except in Enquist's (1985) model where humans score significantly lower than the ESS, but higher than the non-communicating ES Set) suggests that Gigerenzer's (2000) interpretation is closer to the truth in our case. When we compare the strategy of players to the equilibria, it is essential to remember that equilibria strategies are only the best strategies to play when your opponent (and in fact the whole population) is also playing them. As we see in all three games, the equilibrium strategies, when played against the average human strategy, do no better than the human players do against themselves. Equilibrium solutions are precise and inflexible; whereas the human's intuitive heuristic strategies seem robust and adaptive.

4.2 Future Research

Encouraging Communication: In Chapter 3, where we see both sending and receiving information, the context of play is made very clear by the signal and behaviour types that are available. It makes intuitive sense, for example, that strong players would choose an action like attack and weak players would choose an action like flee. We do not see the same kind of information use in Chapter 2. Perhaps if the contextual language were framed in another way so that it was more intuitively an aggressive game with signals that line up with future behaviours, we may see more communication happening. Other studies which found communication in sender-receiver games (Blume, DeJong, Kim and Sprinkle 1998) provided subjects with a summary of the history of how the game had been played in 'previous sessions' thus hand feeding them ideas about how the game ought to be played. Providing players with a historical report emphasizing communication prior to their play may also encourage communication.

Gender Effects: The effects of gender need to be studied more systematically than was done in this thesis. For all of the experiments presented, players were in groups of three that they put themselves into, so groups could be composed of all males, all females or a mix thereof. There are two ways to address this issue. First, experiments could still be run in groups of three, but the experimenter would choose the gender of participants for each group. This would allow for a comparison of male and female strategies when playing against their own sex. Second, in order to investigate how the genders play against each other, subjects would have to play in pairs, rather than in trios.

Age Effects: Although we did not consider the effect of age, it would also be interesting to examine whether there is a relationship between the age of the player and their strategy choice. I would expect that younger subjects would choose strategies that are more risky than their older counterparts. This could also be coupled with studying gender to determine whether older male subjects (who may choose less risky strategies) play similarly to young female subjects (who may also choose less risky strategies than young males).

Subjective Payoff Value: In listening to the comments that players made while playing the game, they sometimes seemed very concerned with whether their payoff was greater than their opponent's. A few subjects even indicated that they were choosing behaviours that would reduce the potential payoff to themselves if it also reduced the payoff for their opponent. In order to begin to examine this, a simple questionnaire could be administered at the end of play asking question such as: did the score of your opponent influence your decision to choose behaviours. It would also be interesting to investigate the effect of monetary rewards on subjects' evaluation of payoffs.

Learning: Although other experiments show effects of learning, by showing a change in strategy use over time (Blume, DeJong, Kim and Sprinkle 1998; Sermat 1967), an informal examination of our data indicated that our players did not change their signal or behaviour choices over time when comparing the first and last ten trials. Given that other experiments, which did find a learning effect, had players often playing over 300 trials, our lack of evidence for learning is not entirely surprising. Future studies involving the models we used would benefit greatly from having players engage in many more rounds of play in order to be able to compare strategy choice at the beginning and end of sessions of game play. Blume and Gneezy (2000) report that for optimal learning to occur in repeated coordination games, researchers must limit both the cognitive demands on, and amount of information available to, players. To the best of my knowledge, the experiments in chapters two and three only provided information that was strictly necessary for participants to complete the task; however, it could be argued that the cognitive demands were fairly high, at least for the E'85 model, and that by making the task easier, along with increasing the number of trials, we would maximize the likelihood that learning would occur.

4.3 Implications for the use of Game Theory Models

In this thesis I have shown that non-equilibrium strategies can (and do) payoff well enough to the individual to be considered reasonable strategies. Also, the messy nature of the non-equilibrium strategies that our players used looks a lot like empirical data of communication in real life. It is possible, that rather than needing to create more elaborate models of communication, as suggested in the introduction, the current simple models may be sufficiently accurate, and the variability that we see in behaviour in nature is there because animals do not communicate using an equilibrium strategy. My results suggest that too much importance is placed on equilibrium solutions to the general problem of communication. This does not necessarily mean that we should abandon the investigation of models and equilibrium strategies for communication problems. We should however, employ more empirical techniques when studying models of communication, and other social behaviour, to determine under which circumstances individuals with conflicting interests do communicate.

REFERENCES

Blume, A., DeJong, D., Kim, Y.-G., Sprinkle, G. (1998). Experimental evidence on the evolution of meaning in messages in sender-receiver games. *The American Economic Review, 88,* 1323-1340.

Blume, A. & Gneezy, U. (2000). An exerimental investigation of optimal learning in coordination games. *Journal of Economic Theory, 90,* 161-172.

Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour, 33,* 1152-1161.

Gigerenzer, G. (2000). *Adaptive Thinking: Rationality in the Real World.* New York: Oxford University Press.

Hurd, P. & Enquist, M. (2001). Threat display in birds. *Canadian Journal of Zoology, 79,* 931-942.

Kim, Y. G. (1995). Status signaling games in animal contests. *Journal of Theoretical Biology, 176,* 221-231.

Sermat, V. (1967). The effect of initial cooperative or competitive treatment upon a subject's response to conditional cooperation. *Behavioral Science, 12,* 301-313.

Tversky, A., & Kahneman, D. (1974). Judgement under uncertainty; heuristics and biases. *Science, 185*, 1124-1131.