ALTRUISM AS A SIGNAL OF STATUS

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By

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Abstract

From an evolutionary point of view, it is difficult to explain the existence of altruism that is not directed at kin or at friends. But humans demonstrate this form of altruism commonly, in such ways as donating to charity or heroically saving another's life. One explanation of these behaviours that is still consistent with evolutionary theory is the idea that altruism may function as a signal. Altruists gain a positive reputation through their deeds that may ultimately return to increase their biological fitness. Here I test this idea in a variety of ways, focusing on altruism as a signal of status. In the laboratory, I conducted an experiment where participants had the incentive to signal their personal wealth to others. In another experiment, I manipulated participants' relative status in an attempt to reduce costly conflict between participants. Outside the laboratory, I investigated the connection between heroism and reproductive success through a sample of WWI heroes. The background, methods, and conclusions of these studies are detailed within.

Acknowledgments

I came to McMaster University to enter into the business of science after having spent many nights alone marvelling at the discoveries of others. Now was my chance to engage with others of a similar mind and see what amazement and wonder I could inspire, all with the support offered to a graduate student. Two years later, my ambitions have mostly been realized, through a lot of hard work and some judicious reassessments. One thing I rarely doubted was the support of my supervisors, my thesis committee, my graduate program and my department, or the quality and friendliness of my peers and colleagues. For this I must thank Martin Daly, Margo Wilson and Andy Muller, Bruce Milliken and Allison Sekuler, and all the staff and faculty of the department; my labmates, Daniel Krupp, Toko Kiyonari, Steve Stewart-Williams, Andrew Clark, Pat Barclay, Julie DesJardins; and the members of the Animal Behaviour Journal Club. One extra thanks to anybody who has taken the time to open these pages. They are the product of a sincere effort!

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Chapter 1:
General introduction

Background

Homo sapiens is a cooperative animal. Across cultures, humans have been found to live in communities, form friendships and care for others (Henrich, 2001). This widespread tendency to cooperate actively with others is a problem for an evolutionary account of human nature because natural selection favours the evolution of selfish behaviours. To be precise, natural selection selects for heritable behaviours that increase the fitness of individual organisms without respect to other organisms' fitness. Behaviours that impose a fitness cost on an organism and grant a fitness benefit to another organism—the biological definition of altruism—will be selected against. Nevertheless, apparently altruistic behaviours are ubiquitous in human society.

Since the theory of evolution by natural selection was first proposed (Darwin, 1859), scientists have grappled with this problem, including both Darwin (1874) and Wallace (1869). Currently, several complementary explanations have been accepted to account for distinct types of altruism. First, the theory of kin selection (Hamilton, 1964) shows altruism can be evolutionarily stable when it is directed towards related kin, such as children, siblings, cousins, uncles, aunts, etc. In essence, the theory of kin selection expands the concept of an individual's fitness to include the fraction of genes of other individuals that are necessarily shared by common descent. Second, the theory of reciprocal altruism states that altruism directed towards non-related individuals can be selected for when it engenders future reciprocation (Trivers, 1971). This theory formally embodies the idea "You scratch my back, and I'll scratch yours." It can be considered the ultimate basis of economic exchange. Third, the theory of indirect reciprocity (Alexander, 1979) proposes that reciprocal altruism can be generalized to networks of indirect exchange when group members can keep track of others' past behaviour.

Finally, the theory of altruism as a signal can explain altruism among non-kin that is not reciprocal, such as donations to a charity. Altruism will be selected for as a signal whenever it conveys information about the altruist that advances the altruist's biological interests (Zahavi, 1977). In a social environment, altruism may be a means to inform others about one's resources, status, friendliness or sexual attractiveness. Altruism is a reliable signal of these personal qualities because it is tied to one's ability to give to others. For example, only a truly rich or generous person could donate a large amount of money to charity. Costly signals of this kind have been shown to be evolutionarily stable because they guarantee their own honesty (Grafen, 1990). Altruism is also an effective signal because it attracts the attention of its recipients.

Altruism as a signal

A conspicuous example of altruism as signal is the tradition of potlatches observed during the late 19th and early 20th centuries among the Kwakiutl and other nearby Native Americans of coastal British Columbia. In these public feasts, hosts competed to give away gifts to guests, often to an extreme degree. Prestigious items such as clocks, sewing machines, tables and blankets were bestowed in quantities out of all proportion to their practical utility (Goldman, 1937; Rohner & Rohner, 1970). Such was the social necessity of the potlatch that hosts acquired private loans to finance their public generosity (Drucker & Herizer, 1967).

In recent years, field researchers have investigated similar traditions that exist on a smaller scale. The anthropologists Smith and Bliege Bird (2000) invoke signalling to explain the tradition of turtle hunting and public feasting among the Meriam people of the Torres Strait Islands. For the Meriam, turtle hunting is a costly and dangerous activity that yields fewer calories per unit of time than comparable food gathering activities. The few hunters who successfully capture a sea turtle share it entirely with the surrounding community, keeping little for themselves. Despite these disincentives, a minority of Meriam consistently choose to hunt turtles. Smith and Bliege Bird argue that the activity is sustained by the reputational benefits it brings to the hunters. They show that hunt leaders are more respected within their community, marry earlier, marry more fertile mates, and have more children.

Harbaugh (1998) presented an example from a Western society—donations by lawyers to their alma mater. The lawyers were free to donate any amount, but their donations were reported to other alumni in categories of $0-500, $500-1000, $1000-2500, etc. Harbaugh found that the lawyers donated amounts near the lower thresholds of categories more often than would be expected if they gained satisfaction only from donating their money.

Signalling status

Altruism clearly functions as a signal in some contexts but the information being conveyed is not always clear. The most obvious message is that the signaller can afford the signal. Beyond that, the signal may communicate a willingness to cooperate or a warning to competitors, depending on context. The former idea, altruism as a signal of cooperation, has been tested with economic games by Barclay (2004). My thesis research is focused on testing altruism as a signal of competitive ability.

In the rest of this report, I recount my efforts in detail. First, I tried to demonstrate altruism as a signal of status by engineering in the laboratory a social situation conducive to the phenomenon. Participants were presented with the opportunity to signal their relative wealth by giving to a common fund, and they had an incentive to do so because they also had to compete with others in a spending game. Second, I tried to refine the War of Attrition game as a measure of a dyadic competition. Participants played multiple War of Attrition games with either the status of "owner" or "non-owner". Third, as a methodological exercise, I analyzed the evolutionary stability of the War of Attrition as I had been implementing it in the laboratory. Fourth, I investigated instances of altruism in a natural population to support the hypothesis that altruism as a signal yields actual reproductive benefits. The population was a group of American World War I veterans who received medals for heroism in combat.

Chapter 2:
Demonstrating altruism as a signal of status

Introduction

In its simplest form, altruism as a signal of status should be a donation that is observable by others who have an interest in the donor's status. Gintis et al. (2001) mathematically modeled this social situation, and they found that the decision to signal altruistically depends on the cost of signalling, the proportion of high and low status types in the population, and the benefit of interacting with a known type. By creating a laboratory environment with a positive incentive to signal through altruism, I hoped to demonstrate that people will spontaneously use altruism as a signal of status. Already, high status people have been shown to receive better offers in bargaining and sharing experiments (review in Ball & Eckel, 1998).

The experiment used groups of participants in which one member of each group was given more resources than other group members. This relative inequality in resources was made relevant by a game of costly competition that was won by whoever was willing to spend the most resources. The high resource group member could have won the game every time by outspending his or her rivals, but his or her net profit depended on the amounts that the losing participants chose to spend. Consequently, the high resource group member had an incentive to discourage spending by low resource group members.

In the experiment, altruism was enabled as a means to deter this costly competition. Preceding the competitive game, groups participated in a cooperative game that presented group members with the opportunity to contribute to a common fund that was redistributed to the entire group. Group members thus entered the game of costly competition knowing how much each individual member contributed to the common fund. The expected outcome was that high resource individuals would contribute an amount to the common fund that signalled their dominant position for the subsequent game of costly competition, the economically rational behaviour.

Methods

Groups of participants were engaged by the experimenter for approximately 45 minutes. Each group went through a sequence of instructions, experimental trials, questionnaire and debriefing/payment.

Participants

48 undergraduates from the McMaster Psychology subject pool participated in the experiment, divided into 12 groups of 4. The participants signed up for the experiment using the experimetrix.com online registration system. The experiment was advertised to students as an opportunity to earn course credit and a variable amount of money up to $15 Canadian. The maximum that any participant could have earned was $15.00 and the minimum any participant could have earned was $2.50.

71% of the participants were female and 29% were male. The average age of participants was 19.7 years. 96% of the participants had participated in a psych experiment before. All reported speaking English proficiently for at least 8 years. Nearly all reported majoring in the social or life sciences.

Pre-experiment

Before completing any trials of the experiment, each group was first brought through a routine sequence of events by the experimenter. First, the group as a whole was given a brief verbal introduction to the experiment, which was described as a decision-making game for money, where the pay-off to each individual depended on the decisions of others in the group. Next, group members were given consent forms to read over individually and sign. Once the forms had been signed, the group was brought into the small computer lab where the actual experiment took place. Each group member was seated at a computer desk that was partially hidden from other group members by office dividers. Participants were told not to communicate with each other. The experimenter then verbally introduced the group to the computer program that would guide them through the experimental procedure, started the program, and left them to complete the on-screen instructions (see Appendix 1) and practice questions[1]. After approximately 15 minutes, the experimenter returned to the computer room, at which time the participants were usually finishing the practice questions. If any of the group members were unable to complete one of the practice questions, the

[1] The practice questions that followed the on-screen instructions were designed to test the participants' understanding of the essential features of the games and the experimental procedure. The questions demanded that the participants' perform some simple arithmetic calculations from word problems, and that they remember several important numbers from the instructions. A sample question from the practice questions is, "In the first game, suppose you contributed $6 and the rest of group contributed a total of $4. How much would you get from the group fund?" Whenever a participant did not answer a question correctly, the event was recorded by the computer program.

experimenter intervened quietly and tried to ensure that the participant understood the concept relevant to the question. Once all of the group members had finished the practice questions, the experimenter asked if there were any more questions, and if not, started the first trial of the experiment, and left the room until the fifth trial was completed.

Experimental trials: The Public Goods Game and the War of Attrition

The two games used in the experiment were modified versions of economic games known to experimental economics and evolutionary biology, the Public Goods Game (PGG) and the War of Attrition (WoA).

The PGG has been used in hundreds of experiments over the past three decades to examine behaviour in the face of conflicting individual and collective incentives[2] (Ledyard & Kagel, 1995). The PGG is equivalent to a multi-player Prisoner's Dilemma. The basic structure of the linear PGG is as follows: There are n players in a group. Each player starts with an initial endowment e, and each must player must choose how much of the endowment to contribute to the public good x_i and how much to keep for him or herself $e - x_i$. The individual payoff y is a function of the total contributions from all group members.

$$y_i = (e - x_i) + \frac{m}{n}\sum_{j=1}^{n} x_j$$

[2] The PGG is used as a model of many real life situations, such as fishing from a body of water, letting animals graze on communal land, defending a territory during a war, and cleaning dishes in a shared household. In each of these situations, individuals can maximum their payoff by acting selfishly, but the collective good suffers as a result.

The variable *m* is a multiplier that determines by what factor contributions are multiplied before being divided among the *n* group members. When *m* is greater than 1 and less than *n*, group members have individual incentive to contribute nothing, and a collective incentive to contribute everything.

In the present experiment, a PGG was conducted with groups of 4 participants. Participants could make contributions up to the amount of their starting endowments in increments of $0.50. Contributions were multiplied by a factor of 1.6 before being divided equally among group members. In these respects, the setup was similar to other recent PGG experiments (Barclay, 2004; Fehr & Gächter, 2002). However, since the present experiment was concerned with the effect of contributions on perceived status, the starting endowments of group members were varied to create differences in relative status[3]. At the beginning of each trial, one of the four group members was randomly selected to start with $7 (the high resource member) while the remaining group members each received $5 (the low resource members). Participants were informed of this heterogeneity, but they were not informed of other group members' specific endowments. That information could only be revealed by the size of individuals' contributions.

Along with their endowments, participants were assigned pseudonyms that appeared on screen at the beginning of every trial. The pseudonyms were selected from a list of Greek names that had previously been rated as neutral with respect to gender and likeability. The purpose

[3] While PGG experiments with heterogeneous endowments are rare, some have been conducted. In a meta-analysis of Public Goods Games, Zelmer (2001) found that heterogeneous endowments decreased contributions by 15% ($p < 0.05$), although Chan et al. (1999) found that heterogeneous endowments in a non-linear PGG increased contribution levels.

of the pseudonyms was to give each group member a distinct identity within each trial.

Once group members had decided on their individual contributions, the contributions and payoffs of all group members were displayed for all to see. Next, group members entered the second stage of the experimental trial, as instructed beforehand, in which each group member engaged in simultaneous, two-player War of Attrition games with each of the other three group members. In other words, a total of 6 contests took place, corresponding to all possible two-person interactions in the group of 4 participants (see Figure 1).

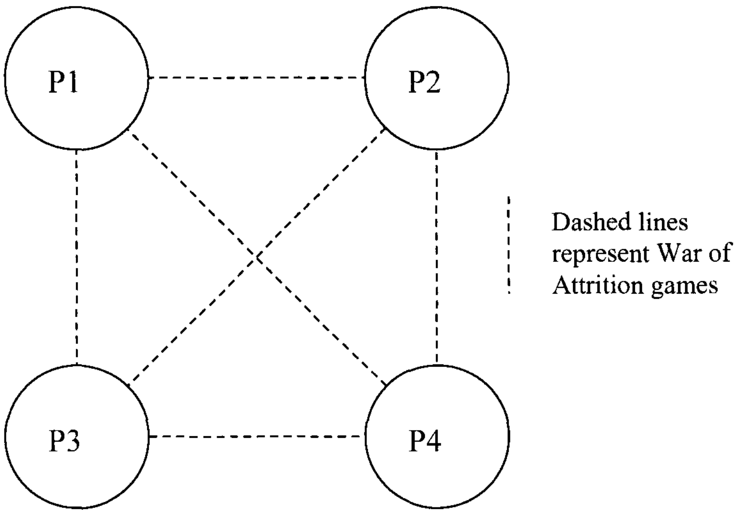


Figure 1: Diagram of dyadic War of Attrition interactions in group of four participants.

The WoA game was first analyzed theoretically by Maynard Smith (1976). It was designed to model situations where two animals must compete for a non-divisible resource (territory, mate, job position, etc.) while incurring some non-recoverable cost (time, effort, money, etc).

The basic structure of the game is as follows: There is a prize of some value v. Both players start with a positive endowment e_i. Each player must decide how much of e_i to spend in the contest x_i. Whoever decides on the higher value of x is considered the winner, and whoever decides on the lower value is considered the loser. If the value of x is the same for both players, then a tie is declared (although with perfectly continuous variables this is assumed never to happen). The payoff y to each player is given by the following equations:

$$y_{win} = e - x_{lose} + v$$
$$y_{lose} = e - x_{lose}$$
$$y_{tie} = e - x_{tie} + v/2$$

An important feature of the WoA is that the winner's cost is determined wholly by the loser's willingness to spend x_{lose}. This means that each player must only consider the probability that their willingness to spend will exceed the other's, and not the magnitude of any difference.

In the present experiment, the value of the prize in every WoA was \$5. Participants could spend an amount of money up to the value of their starting endowments in increments of \$0.50. The starting endowments were equal in value to the endowment that each participant had received in the PGG (except in the control condition—discussed below). Thus, three participants in each group played their WoA games with endowments of 5\$ and one participant played their WoA games with endowments of \$7. The profits that participants might have earned in the PGG remained separate from starting endowments in the WoA games.

In the control condition, the starting endowments of group members were re-randomized before the WoA games. One member of each group was still selected to be the high resource member with $7, but the selection was orthogonal to selection in the PGG. In the experimental condition, the relative status of group members was constant across both parts of a single trial (the PGG and the WoA games), whereas in the control condition the relative status of group members was reshuffled between the two parts of a single trial. Therefore, participants in the control condition could not infer anything about other individuals' status in the WoA by their behaviour in the PGG.

Once all members of a group had indicated their willingness to spend (termed "bids" for actual participants) for each of their WoA contests, the results of their contests were displayed in detail. Next, participants were shown an individual summary screen that totalled their profits from the PGG and their profits from their WoA contests. Then, the group began another trial until all 5 trials had been completed.

Post-experiment

After the trials, participants completed a short, 26-item questionnaire that asked about their motivations at various stages in the experiment (see Appendix 1), plus some simple demographic information. After all group members had completed the questionnaire, the experimenter re-entered the computer room and began the payment process. One of the 5 trials was randomly selected for payment by rolling a six-sided die in full view of all group members (re-rolling on an outcome of six). Individuals' profits from the selected trial were divided by a factor of 3 and paid out privately in cash.

Results

The average amount that participants earned was $7.85, with a minimum of $3.25 and a maximum of $12.50. (Final amounts were rounded up to the nearest quarter dollar.)

Public Goods Game

Groups contributed a mean of $12.95 to the public good, 59% of the maximum possible contribution of $22.00. This proportion is at the upper end of the normal range of 40 to 60% according to Ledyard & Kagel (1995). Group contributions were significantly different between groups ($F_{11,48} = 7.01$, $p < .01$). Group contributions were not significantly different over trials ($F_{4,55} = 1.03$, $p = .40$), contrary to the normal expectation of a change in contributions over repeated rounds of the PGG, although there was some evidence of a difference between the mean group contributions in the 4th and 5th trial ($t_{22}=1.68$, $p=.11$), evidence of an end-game effect. There was no evidence of a difference between the experimental and control conditions ($t_{58}=0.78$, $p=.45$). These findings are reflected in Figure 2.

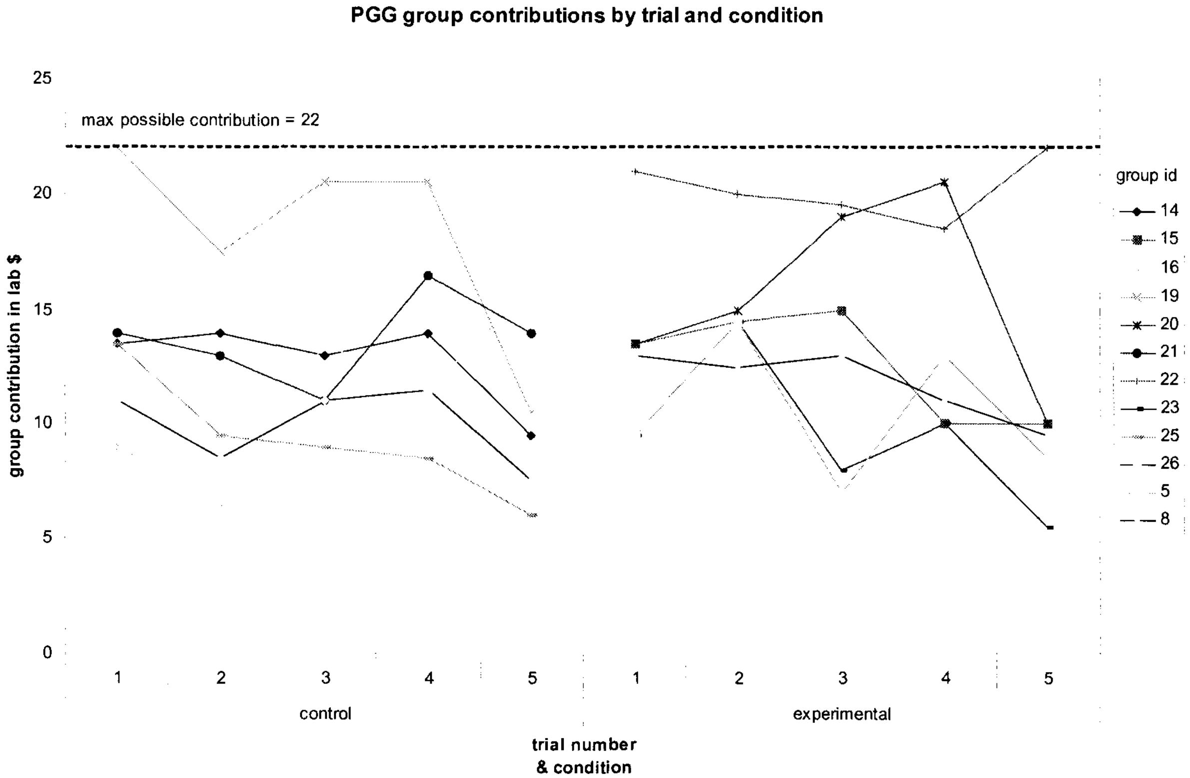


Figure 2: Group contributions over trials in experimental and control treatment conditions.

Individual contributions averaged $3.16 for participants endowed with $5, and $3.47 for those endowed with $7. Low resource participants tended to contribute the maximum of $5, whereas high resource participants did not show any strong modal tendency. This pattern is illustrated in Figure 3.

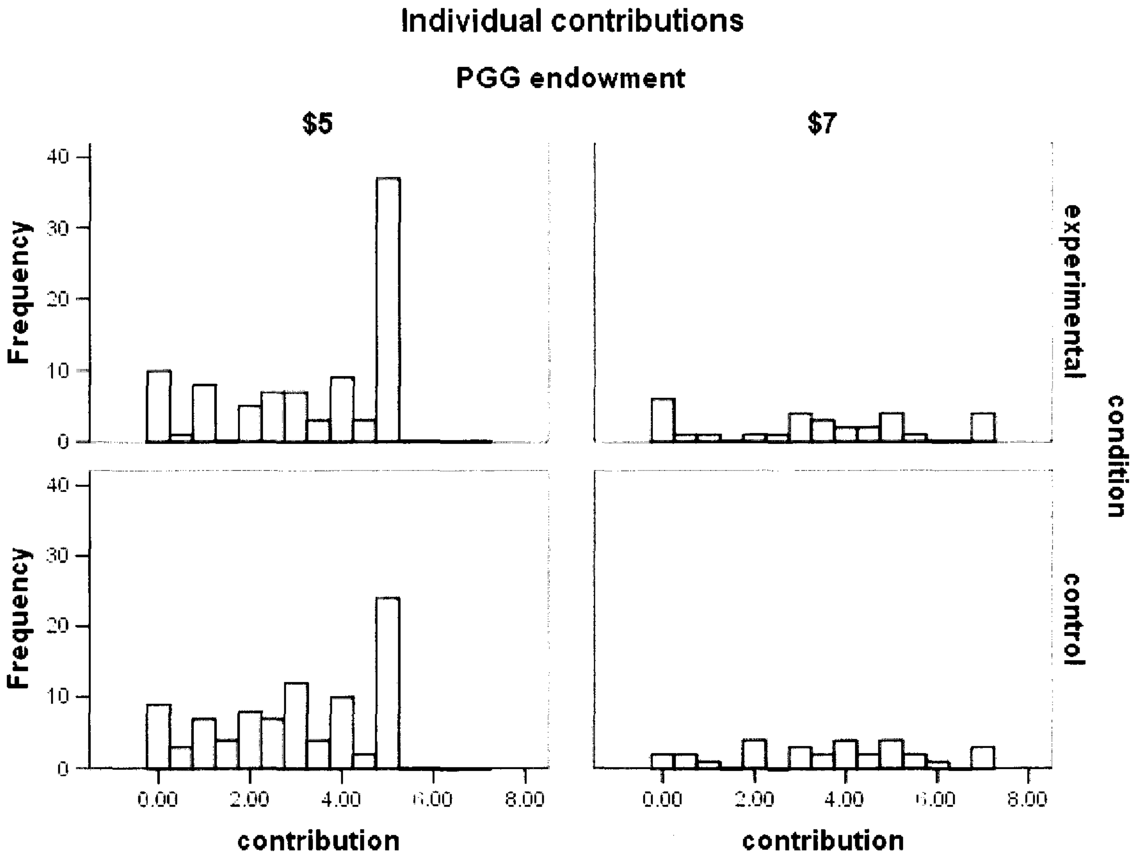


Figure 3: Histograms of individual contributions by endowment and condition. Note: Endowments of $7 were assigned to one member in every group of four.

The main prediction for individual contributions was that high resource group members in the experimental condition would contribute a greater amount than high resource group members in the control condition. In a two-way ANOVA, this would result in an interaction between PGG endowment and treatment condition. No significant effect was found ($F_{1,236} = 1.68$, $p = .20$). Moreover, the interaction is not in the predicted direction. The mean contribution of high resource individuals in the experimental condition was actually less than the mean of high resource individuals in the control condition. This difference was not due to overall differences in conditions, because the experimental group contribution level was higher than the control group.

War of Attrition

Participants were willing to spend a mean of $3.70 against opponents in the War of Attrition. High resource group members were willing to spend a mean of $4.13, significantly more than low resource participants who were willing to spend a mean of $3.56 ($t_{238} = 2.28$, $p = .02$). The distribution of bids is illustrated in Figure 4. The distribution among low resource participants does not resemble the negative exponential function that may be expected on theoretical grounds (see Chapter 3; and Maynard-Smith, 1974). Among high resource group members, the distribution should be heaviest on the right, because it is a dominant strategy for high resource group members to commit more than $5. In the experimental condition this pattern was observed, but not in the control condition.

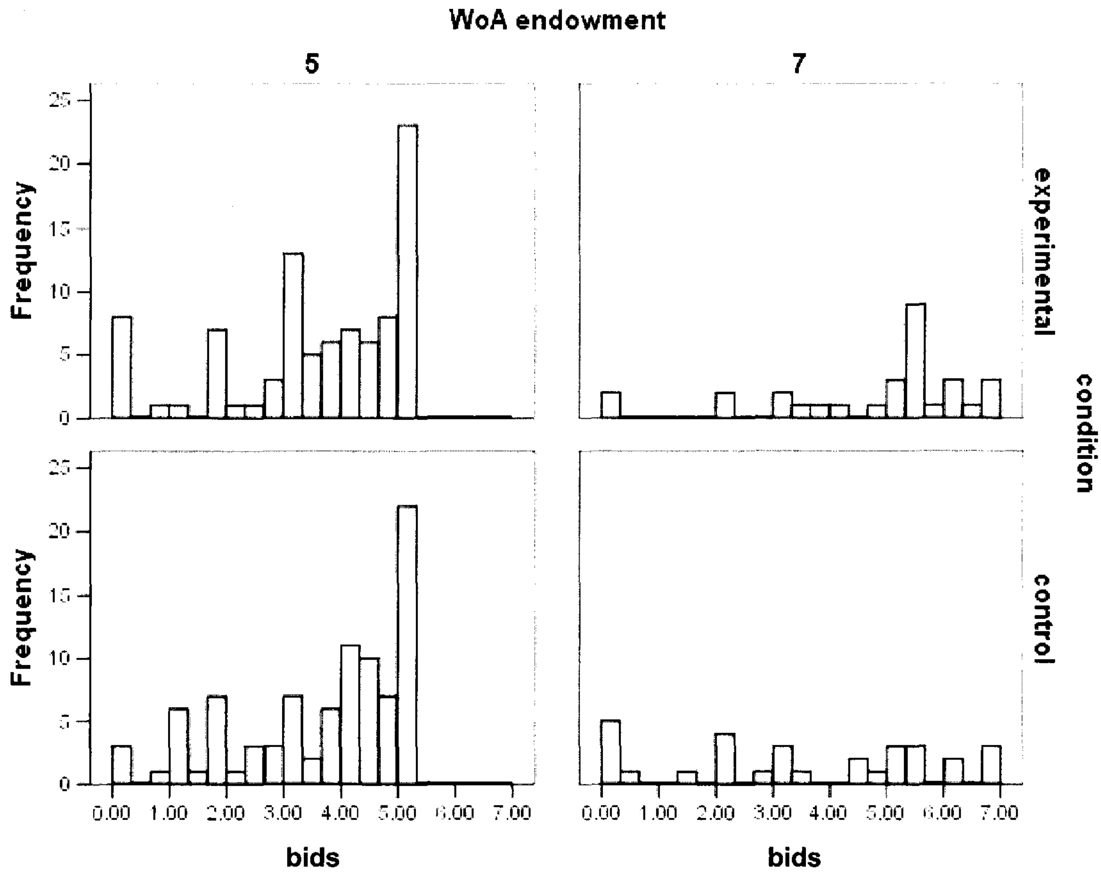


Figure 4: Frequency distribution of bids in the War of Attrition by condition and endowment. Note: Endowments of $7 were assigned to one member in every group of four.

The main prediction in the WoA was that low resource group members would be willing to spend less against high resource group members in the experimental condition. In a two-way ANOVA on the mean bid against individual participants in a round, a significant interaction was found between condition and their WoA endowment for that round ($F_{1,236} = 4.95$, $p = .03$). Post-hoc t-tests revealed that mean bids against high resource group members were significantly less than bids against low resource group members in the experimental condition, whereas there was no difference in the same comparison in the control condition.

PGG-WoA interactions

The two main results of the analysis of the PGG and the WoA conflict. Treatment condition did not significantly affect contributions by high resource group members in the PGG, but treatment condition did significantly affect behaviour toward high resource group members in the WoA. Examination of the histograms in figure 2 reveals that a proportion of high resource group members in the experimental condition contributed close to nothing to the public good, so it is reasonable to suppose that any signals of status were statistically obscured by free riding behaviour. To explore this possibility, two new variables were created: top contributor and high contributor. Top contributors were those participants who contributed the most out of their group to the public good. High contributors were those participants who contributed more than $5, unambiguously revealing their status as high resource group members. Two-way ANOVAs on willingness to spend in the WoA were performed with the two new variables. No significant interactions with condition were found (top contributor and condition, $p = .63$; high contributor and condition, $p = .52$). That is, neither participants who were the top contributors in their groups, nor participants who contributed more than $5, were treated any differently in the WoA in the experimental condition.

Discussion

The present experiment was designed to test the idea that altruistic behaviour can be induced by the prospect of costly competition. However, participants did not behave more generously when they had an incentive to advertise their higher status. Participants were willing to spend less in contests with higher status group members, but the way in which they identified higher status group members is unclear. Indeed, participants reported in the post-experiment questionnaire that their decisions in the WoA were not strongly influenced by others' actions in the PGG (3.3 on a 5 point Likert scale). In light of these results, the present experiment must be considered to have failed to demonstrate altruism as a signal of status. The rest of this discussion will be devoted to explaining this failure and to suggesting improvements.

Design weakness #1

Participants did not understand the War of Attrition. The mean willingness to spend in the War of Attrition was $3.70, much higher than a predicted mean of roughly $2.50 (assuming that high resource group members always bid $5.50). Low resource group members lost $1.53 on average. That is, low resource group members could have profited more by committing nothing, given the distribution of commitment levels that existed. Interestingly, female participants ($n = 33$) were willing to spend a mean of $4.11, while male participants ($n = 15$) were willing to spend a mean of $2.81, a highly significant difference ($p < .01$). Perhaps the strongest evidence of misunderstanding is that the modal commitment of low resource group members was $5 (refer to figure 4), when theoretical models (Maynard-Smith, 1974) predict a mode of $0. The behaviour of high resource group members strongly contradicted expectations as well, since they were willing to spend more than $5, which was the profit maximizing strategy, only 43% of the time.

The cause of any misunderstanding of the WoA may lie in the computer interface that participants used. The computer screen for the WoA required that participants simultaneously calculate their desired commitment levels against all three other group members without providing any immediate sense of the costs involved (see Appendix 1). In addition, the use of the term "bid" might have implied to participants that only the winner of each contest had to spend money, despite instructions to the contrary.

Design weakness #2

Participants did not have enough practice. Although participants reported that they understood the experiment (4.05 on a 5 point Likert scale), they may not have had enough experience with the most important aspect of the experiment, the interaction between high and low resource group members. With random assignment, participants averaged only 1.25 trials as high resource group members. Assuming that high resource group members do not dominate in the WoA, low resource members have no incentive to attend to status differences. To solve this problem of inexperience, participants could be asked to complete more trials. Alternatively, participants could be directly informed of optimal strategies for the WoA, leaving only PGG contributions as a strategic consideration.

Design weakness #3

Participants did not perceive the different resource endowments as psychologically meaningful differences in status. Participants may have had difficulty equating the dollar amounts randomly assigned by computer with cues of status in natural settings. One method to solve this problem would be to explicitly frame the resource endowments as "rich" and "poor". High resource group members would be referred to as "rich" and low resource group members would be referred to as "poor". This might have the effect of inducing participants to act as a "rich person" or as a "poor person".

Conclusion

Despite the fact that participants had an incentive to avoid conflict in the War of Attrition, their invariably high spending behaviour meant that altruism in the Public Goods Game could not have acted as an effective deterrent. Whether altruism as a signal of status can be demonstrated is a question that must be resolved by better experiments.

Chapter 3:
The War of Attrition with ownership framing

Introduction

The War of Attrition is a well-studied model of contest behaviour in non-human animals. Economists have analyzed the model and related models because of their applicability to economic situations (Bulow & Klemperer, 1999), although they have been slow to test these models empirically. Only Kirchkamp (2004) has explicitly conducted a War of Attrition with human participants, and this was with asymmetrical cost functions drawn randomly from a uniform distribution. Therefore, the present study was undertaken with two goals in mind: 1) to test the War of Attrition as a model of contest behaviour in human dyads; and 2) to manipulate the status of the contestants in a way that is analogous to manipulations that have been done with non-human animals.

The War of Attrition as a mathematical game was first described and analyzed by Maynard Smith (1974). It is intended to model any contest between two animals over an indivisible resource. The animals each have to decide how much effort to invest in winning the resource, the winner being the animal that invests the most. The effort invested may be in the form of energetic costs, time costs, survival costs, or other currencies depending on the ecology of the animals. Note that the nature of the "decision" — conscious or unconscious, innate or learned — is not important to the logic of the game.

Biologists have used the War of Attrition to explain the general distribution of contest durations in male dung flies (Parker & Thompson,

1980) and male butterflies (D. J. Kemp & Wiklund, 2001). This distribution is a negative exponential distribution where the minimum contest duration is the most frequent and greater durations decrease in frequency at a decelerating rate. To see why this is the expected distribution, we will formalize the structure of the game.

Denote the variables

V	Value of the resource
m_A	The cost to Player A
m_B	The cost to Player B

Then the payoffs to Player A and B are

	Player A	Player B
A wins: $m_A > m_B$	$V - m_B$	$-m_B$
A ties: $m_A = m_B$	$V/2 - m_B$	$V/2 - m_B$
A loses: $m_A < m_B$	$-m_A$	$V - m_A$

No pure strategy can be an evolutionarily stable strategy (ESS). To see this, suppose the members of a population play pure strategy m. A mutant that plays $m+1$ would always win against the population and therefore get a higher payoff. And if the payoff to a winning strategy is ever less than zero ($V-m<0$), a mutant that plays $m=0$ could also invade.

Maynard Smith (1974) showed that the stable strategy is to play m with the probability

$$p(m) = \frac{1}{V} e^{-m/V}$$

Players that employ this type of mixed strategy will produce a distribution of contest costs similar to what has been observed in non-human animals. The first goal of the present study was to replicate these findings with humans.

The second goal of the study was to test whether the perceived status of contestants could be manipulated in such a way as to change their degree of escalation in the game. Such manipulations are common with animal subjects. Kemp and Wiklund (2001) made butterflies fight harder over territory by letting both of them spend time alone on the territory before the contest. This is known as the *residency effect* in the study of animal behaviour. An analogous phenomenon is known in humans as the *endowment effect*. Kahneman et al. (1990) found that undergraduates who were randomly given souvenir mugs demanded substantially more money to sell them than other students were willing to pay to buy them.

The fact that perceived status can affect human behaviour in a competitive situation is important for the hypothesis that altruism specifically serves as a signal of status. Unless people can be shown to respond to more direct cues of status in economic games, it would be unwise to experiment with altruism as a cue of status.

Together, the residency effect and the endowment effect may be conceptualized as an *ownership effect*. For reasons debated elsewhere (D. Kemp & Wiklund, 2004), the owner of an object values that object more than non-owners, merely by being the owner. Consequently, the owner tends to win contests over objects in his possession. In such contests, non-owners will also tend to respect the local difference in status. Hoffman et al. (1994) found that non-owners were more willing to accept unequal offers in the Ultimatum Game.

The present experiment manipulated the ownership status of participants in a War of Attrition in two complementary ways. In the *framed* condition, one participant in each contest was addressed as the owner of the prize being contested. In the *earned* condition, one participant was again addressed as the owner of the prize, but only after having "won" a reaction-time test. I expected both conditions to produce ownership effects, with the *earned* condition producing a stronger effect. Specifically, I expected owners in the two experimental conditions to be willing to spend more in the War of Attrition than participants in an unframed control condition, and I expected non-owners to be willing to spend less. As a result, the total contest cost to dyads should have been less in the *framed* condition than in the *unframed* condition, and smallest in the *earned* condition.

Methods

Participants

52 undergraduates from McMaster University participated in the experiment. 46% of the participants were male and 54% were female. The average age of the participants was 19.3 years.

The 52 participants were divided into 13 one-hour sessions of 4 participants. Each session was conducted under a single condition: 5 sessions were of the *unframed* control condition, 4 sessions of the *framed* condition, and 4 sessions of the *earned* condition.

In each session, players played between 15 and 30 rounds of the War of Attrition. Only the first 15 rounds of sessions were analysed in order to include all player's data.

For each round, each participant was randomly assigned a partner. Because participants were isolated from one another and no cues of individual identity were provided, it was expected that participants could not form ongoing dyadic relationships.

The experiment was programmed and conducted with the software z-Tree (Fischbacher 1999).

The War of Attrition

Participants were informed of the rules of the game in written instructions. They had to pass a set of questions based on the instructions before being allowed to continue with the experiment.

In each round, participants were given $10 CAN to play with. The prize for winning the War of Attrition in any given round was $5. At the end of the experiment, participants were each paid their average total profit over all rounds.

The War of Attrition was realized with a computer program running on standard desktop computers (see Appendix 2). The decision of how much to bid in the contest, between $0.00 and $10.00, was presented on the first screen. On the following screen, the bids of the two players in the contest were represented by animated bar graphs. Next, in a summary screen, players were informed of the amounts the loser and winner had to spend, their net profit for the round, and their average profit over all rounds. Note: the highest bidder was made to pay one cent more than the lowest bidder, a slight deviation from the standard rules of the War of Attrition, in order to promote understanding.

Framed and *earned* conditions

In *framed* and *earned* conditions, participants were randomly assigned the status of either owner or non-owner every round.

In the *framed* condition, one participant in each contest was consistently addressed as the owner of the prize by using language related to possession. On the critical decision screen, the *owner* was informed: "You own the prize. How much are you willing to spend to keep it?" The *non-owner* was informed: "The other player owns the prize. How much are you willing to spend to take it?" In contrast, in the neutral *unframed* condition, both players were merely asked: "How much are you willing to spend to get the prize?" In addition, the instructions for the *framed* condition were modified to be consistent with the language used in the game itself (see Appendix 2).

In the *earned* condition, all the same text was used as in the *framed* condition. In addition, before each round of the game a reaction-time test was conducted. Participants were asked to click on a button as soon as it appeared after a random delay of 5 to 15 seconds. Following the reaction-time test, the randomly assigned "owner" of the prize was announced, creating the illusion that the test affected ownership status in the game.

Results

Participants' strategies in the War of Attrition

The *unframed* condition produced a distribution of bids that only somewhat resembled the distribution predicted from the game theoretic analysis of the War of Attrition. As shown in Figure 5, participants bid upwards from 0 dollars with declining frequency, but they were willing to spend between 4 and 6 dollars much more frequently than expected. Finally, they bid 9 or more dollars most frequently of all, instead of the least frequent. Most of these bids were the maximum bid of 10 dollars. Overall, the mean bid of \$5.49 was significantly higher than the expected mean of \$5.00 (t_{299}=2.33, p=.02), based on the ESS for the classic WoA.

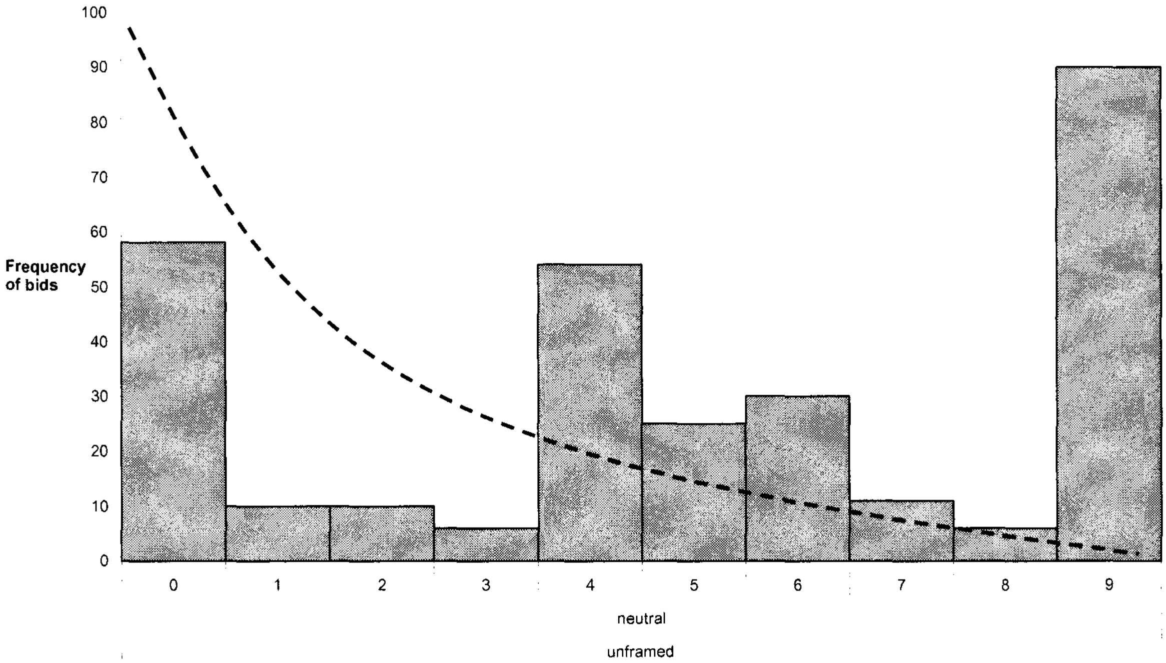


Figure 5: The frequency distribution of bids (willingness to spend) in the *unframed* condition. The dashed line (- - - -) shows a rough prediction based on the ESS for the basic War of Attrition.

Mean profits of \$9.25 in the *unframed* condition were thus significantly lower than the expected profit of \$10.00 in equilibrium (t_{299}=3.22, p<.01). Across the distribution of bids, the minimum bid of zero was more profitable than expected as were bids between 6 and 7 dollars (see Figure

6), which were just above the frequently occurring bids between 4 and 6 dollars.

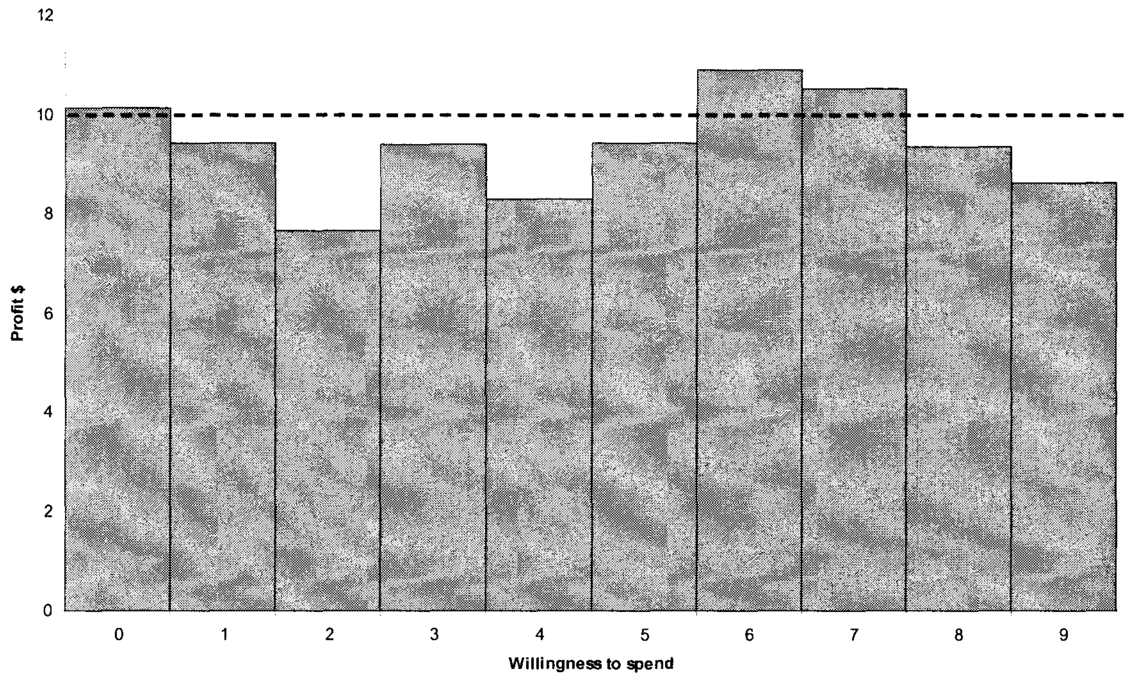


Figure 6: Mean profit by bid. The dashed line (- - - -) shows the expected equilibrium profit of $10 for all bids.

The effects of ownership in the War of Attrition

Across the two experimental conditions, participants did not change their behaviour in the directions predicted (see Figure 7). In the *framed* condition, both owners and non-owners were willing to spend more ($7.37 and $6.72) to get the prize than neutral participants in the *unframed* condition ($5.49). In the *earned* condition, both owners and non-owner were willing to spend slightly more ($5.77 and $5.82) than the neutral condition participants ($5.49).

In a within-subjects GLM test on willingness to spend, the effect of condition was not significant ($F_{1,49.0}$=1.63, p=.21), the effect of ownership was nearly significant ($F_{1,730.1}$=3.20, p=.07), and the interaction of condition and ownership was nearly significant ($F_{1,730.1}$=2.47, p=.12). The interaction effect is mostly due to the fact that non-owners bid $0.65 more on average than non-owners in the *framed* condition, contrary to prediction (see Figure 7).

When the GLM test was done on subjects' *mean* willingness to spend, the results were nearly identical. None of the effects were significant (condition: $F_{1,46.4}$=1.33, p=.25; ownership: $F_{1,30.0}$=2.85, p=.10; interaction: $F_{1,30.0}$=2.85, p=.146).

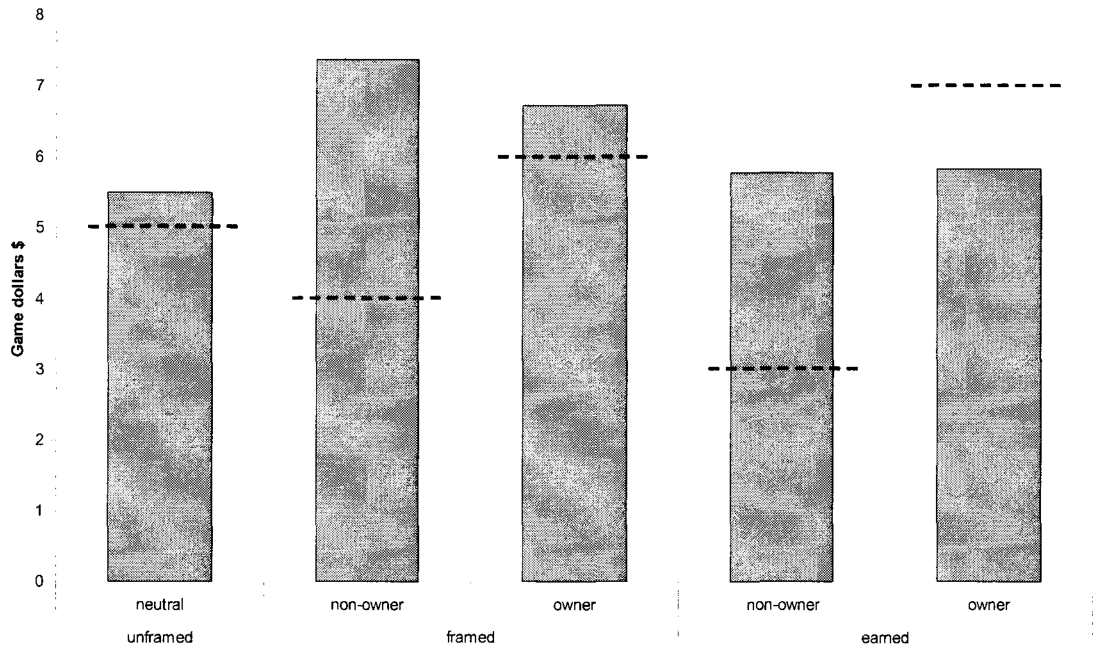


Figure 7: Mean willingness to spend across all ownership conditions, by individuals' ownership status. The dashed lines (- - - -) show qualitative predictions based on framing.

The higher mean willingness to spend in the *framed* condition than in the *earned* condition appears to be mostly the result of fewer low bids of $0.00 to $0.99 in the *framed* condition (see Figure 8).

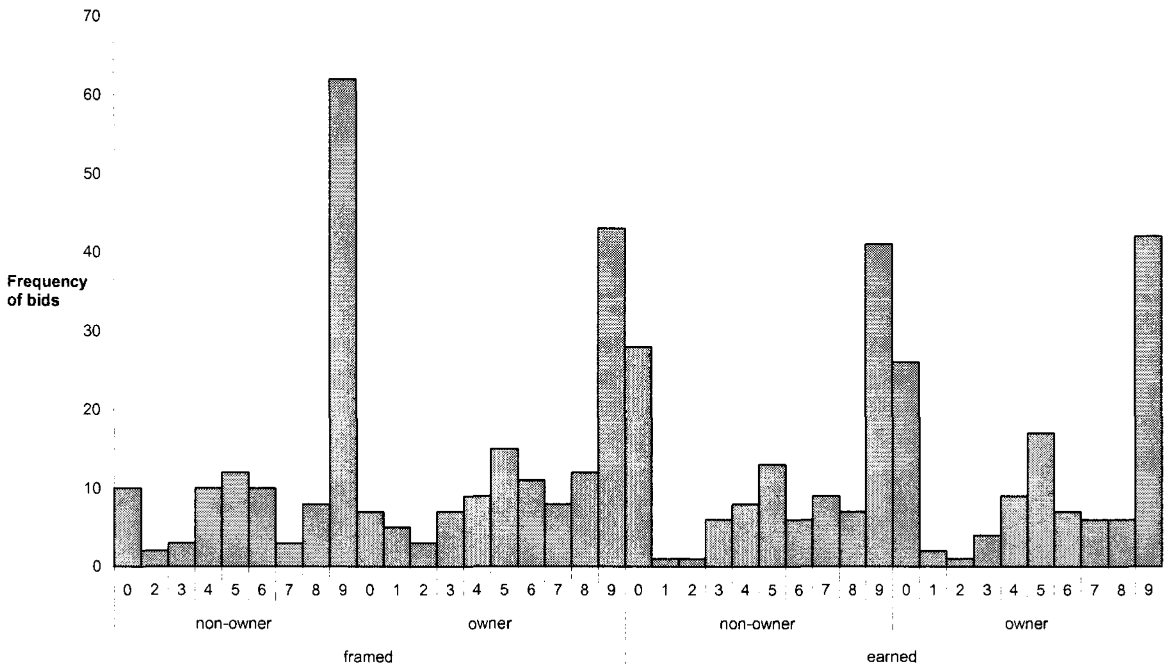


Figure 8: The frequency distributions of bids (willingness to spend) across conditions. Bins are 0.00 to 0.99, 1.00 to 1.99, and so on, up to 9.00 to 10.00.

The manipulations in the *framed* and *earned* conditions were expected to be most effective in earlier rounds, before participants learned of their irrelevance to payoffs, but there was no clear trend either upwards or downwards in contest escalation over time (see Figure 9). When round number was tested in a two-way within-subjects model with condition, it was not a significant factor ($F_{14,686}$=1.14, p=.32), nor was the interaction of round and condition ($F_{28,686}$=.92, p=.59).

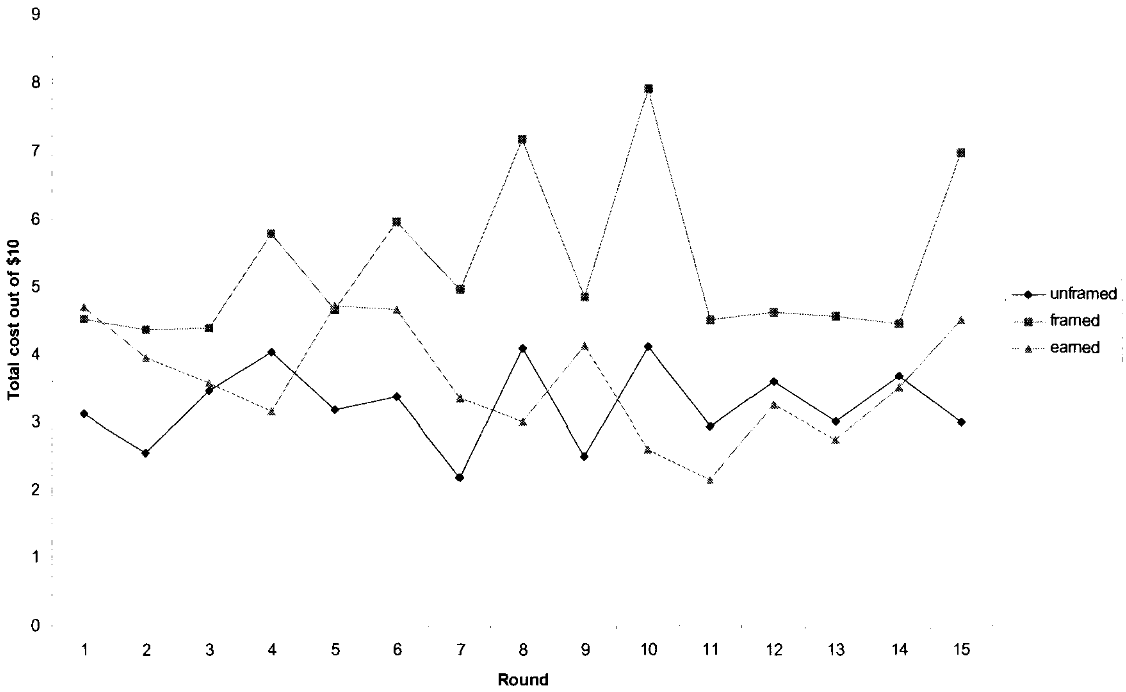


Figure 9: The mean total cost of contests by round and condition. Total cost is the amount the winner of each contest had to pay.

Females were willing to spend more ($6.14) than males ($5.48) in all conditions, although sex was not a significant factor in a model that included interactions with condition and ownership. The interaction of ownership and sex was nearly significant ($F_{1,614}$=2.421, p=.12), indicating that males and females may have been affected differently by the ownership manipulation. In the *framed* condition, females were willing to spend more as non-owners than owners, whereas males were willing to spend roughly the same amount as non-owners or owners (see Figure 10). In the *earned* condition, females were again willing to spend more as non-owners than owners, whereas males were willing to spend more as owners than non-owners (see Figure 11). In short, females behaved opposite to expectations, and males behaved consistent with expectations in the *earned* condition.

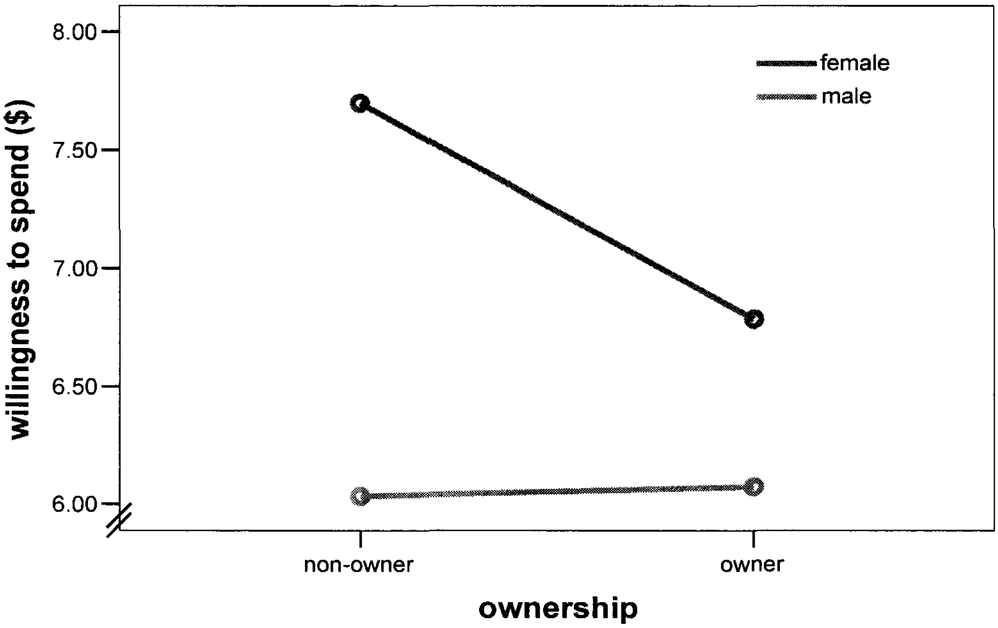


Figure 10: Male and female willingness to spend as a function of ownership in the *framed* condition.

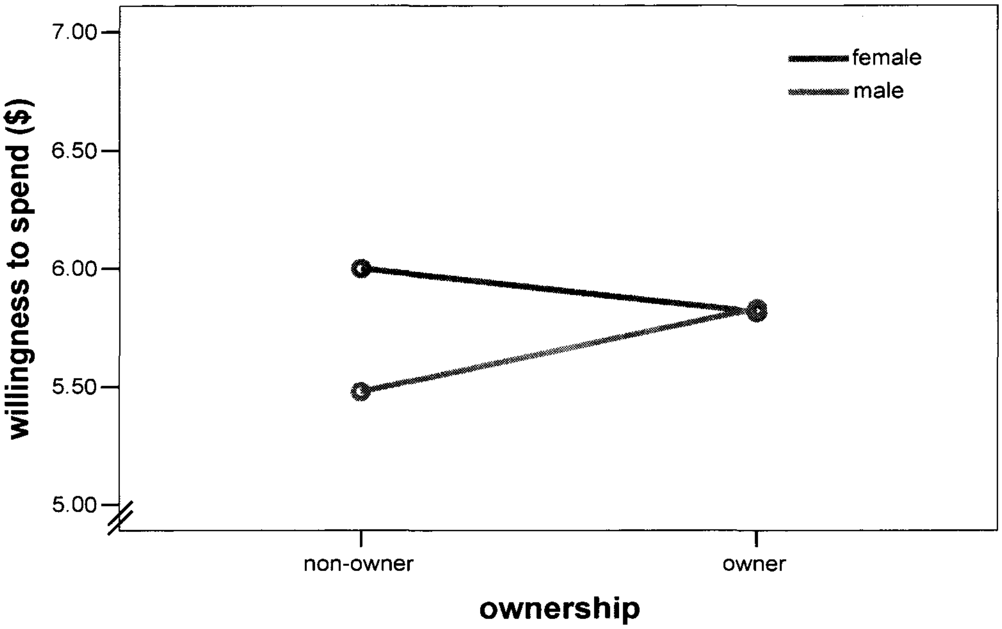


Figure 11: Male and female willingness to spend as a function of ownership in the *earned* condition.

Discussion

Explaining the observed distribution of bids

The behaviour of participants in the *unframed* War of Attrition only weakly resembled the behaviour predicted theoretically. Bids did not decline smoothly in frequency from $0 to $10. Here I propose several complementary explanations for this fact:

1) Bids in the middle of the distribution ($4 to $6) may have been especially salient. People who are unsure of good strategies for a game are known to choose a strategy away from extremes (Camerer & Weber, 1992). In support of this idea, participants in an unpublished pilot study (Dingle, 2006) who played a version of the War of Attrition

that gave them incremental feedback did not exhibit the same spike in bidding frequency in the middle of the distribution.

2) The upper limit of $10 in this laboratory version of the War of Attrition may have altered the evolutionarily stable strategy. The original War of Attrition assumes an infinite domain for escalation of the contest. Reanalyzing the game with an upper limit, I found that the original ESS does not apply (see Chapter 4). Moreover, no new ESS was found. It may be that a monotonically decreasing frequency distribution depends on players always being able to increase their bids.
3) A substantial number of participants believed they were playing against a computer programmed strategy instead of a real person. A post-experiment questionnaire of 12 participants (see Appendix 2) revealed that the mean agreement with this proposition was 3.33 on a five point scale, where 1 was "completely disagree" and 5 was "completely agree". No subjects completely disagreed. Statements by participants after the experiment suggested that participants that believed they were playing a computer strategy also believed that the computer would always win. When asked about the purpose of the experiment, one participant wrote: "See if we still bet money when there is no chance to win."
4) A substantial number of participants failed to grasp the fact that if they bid $0 they would at least get a $10 payoff. In a post-experiment questionnaire of 48 participants (see Appendix 2), the mean agreement with this proposition was 3.4 on a five point scale, where 1 was "completely disagree" and 5 was "completely agree".

Weak framings

The framing manipulations on the War of Attrition did not produce the expected effects. Owners did not bid more for the prize than non-owners. In fact, the data point to the opposite conclusion. Only male participants responded to the manipulations in a way that was somewhat consistent with predictions.

The fact that the ownership manipulations did not produce significant results may be because the framings used were too weak. In the *framed* condition, only the on-screen text was changed. Participants could have easily ignored the text and proceeded through the game by pushing the on-screen button (see Appendix 2). In the *earned* condition, the reaction-time contest was designed to induce a greater feeling of ownership (and non-ownership) over the prize. However, the contest was still trivial compared to most everyday contests (sports, school exams, etc). Hoffman et al. (1994) used a much more challenging written test for their successful manipulation. After many repetitions of the reaction-time contest, participants may have lost interest or learned to doubt its reliability, although a sample of reaction-times collected did not support these possibilities.

Finally, in both ownership conditions, individual participants had to act as both owners and non-owners repeatedly. This might have diminished any feelings of entitlement or deference. Also, Kahneman et al. (1990) found that the endowment effect did not occur when participants in their experiment were given cash credits instead of souvenir mugs. Participants' ownership psychology may not have been activated sufficiently by the abstract and unfamiliar "prize" presented in the experiment.

Ownership manipulations modulated by competitiveness

The fact that non-owners were willing to spend more than owners may be due to competitiveness. Arbitrarily labelling a participant as a non-owner may motivate that participant to compete more strongly against the owner in order to diminish the status difference between them. This variety of inequality aversion would explain why non-owners in the *framed* condition bid more than non-owners in the *earned* condition, since the latter designation may have been perceived as less arbitrary.

Many participants' post-experiment statements indicated that winning the prize alone was most important to them. Describing his or her strategy, one participant wrote: "Offer 10 dollars as my amount each time because regardless of whether I had to spend that amount, in the end, it would either beat or tie the other person so that I either spent less and got the prize, or I spent the same and had to share with them but either way I wasn't losing."

Male-female differences

Why were females willing to spend more on average than males? Post-experiment questionnaires showed that males were significantly more likely to take the game seriously (t_{50}=2.35, p=.02), more likely to believe they would receive their money at the end of the experiment (t_{50}=3.58, p<.01), less likely to believe they were playing against a computer programmed strategy (t_{10}=-2.39, p=.04), and more likely to realize that a bid of $0 would yield a payoff of at least $10 ($t_{46}$=2.04, p=.05)

Why did females and males appear to respond in opposite directions to the ownership manipulation? Females could be more sensitive to inequality (Andreoni & Vesterlund, 2001) and less respectful of status differences in a competitive context, since males have faced more intra-sexual competition over evolutionary history than females (Daly & Wilson, 1988).

Final remarks

In this study, I tried to test predictions derived from a theoretical analysis of the War of Attrition on contest behaviour with human participants. I also tried to manipulate the perceived status of participants to change their behaviour in the game. The results of the study did not support any clear conclusions in either case.

Whether the War of Attrition should be used as a model of contest behaviour in humans should therefore be questioned. Non-human animals are usually more motivated to fight than human participants and they are not subject to the same ethical considerations. Non-human animals can compete with their own resources but human participants must be given resources by experimenters. The reanalysis of the War of Attrition with an upper bound (in Chapter 4) shows that the principle of infinite escalation is important to evolutionary stability in the game. This presents a methodological problem to laboratory experimentation that should be solved before more Wars of Attrition are conducted.

Chapter 4:
Limited escalation and evolutionary stability in the War of Attrition

Greg Dingle and Brad Wagner

Introduction

The original, symmetrical War of Attrition had never been tested with human participants previous to the study described in Chapter 3. A problem with this task is that participants must play with resources (typically money) provided to them by the supervising researchers (for ethical reasons) and so the potential escalation in the game is limited by the researchers' budget. This problem could be avoided if the War of Attrition can be played with an upper limit on potential escalation while retaining a predictable character.

Thus, here we attempt to answer the question: What effect does a restriction on effort have on evolutionary stability in the War of Attrition? First, we reproduce the original analysis of the War of Attrition; second, we analyze the War of Attrition with an upper bound; last, we analyze the War of Attrition as a discrete game with an upper bound as an alternative approach.

Analyses

The original War of Attrition

In the original formulation of the War of Attrition, Maynard Smith (1974) found a stable mixed strategy that invests a given level of effort with a diminishing probability over the domain of zero to infinity, converging to a probability of zero at infinity.

First, we reproduce Maynard Smith's original solution. Denote

V	Value of the resource
m_A	The cost to Player A
m_B	The cost to Player B

where V is a positive constant, and m_A and m_B can take on values in the set $[0, \infty]$. Then the payoffs to Player A and B are

	Player A	Player B
A wins: $m_A > m_B$	$V - m_B$	$- m_B$
A ties: $m_A = m_B$	$V/2 - m_B$	$V/2 - m_B$
A loses: $m_A < m_B$	$- m_A$	$V - m_A$

No pure strategy can be an ESS. To see this, suppose the members of a population play pure strategy m. A mutant that plays $m+1$ would always win against the population and therefore get a higher payoff. And if the payoff to a wining strategy is ever less than zero ($V-m<0$), a mutant that plays $m=0$ could also invade.

Therefore, if there is an ESS, it must be a mixed one. Let I be a strategy defined by the probability density function $p(x)$. That is, the probability of accepting a cost between x and $x + dx$ is $p(x)dx$. To find $p(x)$, we make use of the Bishops-Cannings theorem (1978), which in the present context states that, if m is a pure strategy in the "support" of I (i.e.

p(m) does not equal zero), then the expected payoff to *m* against *I* is constant when *I* is stable.

The expected payoff to *m* against *I* is

$$E(m, I) = \int_0^m (V - x)p(x)dx - \int_m^\infty mp(x)dx$$

The first integral represents the expected payoff to *m* when *m*>*x*, and the second integral represents the expected payoff to *m* when *m*<*x*.

We have to find *p(x)* such that $\partial E(m,I)/\partial m = 0$, subject to the constraint

$$\int_0^\infty p(x)dx = 1.$$

We differentiate with respect to *m*

$$\frac{\partial E(m,I)}{\partial m} = (V - m)p(m) + mp(m) - \int_m^\infty p(x)dx$$

$$\frac{\partial E(m,I)}{\partial m} = Vp(m) - \int_m^\infty p(x)dx$$

We set $\partial E(m,I)/\partial m = 0$ and take the derivative

$$0 = Vp'(m) + p(m)$$

$$p(m) = -Vp'(m)$$

A differential equation of this form has the solution

$$p(x) = \frac{1}{V} e^{-x/V}$$

which is the required function. This shows that $I = p(x)$ is a candidate ESS; to show that it is stable, we must also show that

$$E(I, m) > E(m, m)$$

This has been done by Maynard Smith (1974). It has been proved by Bishops and Cannings (1978) for the more general case when *m* can be any mixed strategy different from *I*.

The War of Attrition as a continuous game with an upper boundary

We turn now to the case of the War of Attrition with an arbitrary upper boundary *b*. Let *b=1* without loss of generality. The expected payoff to *m* against *I* is then

$$E(m, I) = \int_0^m (V - x)p(x)dx - \int_m^1 mp(x)dx$$

We again have to find *p(x)* such that $\partial E(m,I)/\partial m = 0$, subject now to the constraint

$$\int_0^1 p(x)dx = 1.$$

We differentiate with respect to *m*

$$\frac{\partial E(m,I)}{\partial m} = (V-m)p(m) + mp(m) - \int_m^1 p(x)dx$$

$$\frac{\partial E(m,I)}{\partial m} = Vp(m) - \int_m^1 p(x)dx$$

We set $\partial E(m,I)/\partial m = 0$

$$0 = Vp(m) - \int_m^1 p(x)dx$$

$$p(m) = \frac{1}{V}\int_m^1 p(x)dx$$

$$p(m) = -Vp'(m)$$

The solution to the differential equation is the same as before

$$p(x) = \frac{1}{V}e^{-x/V}$$

But notice that the limit of p(x), as *x* goes to 1, the upper boundary

$$p(x)_{\lim x \to 1} = p(1)$$

$$p(1) = 0.$$

Thus, there can be no candidate mixed ESS. Intuitively, we can see that a mutant that plays the pure strategy at the boundary would always get a higher expected payoff than one slightly below it. Therefore, there is no mixed ESS in the War of Attrition with an upper boundary. It appears that evolutionary stability in the original War of Attrition depends on the fact that players can always escalate the contest to a higher cost.

The War of Attrition as a discrete game with an upper boundary

As an alternative approach, we now model the restricted War of Attrition as a discrete game. The cost domain is divided into a set of cost intervals of equal distance. As in the continuous version of the game, there exists no pure strategy ESS in the discrete War of Attrition. If an ESS exists, it must be a mixed strategy.

Now we work through the case where the set of costs are the integers 0 through 10. We choose this case because it corresponds to a laboratory War of Attrition one of the authors conducted using increments of 0 dollars up to 10 dollars (Dingle, unpublished).

Let I be a mixed strategy composed of the pure strategies i = 0 to 10. Let p_i be the probability that the pure strategy i is played in support of the mixed strategy I, subject to the constraint

$$\sum_{i=0}^{10} p_i = 1$$

Let W be the payoff to a mutant strategy playing a pure strategy of cost m = 0 to 10 against a population playing the mixed strategy I. The rows correspond to the possible cost levels of the mutant strategy and the columns correspond to the cost levels in the mixed strategy *I*.

W =

$$\begin{bmatrix} v/2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ v-1 & v/2-1 & -1 & -1 & -1 & -1 & -1 & -1 & -1 & -1 & -1 \\ v-2 & v-2 & v/2-2 & -2 & -2 & -2 & -2 & -2 & -2 & -2 & -2 \\ v-3 & v-3 & v-3 & v/2-3 & -3 & -3 & -3 & -3 & -3 & -3 & -3 \\ v-4 & v-4 & v-4 & v-4 & v/2-4 & -4 & -4 & -4 & -4 & -4 & -4 \\ v-5 & v-5 & v-5 & v-5 & v-5 & v/2-5 & -5 & -5 & -5 & -5 & -5 \\ v-6 & v-6 & v-6 & v-6 & v-6 & v-6 & v/2-6 & -6 & -6 & -6 & -6 \\ v-7 & v-7 & v-7 & v-7 & v-7 & v-7 & v-7 & v/2-7 & -7 & -7 & -7 \\ v-8 & v-8 & v-8 & v-8 & v-8 & v-8 & v-8 & v-8 & v/2-8 & -8 & -8 \\ v-9 & v-9 & v-9 & v-9 & v-9 & v-9 & v-9 & v-9 & v-9 & v/2-9 & -9 \\ v-10 & v-10 & v-10 & v-10 & v-10 & v-10 & v-10 & v-10 & v-10 & v-10 & v/2-10 \end{bmatrix}$$

Let P be the probability that *I* plays the pure strategy *i* with probability p_i.

$$P = \begin{bmatrix} p_0 \\ p_1 \\ M \\ p_9 \\ p_{10} \end{bmatrix}$$

Let *k* be the expected payoff to mutant *m* against *I*, which is a constant assuming that the Bishop-Cannings theorem applies. Then let K be a vector the same size as P but filled with *k*.

The expected payoff to mutant *m* against *I* is then the matrix multiplication

$$WP = K$$

We rearrange to isolate *P*

$$P = W^{-1}K$$

Using the computer program Matlab to solve for *P* when V=5, we find that there is no solution where $0<p_i<1$ for all p_i. This means that there is no stable mixed strategy in the discrete War of Attrition over the integers 0 to 10. Nonetheless, we expect a stable strategy to emerge in the discrete game if we included the integers up to infinity, since then the discrete game becomes indistinguishable from the continuous game.

Discussion

In view of the fact that we found no ESS in the restricted War of Attrition in either the continuous version or in the discrete version we tested, we conclude that game theoretic analysis cannot provide a reasonable expectation of evolved optimal behaviour in a restricted War of Attrition. This result is important for researchers who wish to experiment with animal contests, since contests in laboratories are typically limited by ethical and other considerations. With humans in particular, researchers must typically provide the money or other resources with which participants can compete. This ties the maximum possible escalation of a contest to the researcher's budget.

Researchers may be able to avoid the problem of limited escalation by providing a very large amount of less valuable resources, but then the motivation of participants becomes a problem. Alternatively, researchers could reduce their study of contest behaviour to a Hawk-Dove game, which may be considered a two-action discrete War of Attrition. Theoreticians may be able to suggest other models of animal contests that may be more suitable for laboratory experimentation. Indeed, theoreticians should re-analyze any other continuous games that assume an infinite domain to check if their solutions rely on that assumption like the War of Attrition.

Chapter 5:
The reproductive success of war heroes

When honor scorns to compromise with death—that is heroism.
-Robert Green Ingersoll

Introduction

Altruism directed at non-kin is difficult for evolutionists to explain, because natural selection would have favored individuals who behaved without concern for the welfare of unrelated individuals. Altruism may arise in the context of repeated interactions when one individual can expect another to repay its gifts (Trivers, 1971), but such reciprocity cannot account for altruism in situations that preclude exchanges between donors and recipients, thus there is a one-way transfer of benefits. In the most extreme cases, one individual risks his or her life for the survival of others.

The term "heroism" is well-suited to describe this type of behaviour. Dictionaries define heroism as an act of a hero, a person who is noted for feats of courage and nobility of purpose ("American Heritage Dictionary", 2006;, "Oxford English Dictionary", 2006). Becker and Eagly (2004) argued that only the conjunction of risk-taking and service to a socially valued goal yields heroic status. The Carnegie Hero Fund, in operation since 1907, has two conditions for its heroes: first, a hero must "voluntarily risk his or her own life to an extraordinary degree in saving or attempting to save the life of another person", and second, "the act of rescue must be one in which no full measure of responsibility exists between the rescuer and the rescued." (*Carnegie Hero Fund Commission: Annual report*, 2004).

A similar concept of heroism is known across a diverse range of cultures. Klapp (1949) wrote that the "defending or delivering hero" is represented by many historical and mythical figures; Beowulf, Achilles, David, Rama and Guan Yu are examples of heroes that in some way saved their countrymen from danger. As much as heroes are known around the world, they are viewed in a similarly positive light. Beowulf, after slaying a monster that had been terrorizing the local people, returned to much praise, celebration, and gift-giving ("Beowulf", 2006). Guan Yu, who fought against bandits in 2nd century China, is still revered today in Chinese police stations as a symbol of brotherhood and righteousness ("Guan Yu", 2006).

Undoubtedly, people who have made sacrifices for others have always been celebrated by their communities, regardless of whether their stories are still being told. The attention and praise that are given to people who perform heroic acts suggest possible reproductive benefits. As a result of their actions, heroes may be perceived as more socially dominant and more attractive. In a mating context, heroism may be considered a reliable signal of a person's competence, risk proneness or general concern for others' welfare. Heroism could be an especially good signal because the costs of failure are high.

Some evidence for a relationship between heroism and reproductive success exists already. In a study of the Torres Strait Islanders, Smith and Bird (2000) found evidence to support the argument that big-game hunters who contributed to public feasts were rewarded with social prestige and mating success. Among the Yanomamö of the Amazon basin, Chagnon (1988) found that men who had killed enemies in combat, arguably a public service, had higher reproductive success than other men. In a survey of US undergraduates, Farthing (2005) found that both males and females preferred heroic risk-takers as mates over risk-avoiders and non-heroic risk-takers, and the preference for heroism was stronger in females than in males. Similarly, Kelly and Dunbar (2001) found that females preferred heroic risk-takers.

R.A. Fisher (1958, pp. 247-274) speculated that clan-based cultures, typified by ancient Northern Europeans and Central Asians, selected for heroism. Fertility in such cultures was strongly associated with social status, and males could attain social status for themselves and their kin by performing heroic acts, such as leading an attack on a rival clan. The fitness costs of premature death would have been mitigated by the status benefits to surviving kin.

To be sure, there are many reasons why heroism may not confer higher fitness, even when the hero survives. The attention given to heroes may be too short-lived. Any promotion in social status may be a transparent ploy by political elites, especially in wartime. Or, the risk-taking for non-kin that heroes exhibit may be perceived as undesirable in a potential parent.

To test whether heroism confers increased reproductive success, I investigated the lives of 57 male WWI war heroes who received the US Medal of Honor. I retrieved their demographic information from the 1930 US Census, which was taken approximately 11.5 years after the end of the war, leaving enough time for the heroes to start families. For comparison, I also recorded the demographic information of 114 WWI veterans from the same neighborhoods as the heroes. For an additional comparison, I obtained a random sample of 13637 WWI veterans from the 1930 US population (Ruggles et al., 2004). I then tested differences between the heroes and the two control groups in marriage likelihood and marital fertility. To pinpoint any effect of the Medal of Honor, I analyzed rates of marriage over time, both before the war and after the war. Finally, to test whether aggressiveness was confounded with heroism, I compared heroes who received their Medal of Honor through violent and non-violent actions.

Methods

The Medal of Honor

The Medal of Honor is the highest military medal awarded by the United States government. Every recipient must satisfy a strict set of criteria ("Military Awards", 1995), the main part of which is reprinted below:

> The Medal of Honor is awarded by the President in the name of Congress to a person who, while a member of the Army, distinguishes himself or herself conspicuously by gallantry and intrepidity at the risk of his or her life above and beyond the call of duty while engaged in an action against an enemy of the United States; [...] The deed performed must have been one of personal bravery or self-sacrifice so conspicuous as to clearly distinguish the individual above his comrades and must have involved risk of life. Incontestable proof of the performance of the service will be exacted and each recommendation for the award of this decoration will be considered on the standard of extraordinary merit.

Interestingly, the Medal of Honor cannot be awarded for saving family members (N. Smith, 2006, personal communication), a tacit acknowledgement of the overlap of genetic interests among kin.

Below is a representative citation from one of the WWI recipients used in the present study.

> "At a critical point in the action, when all the officers with his platoon had become casualties, Cpl. Allex took command of the platoon and led it forward until the advance was stopped by fire from a machinegun nest. He then advanced alone for about 30 yards in the face of intense fire and attacked the nest. With his bayonet he killed 5 of the enemy, and when it was broken, used the butt of his rifle, capturing 15 prisoners."

The extraordinary criteria for the Medal of Honor have made it a very exclusive award. Between 1900 and 2005, a total of 967 medals were awarded ("Medal of Honor Citations", 2005). Medal of Honor recipients receive several special lifetime privileges from the military. Currently, these include a special pension of $200 a month ("Military Awards", 1995). As an indication of the award's popular recognition, at least two Oscar Award winning movies have depicted events that resulted in a Medal of Honor: Sergeant York[4] ("Sergeant York", 1941) and Black Hawk Down ("Black Hawk Down", 2001).

WWI Medal of Honor recipients

In World War I, a total of 120 males were awarded Medals of Honor for actions that occurred during the United States' involvement in the war from June 1917 to November 1918 ("Medal of Honor Citations", 2005). Of these, 33 of the awards were awarded posthumously, leaving 87

[4] Sergeant Alvin C. York was a WWI Medal of Honor recipient who was drafted into the war despite applying for exemption as a conscientious objector. During the first morning of the Battle of the Argonne, York killed 25 Germans and captured 132 prisoners. After the war, he married and had three sons ("Alvin C. York", 2000).

men who survived their heroic actions. These 87 men formed the initial sample. All of the information contained in the heroes' official citations was recorded for later use. This included name, place of birth, date of birth, service (Army, Navy or Air Force), rank and unit, place and date of action, and a short paragraph describing the heroic action.

The information contained in the citations was used to find each hero's record in an electronic database of the 1930 US Census[5]. The database is an electronic copy of the original 1930 census sheets as recorded by the census takers ("1930 Census", 2002). I attempted to locate the initial sample of 87 heroes by matching on first and last name, year of birth, city of birth and WWI veteran status. Only those heroes who had a perfect match or a near-perfect match (e.g. "Phillip" and "Philip") in the census records were included in the final sample used for statistical comparisons. By this method, 57 of the 87 surviving Medal of Honor recipients were successfully identified. Heroes that were not identified were either missing completely from the census or had demographic information that partly contradicted their military records.

Neighborhood veterans

For every hero located in the census sheets, the next and previous WWI veteran were also located and their demographic information was recorded. The order of the persons recorded in the census followed the house-by-house route of the original census taker, so the next and

[5] The 1930 US census is particularly suited to the present study for a variety of reasons: It is a complete record of the entire US population on 1 April 1930 (123 million); it is the most recent (and thus reliable) publicly available US Census (72 years must pass before a US census can become public); it contains information on the war that a veteran fought in; and it was conducted an appropriate number of years (11.5) after a major US war (WWI) for veterans of the war to have started families and to have children in their homes ("1930 Census", 2002).

previous veterans are considered to be the nearest veteran neighbours to each hero. They were typically separated from the heroes by roughly 50 lines in the census sheets, with the maximum distance being 227 lines. (Each line represents a single person.)

US population veterans

In addition to the 114 neighborhood matched veterans, I obtained a sample of 13637 US WWI veterans from the general population of the 1930 US Census. I obtained this large sample (1 out of every 250 WWI veterans in 1930) through the University of Minnesota's *Integrated Public Use Microdata Series* (IPUMS) database (Ruggles et al., 2004).

Measures

Two aspects of reproductive success were measured for all three groups of veterans: marital status at the time of the census, and, given marriage, the number of recorded children living in the same household. This operational definition of offspring had to be used because the 1930 census does not identify parents of children of unmarried couples or parents who are living away from their children's home. Heroes and other veterans were considered married if and only if they reported a living spouse at the time of the census.

Statistical methods

Four main statistical tests were performed to compare marriage and fertility between heroes and the two control groups of neighborhood matched veterans and WWI veterans from the general US population.

To compare the likelihood of marriage between heroes and neighborhood veterans, I performed a logistic regression on marriage as a binary response variable with WWI Medal of Honor status as a predictor. The heroes and neighborhood veterans were treated as independent groups (n_{heroes}=57, $n_{neighbors}$=114) since heroes' marital status did not correlate with either set of matched veterans (φ_{prev}=-0.04, p=.769; φ_{next}=-0.07, p=.625).

To compare the number of children of married heroes and married neighborhood veterans, I performed a matched pairs t-test, since marital fertility was found to be correlated within neighborhoods (r=.41, p=.02). Each hero's fertility score was paired with the average score of the next and previous neighborhood matched veteran. Only those cases where all three in a set were married were used (n=36).

In comparisons with the neighborhood veterans described above, no control factors were used because it is assumed that geographic proximity naturally controls for such factors as socioeconomic status, rural/urban status, and regional differences. While heroes were older on average than neighborhood veterans, preliminary analyses did not show age to be strongly associated with marriage or fertility within this narrow population. In contrast, in comparisons with the US population veterans, I used multiple control factors to isolate heroism as a predictor , which the large sample size afforded. These control factors are listed in Table 1.

Table 1: Control factors used in analyses of heroes and US population veterans.

Variable	Possible values	Notes
Age	Number in years	
Duncan Socioeconomic Index	0 to 100	Popular socioeconomic index based on stated profession; See Blau & Duncan, 1967
Race	white=1, non-white=0	Coded by census takers
Employed	yes=1, no=0	Employment status on the previous regular working day
Region	Northeast, Midwest, South, West	Divides the US into four regions; coded as three dummy variables
Living on a farm	yes=1, no=0	Reported by respondents
Owns home*	yes=1, no=0	Head and owner of household
Rents home*	yes=1, no=0	Head of household but paying rent
		*Persons neither owning nor renting were listed as dependents of others, typically family

The factors in Table 1 were selected from a larger set of demographic variables recorded in the census. They were included in the final models because they robustly predicted marriage likelihood and fertility in preliminary analyses.

To compare the likelihood of marriage between heroes and US population veterans, I performed a multiple logistic regression on marriage as a binary response variable with WWI Medal of Honor status as the predictor of interest and the previously listed factors as additional predictors.

To compare the fertility of married heroes and married veterans from the US population, I performed a multiple linear regression on number of children with WWI Medal of Honor status as the predictor of interest and, again, the previously listed factors as additional predictors.

To pinpoint the potential effect of the Medal of Honor, I compared the odds of marriage over time in heroes and neighborhood veterans, using a survival function with the interaction of hero status and post-war period as the predictor of interest. (Post-war period was defined as April 1919 to April 1930.)

Finally, to test whether aggressiveness was confounded with heroism, I compared heroes who received their Medal of Honor through violent versus non-violent actions, using t-tests on marriage and marital fertility.

All statistical analyses were done with the aid of the computer software SPSS version 13.0.

Results

Table 2: Mean values of measured variables for the three groups of veterans

	WWI Medal of Honor recipients	Neighborhood veterans	Veterans from US population
Sample size	57	114	13637
Married	.93	.81	.78
Children	1.44	0.89	1.19
Age	39.7	36.8	36.1
Duncan SEI	49	45	35
Race	.98	1.00	.92
Employed	.95	.95	.90
Living on a farm	.05	.03	.13
Owns home	.40	.26	.41
Rents home	.47	.52	.54

Medal of Honor recipients and neighborhood veterans

In the logistic regression on marriage, heroes had 3.17 times greater odds of being married ($p=.043$). Controlling for age did not change the significance of this result.

In the matched pairs t-test on fertility, married heroes' mean number of children was significantly higher than the mean of matched veterans ($t_{35}=2.381$; $p=.023$). Controlling for age with age difference as a covariate in a repeated measures design did not change the significance of this result.

Medal of Honor recipients and US population veterans

In the multiple logistic regression on marriage, being a hero was associated with 3.75 times greater odds of being married ($p=.013$), independent of control factors. All control factors were significant at a p-value criterion of .01, except for race and age. The complete list of parameter estimates is shown in Table 3.

Table 3: Logistic regression on marriage

Variable	Exp(B)	S.E.(B)
Medal of Honor	3.745*	.529
Age	1.003	.004
Duncan SEI	1.009**	.001
Race	1.166	.083
Employed	2.055**	.065
Region	(overall) **	-
Living on a farm	.838**	.066
Owns home	2.589**	.086
Rents home	4.424**	.085
R2 = .087	* p<.05, ** p<.01	

In the multiple linear regression on fertility within marriages, being a hero was associated with 0.131 more children, independent of control factors, though the relationship was not statistically significant (p=.495). All control factors except age were significant at a p-value criterion of .01. The complete list of parameter estimates is printed in Table 4.

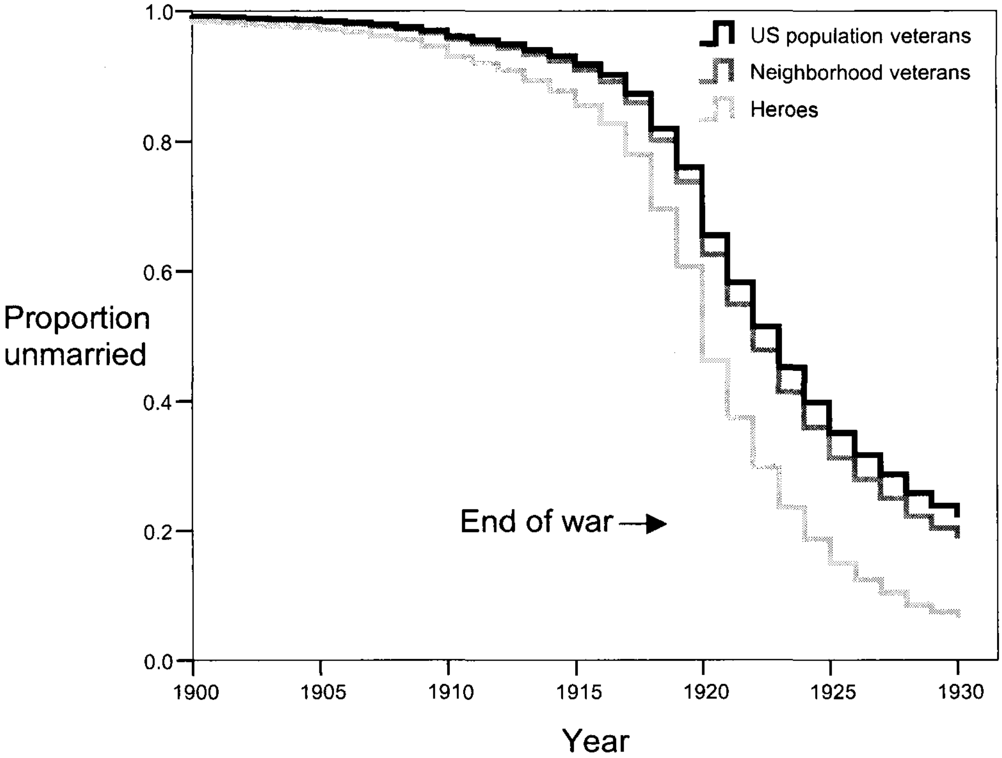
Table 4: Linear regression on fertility within marriages

Variable	Mean in married heroes N = 53	Mean in married veterans N = 10632	B parameter estimate	SE(B)
Number of children, given marriage	1.55	1.52	-	-
Medal of Honor	1.00	.00	.131	.193
Age	39.2	36.1	.004	.003
Duncan SEI	49	37	-.007 **	.001
Race	.98	.93	.556 **	.055
Employed	.94	.92	.137 **	.052
Region	-	-	** (overall effect)	-
Living on a farm	.06	.13	.642 **	.044
Owns home	.43	.39	1.035 **	.080
Rents home	.50	.57	.911 **	.079
$R^2 = .073$			* p<.05, ** p<.01	

The effect of the Medal of Honor

In the survival analysis of marriage with heroes and neighborhood veterans, being a hero was associated with 1.38 times greater odds of getting married over time, though not significantly (p=.36). Being a hero in the post-war period was associated with an additional 1.25 times greater odds of getting married, though again not significantly (p=.58). Marriages over time (Figure 12) suggest that heroes married more in most years, but particularly in the years 1919 and 1920 immediately following the end of the war in 1918.

Figure 12: Marriages over time



In the survival analysis of marriage with heroes and US population veterans (see Figure 12), being a hero was associated with 1.40 times greater odds of getting married over time, although this was not significant (p=.177). Being a hero in the post-war period was associated with an additional 1.42 times greater odds of getting married, though again not significantly (p=.25). These results were obtained controlling for the same list of factors as in the previous regressions with the US population veterans, plus the interaction of age and post-war period.

Aggressiveness and reproductive success in heroes

Among the WWI Medal of Honor recipients, 23 of 57 awards were for non-aggressive actions in which the hero did not personally kill any enemy soldiers. (Most of these actions were either medical or reconnaissance missions.) By 1930, 91% of non-aggressive heroes were married and 94% of aggressive heroes were married. Married non-aggressive heroes had a mean of 1.67 children and married aggressive heroes had a mean of 1.47 children. In t-tests between the two groups, there were no significant group differences in marriage likelihood (t_{55}=-0.67, p=.51) or number of children in marriages (t_{51}=-0.37, p=.72).

Discussion

Compared to neighborhood veterans, heroes were more likely to be married and had more children if married. Compared to veterans from the general US population, heroes were more likely to be married, but they did not have significantly more children if married. After the war, heroes were additionally more likely to marry than neighborhood veterans, but not significantly so. Among heroes, those whose heroism entailed violent action did not show any significant differences in reproductive success from those whose heroism did not.

Why the inconsistent result on fertility?

The disparity in the association of heroism with fertility across the two comparison groups has two possible explanations. First, the method I employed to count the offspring of the heroes and their neighborhood controls may underestimate fertility relative to the method employed for the IPUMS database, although I attempted to follow the same method. Second, assuming that the heroes' neighborhoods are in fact lower in fertility, the multiple regression model used with the US population veterans may not have adequately controlled for whatever neighborhood factors are responsible for the difference in fertility. Only about 7 percent of the total variation in fertility was explained by the model. Heroes' neighborhoods as a whole could differ consistently on some factor that is correlated with lower fertility but that was not captured by the included factors such as socioeconomic status or region. Indeed, the fact that the estimated strength of association between heroism and fertility in the multiple regression model was higher than the mean difference between married heroes and married US population veterans (.13 vs .03) shows that other factors associated with being a hero were also associated with lower fertility (most notably "living on a farm"). Despite the lack of statistical confidence in this association, it should be remembered that the results from all other tests support the general conclusion that WWI Medal of Honor recipients had higher reproductive success than other WWI veterans.

What is the reproductive advantage to heroes?

The measures of reproductive success used here may underestimate the true difference between heroes and ordinary veterans because two major sources of reproductive success were not counted. First, extra-marital offspring were not counted, nor were offspring from previous marriages. High status is known to have a positive association with extra-pair copulations in human males (Kaplan & Hill, 1985; E. Smith, 2004) and with the likelihood of remarriage (Elman & London, 2001; Wolf & MacDonald, 1979). Medal of Honor recipients may have had more children out of wedlock and more children in other marriages than other veterans. Second, reproductive success after 1930 was not counted. Heroes and other veterans, being roughly 37.5 years old in 1930, presumably had some years left in their reproductive careers, and whatever advantage heroes had should have increased over time.

Of course, since heroes survived the war at lower rates than other veterans, the numbers presented thus far overestimate the *expected* reproductive success of heroes. We may wonder: What would the expected future number of offspring be for a young male who is destined to fight in WWI and receive a Medal of Honor? We can estimate this with the following formula.

$$\text{Expected reproductive success} = \text{survivorship} * \text{marriage} * \text{fertility}$$

Survivorship in the war for heroes can be taken from the proportion of non-posthumous Medal of Honor recipients (87/120 = 0.73), and survivorship for non-heroic veterans can be taken from official US military records of casualties in WWI (Bird, 2000). Calculations for the three groups of veterans are presented in Table 5.

Table 5: Calculations of expected reproductive success for the three groups of veterans

	Heroes	Neighborhood veterans	US population veterans
Survival through the war	0.73	0.97	0.97
Likelihood of marriage	0.93	0.81	0.78
Fertility in marriage	1.55	1.09	1.52
Expected reproductive success	1.05	0.86	1.15

Based on these calculations, we should expect the average hero to have 0.19 more children per generation than a neighborhood veteran, and 0.10 fewer children per generation than a veteran from the general US population.

Note that this method of estimating expected lifetime reproductive success makes many simplifying assumptions: 1) survival is based only on the war and excludes any deaths before or after; 2) survival in the war is assumed to be random with respect to future reproduction; 3) heroes and other veterans that died in the war are assumed to have zero offspring; 4) lifetime fertility is based only on the product of marriages existing in 1930, as detailed above.

How is heroism related to reproductive success?

How heroism may affect reproductive success is difficult to ascertain with the data used in the present study. My one effort to identify a specific effect of the Medal of Honor, the survival analysis of marriages over time, was inconclusive. Although the two estimates of the interaction between heroism and post-war marriage indicates that heroes were *additionally* more likely to marry after the war than other veterans, the estimates were not statistically significant. According to power analysis, the sample of heroes would need to be more than three times larger for an interaction effect of the sizes observed to be detected. Therefore, more data or more powerful statistical techniques are needed. One possibility is to focus on the first few years following the war, when any effect of the Medal of Honor is assumed to be strongest. In 1919, 12% of all heroes, 5% of neighborhood veterans and 6% of US population veterans got married, and in 1920, 16% of all heroes, 11% of neighborhood veterans and 11% of US population veterans got married.

Apart from the Medal of Honor, the greater likelihood of marriage and higher fertility of the WWI heroes could be because of various personal traits that may have been expressed even before the heroes' actions in the war. Many traits are commonly associated with heroism. Heroes may be more risk-loving, impulsive, prosocial, vigorous or wealthy; heroes may be perceived by others as more attractive, prestigious, powerful or trustworthy. These traits could influence the reproductive behavior of heroes or of potential mates, as suggested by the attractiveness research of Farthing (2005). Mueller and Mazur (1996) found that West Point cadets who scored highly on facial dominance achieved higher military rank and higher fitness later in life.

Some readers may be skeptical that desirable personal characteristics would be correlated with an increase in fertility in a modern population (58% of the US was urbanized in 1930 ("Urban/rural status", 2006)), since preferred family sizes have declined sharply with the demographic transition. However, in support of an enduring correlation, Hopcroft (2006) found that present day high-status men in the US have more genetic offspring than low-status men.

Although heroism is commonly associated with attractiveness, the extremely violent nature of the actions of some of the heroes in the present study raises the question of whether aggressiveness may be responsible for any reproductive advantage. Psychopathy has been linked to higher mating effort in men (Barr & Quinsey, 2004). However, in the present sample of heroes, aggressive individuals did not have significantly different reproductive success from non-aggressive individuals, suggesting that heroism is not confounded with aggression.

Future studies

The association between heroism and reproductive success suggested here could be clarified by more studies of historical samples of heroes.

To determine whether heroism is associated with reproductive success in proportion to the degree of heroism, researchers could investigate the lives of recipients of the Distinguished Service Cross, the second highest US military award for bravery after the Medal of Honor. Having a slightly lower standard, it was awarded to 6185 soldiers in WWI ("Distinguished Service Cross (United States)", 2006). If the Distinguished Service Cross recipients show higher reproductive success than ordinary veterans, but lower reproductive success than Medal of Honor recipients, that would be evidence in support of a graded association of heroism with reproductive success.

To determine whether the association of heroism with reproductive success is dependent on public recognition, researchers could make use of an interesting group difference in World War II Medal of Honor recipients. Roughly 30 African-American and Asian-American recipients were awarded their medals after a delay of several decades because of racial discrimination in the military. This delay might allow researchers to separate the public recognition of heroism from the trait of heroism as a whole.

An important and unexplored aspect of heroism is its possible association with the reproductive success of kin. Fisher (1958) pointed to the inclusive fitness benefits of heroism as the principal way it could be supported in a population. With electronic family trees becoming more and more complete, it should soon be possible to measure the reproductive success of the brothers and sisters of the WWI Medal of Honor recipients or a similar group of heroes.

Finally, to generalize the basic findings reported here, many more studies of the same type could be conducted with other publicly available lists of heroes. The Victoria Cross, the highest military award for bravery in the British Commonwealth, has been awarded a similar number of times over history as the Medal of Honor ("Victoria Cross", 2006). Fighter aces, starting in WWI, have had their names and number of kills recorded for posterity ("Flying ace", 2006).

Concluding remarks

Evolutionists at least as far back as R.A. Fisher have supposed that even the most noble, self-sacrificing deeds may be consistent with a Darwinian view of human behavior because of the prestige granted to the individuals who accomplish such deeds. Here, I have presented direct evidence that surviving war heroes are more likely to be married and have more children than otherwise similar veterans. If this pattern has persisted over time and across cultures, the human people may have been shaped by a preponderance of heroic ancestors. The evolutionary puzzle of one-sided non-kin altruism may be partly explained by an evolved psychology for heroism.

Chapter 6:
General discussion

Background

An evolutionary account of altruism is an important undertaking. The highly cooperative character of *Homo sapiens* appears to stand in opposition to the selfish process of natural selection. This puzzle has earned itself a place in the top 25 most important scientific questions, according to Science Magazine (Pennisi, 2005).

Altruism as a signal of other qualities holds the promise of explaining many of the cases of altruism that are difficult to explain with the theories of reciprocity and inclusive fitness. However, altruism can convey different messages depending on the context, and its value as a signal depends on its proper decoding by receivers. To be sure, the contexts in human life where altruism functions most strongly as a signal are a product of learned cultural traditions, which makes it difficult to elicit altruism as a signal in the laboratory.

Research

Nevertheless, I set out to substantiate altruism as a signal of status. In the laboratory, I conducted two major experiments. The first was designed to elicit altruism as a signal of status directly by pairing a cooperative game with a competitive game. In effect, the idea was to simulate the cultural conditions of the Meriam described by Smith and Bird (2000). Participants could maximize their personal profits by recognizing the inherent status differences within the group. Critically, these status differences could only be revealed by strategic donations. Despite this positive incentive to donate, high status group members did not donate significantly more than in the control condition where they could not reveal their status. This failure to find evidence of signalling can be attributed to the fact that low status group members did not respect high donations when they did occur, eliminating the expected advantage to signalling.

In my second experiment, I focused on the War of Attrition game. It is a well understood game from evolutionary biology that has not yet been used much with human participants. Unless human participants can learn to respect status differences in the War of Attrition, it would be difficult to test altruism as a signal of status. Thus, I manipulated participants' status with an ownership framing that did not materially change players' positions, but was meant to influence their perceptions of the value of the prize. I found some evidence of a weak effect of ownership across three levels of the framing manipulation, but not in the predicted direction. The reasons for the differences, if any, are still unclear. Participants might have reacted to the somewhat arbitrary assignment of status with indignation and increased competitiveness rather than reduced competitiveness. Furthermore, the general distribution of bids in the War of Attrition revealed some anomalies that demand more explanation.

In an attempt to partially explain these findings, Wagner and I mathematically analyzed the War of Attrition with an upper limit on potential escalation, as it had been implemented in my experiments. I found that with the upper limit the original evolutionarily stable strategy of a smoothly decreasing distribution did not hold. In its place, no stable mixed stage could be found, using either integration over the restricted domain, or by analyzing the game with eleven discrete cost intervals. This result should encourage more ambitious mathematicians to analyze the War of Attrition with an upper limit and it should also inform experimentalists who wish to run a War of Attrition in a laboratory.

Outside of the lab, I investigated the lives of a group of World War I war heroes who had distinguished themselves with acts of extreme bravery in combat. Interpreting this as an example of altruism as a costly signal, I hypothesized that the war heroes should have higher reproductive success than a comparable group of soldiers. Indeed, 11.5 years after the war in 1930, the heroes were more likely to be married and have more offspring within marriage than other WWI veterans from the same neighbourhoods. In addition, they were more likely to be married than WWI veterans from the general US population in 1930, but did not have any more children within marriage. When the higher mortality of the war heroes was taken into account, they still had higher reproductive success than veterans from the same neighbourhood, although they had less than veterans from the US population. Statistical tests could not decide whether the heroes gained their reproductive advantage because of the prestige they received after the war, but the raw data suggest an advantage that existed before the war and grew greater after it. The results from this study should greatly encourage researchers to correlate actual heroic behaviour with life history variables to gain a greater understanding of the evolution of altruism.

Final remarks

Altruism as a signal of status is an idea that needs more work. Despite telling historical anecdotes such as the potlatches of the Kwakiutl, the idea must be demonstrated clearly for it to be taken seriously by social scientists and evolutionary biologists. Mathematical models show that altruism as a signal can evolve under certain conditions but researchers are only beginning to test these models. Scientists and laymen alike accept that reputation is a powerful motivating force in human social interactions. Altruism, because of its ability to attract attention and its costliness, should be a strong and reliable social signal. If this reasoning is correct, natural selection should have made our minds sensitive to altruism and its implications.

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Appendix 1

Instruction screenshots for "Demonstrating altruism as a signal of status". Ordered left to right, top to bottom.

Welcome! You are participating in an experiment that measures certain types of decision making in a social context. The experiment itself consists of two basic "games." In the first game, you will have the choice of giving or not giving to a common group fund. In the second game, you will be matched-up with each group member and you will have the choice of bidding against each of them for a prize. The two games together constitute what will be called a "trial." You are expected to complete 5 trials before leaving the experiment.

The procedure for a single trial will be explained in full detail in the text that follows. Please read carefully, as it is important that you understand the choices you are about to make. At the end of these instructions you will be asked a few questions to test your knowledge before you can proceed to the experiment itself. If at any time you have a question of your own, please do not hesitate to ask.

At the beginning of each trial, you will be randomly assigned a pseudonym or "screen name" for your interactions with the other participants of your group. This screen name will stay with you for the trial and then you will get a new name for the next trial.

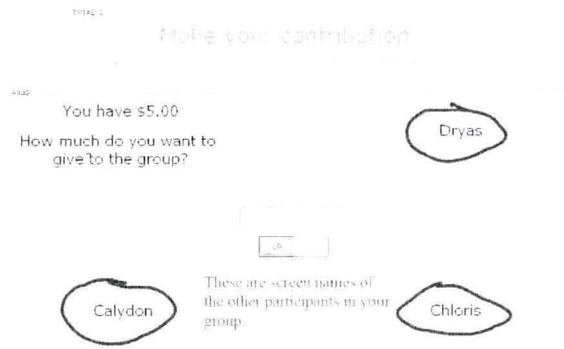
Along with your screen name, you will be randomly assigned a starting amount of money. Your starting amount is the amount of money that you will have available to you at each decision point in the two games.

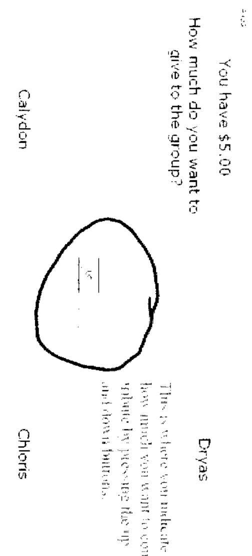
Not all members of the group will have the same starting amounts. Three members of the group will each have $5 as their starting amount of money and one member will have $7 as their starting amount.

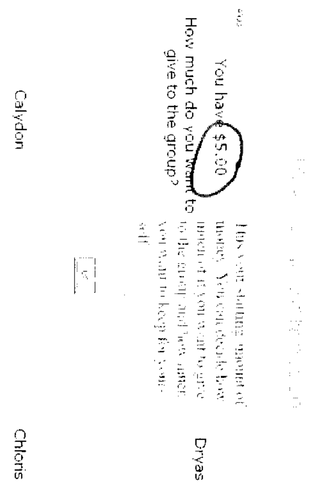
In the first game, you decide how much of your starting amount to give to a group fund. Whatever amount you give to the group fund will be multiplied by a factor of 1.6, then divided equally among all members of the group. So, if you decide to give $5 to the group fund, your $5 contribution will be multiplied to make $8, and each group member, including yourself, will receive $2.

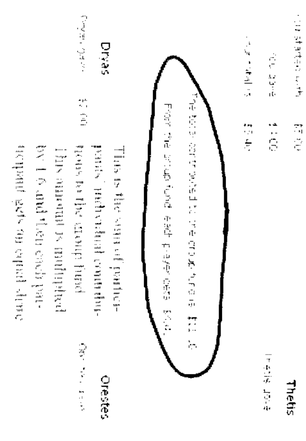
The same formula applies to contributions from all other group members. So, if group members contribute a total of $20, then each participant will get $8 as a result. On the other hand, if group members contribute nothing, each participant will end the game with only their starting amounts.

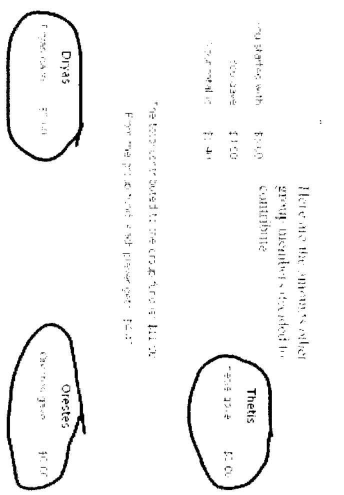
The following screenshots show how you can make a contribution and the feedback you will receive after all group members have made their decisions. Please note that the screenshots are static copies of screens from an actual trial. When you have finished looking at a screenshot, click on the continue button to advance to the next screen.




You have $5.00
How much do you want to give to the group?
Calydon
Dryas
Chloris


You have $5.00
How much do you want to give to the group?
Calydon
Dryas
Chloris

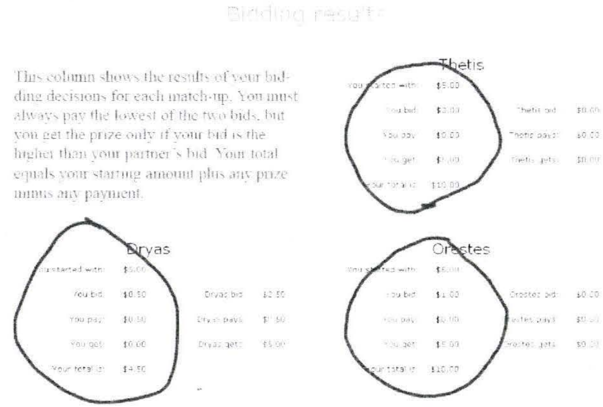

Dryas
Thetis
Orestes

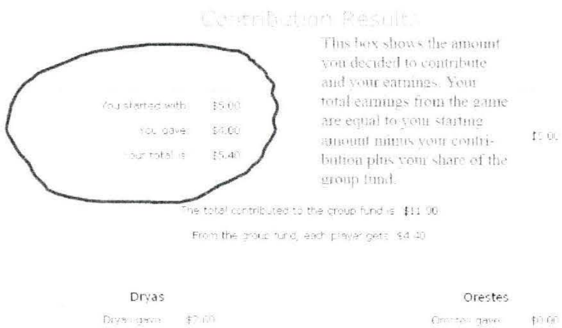

Dryas
Thetis
Orestes

In the second game, you will be matched-up with each of the group members in two-person bidding contests. In each match-up, both participants will have the chance to bid for a $5 prize. Both participants must pay the lowest of the two bids, but only the participant who made the highest bid will get the $5 prize.

So, if participant A bids $6 and participant B bids $4, then both participants will pay $4, and participant A will get the $5 prize. If both participants bid the same amount, the $5 prize will be split in half, with $2.50 going to each participant.

The following screenshots show how you can make your bids and the feedback you will receive after all group members have decided on their bids.

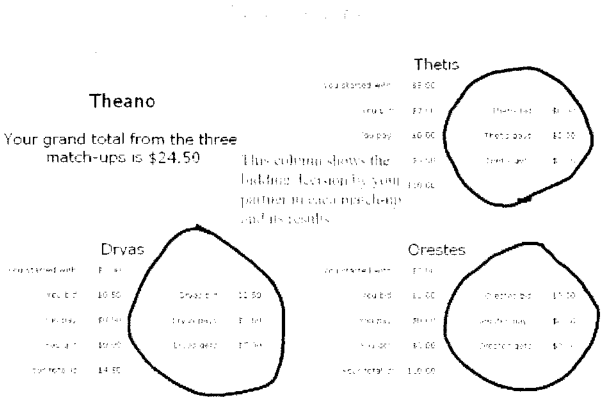




After the second game is complete, a combined total for the current trial will be calculated from the total amounts you earned in the first and second games.

After all five trials of the experiment, one trial out of the five will be selected at random and your combined total for that trial will be converted into real dollars for you to keep, at a rate of 1 Canadian dollar for every 3 lab dollars earned. So, if you earned $27 in the selected trial, you will walk away with $9 in real money.

The instructions are now complete. Now you will be asked a few questions to make sure that you fully understand the experiment and the choices you are about to make.



Post experiment questionnaire and results. All questions were answered with 5-point Likert scales, anchored "strongly disagree" to "strongly agree" unless otherwise specified.

- How much people understood of the experiment
    - I understood how the experiment worked after reading the instructions.
    - I understood how the experiment worked after going through the first trial.
- The contribution game
    - I felt generally more: cooperative ... competitive
    - How did you feel towards group members who contributed a small amount? Angry ... grateful
    - How did you feel towards group members who contributed a small amount? Inferior ... superior
    - How did you feel towards group members who contributed a large amount? Angry ... grateful
    - How did you feel towards group members who contributed a large amount? Inferior ... superior
    - I felt other group members should have contributed as much as me.
- The bidding game
    - I felt generally more: cooperative ... competitive
    - I was influenced by other group members' actions in the contribution game
    - I changed my bidding based on my own actions in the contribution game
    - I bid higher against group members who had contributed a small amount in the contribution game in order to "teach them a lesson"
    - I bid higher against group members who had contributed a small amount in the contribution game because I expected them to bid low as well
- General feedback
    - I enjoyed participating in this experiment.
    - I would do another experiment again of this type.
    - What do you think this experiment was about?

Appendix 2

Instructions for "War of Attrition with ownership framing".

Manipulated sections of text are indicated for the [*framed*] condition and <*earned*> condition.

Welcome! You are participating in an experiment that measures certain types of decision making in a social context. The experiment consists of a simple **two-person game** that you will play repeatedly in rounds. For **each round**, you will be **randomly paired** with another person in your group. You will not know the true identity of your partner in any single round, and, likewise, your partner will not know your identity.

BASIC RULES

In this game, you and the other player have **the chance to earn money**. <To start, you and the other player will do a **reaction time test**, after which **one player** will be awarded a **prize** equal to a certain amount of money.> Each of you will get an equal amount of money at the beginning of each round. [In addition, **one player** will be randomly awarded a **prize** equal to a certain amount of money.]

You can choose to keep this starting money or to spend it on winning a [<the>] prize. You can spend any amount, from zero to your starting amount. In each round, you must decide how much you are **willing to spend**. [<In a round of the game, **if you own the prize**, you must decide **how much** of your starting money **you are willing to spend to keep it. If you do not own the prize**, you must decide **how much** of your starting money **you are willing to spend to take the prize** from the other player.>]

Whoever is willing to spend the **highest amount gets the prize**. The losing player must **pay the amount he or she entered**. The winning player must only **pay 1 cent more** than the losing player. This means that you will not always have to pay what you are willing to spend. The amount that you have to pay will always depend on the actions of the other player.

At the end of a round, whatever money you have remaining will be added to whatever prize money you earned and that total will be recorded as your total payoff for that round.

For example, suppose that:

> The prize is $5
> You start with $10
> The other player starts with $10
> You decide to spend up to $4
> The other player decides to spend up to $3

The result of this example would be that:

> You get the prize of $5 because you were willing to spend more than the other player
> You have to spend $3.01
> Your money remaining is $6.99
> Your total payoff is $11.99
>
> The other player spends $3
> The other player's money remaining is $7
> The other player's total payoff is $7

In the case that you and the other player **both** spend the **same** amount of money, **the prize money will be split equally**.

For example, suppose that:

The prize is $5
You start with $10
The other player starts with $10
You decide to spend up to $10
The other player decides to spend up to $10

The result of this example would be that:

You get half of the prize of $5 because you were willing to spend the same amount as the other player
You have to spend $10
Your money remaining is $0
Your total payoff is $2.50

The other player gets half the prize of $5
The other player spends $10
The other player's money remaining is $0
The other player's total payoff is $2.50

THE COMPUTER INTERFACE

All of the information relevant to the game will be displayed on screen. **You are not allowed to discuss the game with the other people in the room** while the experiment is in progress. If you have a question, please ask the experimenter.

Please **do not attempt to quit the computer program** that runs the game or try to access other programs while the program is running. If you are having trouble with your computer, please call over the experimenter who will assist you.

BEFORE THE GAME

Before the game starts, you will be asked to complete a set of **practice questions** to ensure that you know the rules. You won't be allowed to proceed until you have answered all of the practice questions correctly. If you are having trouble answering one of the questions, please call over the experimenter who will explain the answer.

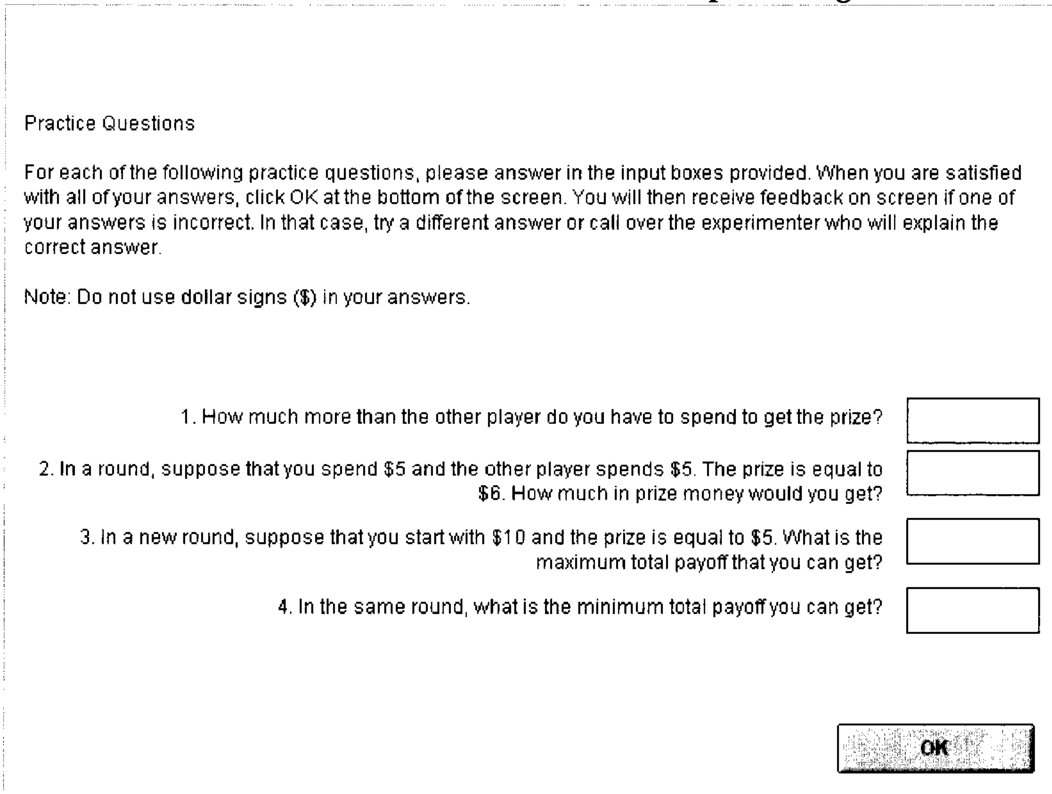
After successfully completing the practice questions, you will go through a single **practice round** that will allow you to familiarize yourself with the computer interface without having to play for real money. The beginning of the real game will be indicated on screen.

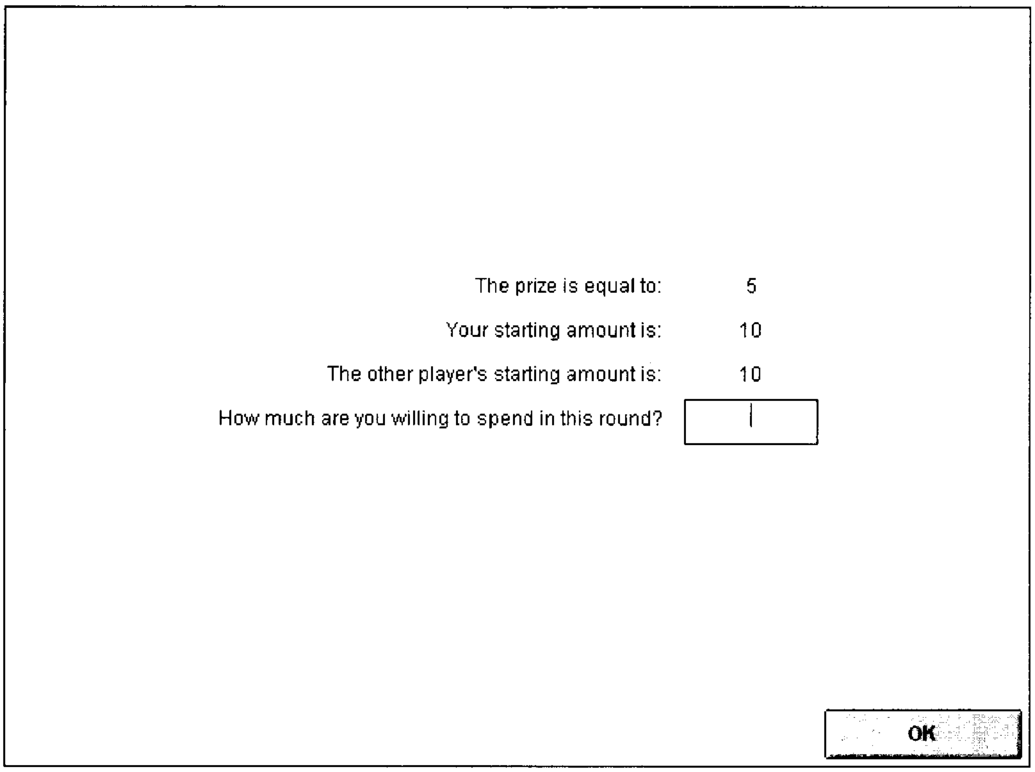
AFTER THE GAME

When you have finished all of the rounds of the game, you will be given a brief **questionnaire**. The questionnaire is a list of questions that will ask you your impressions of the experiment and some demographic information.

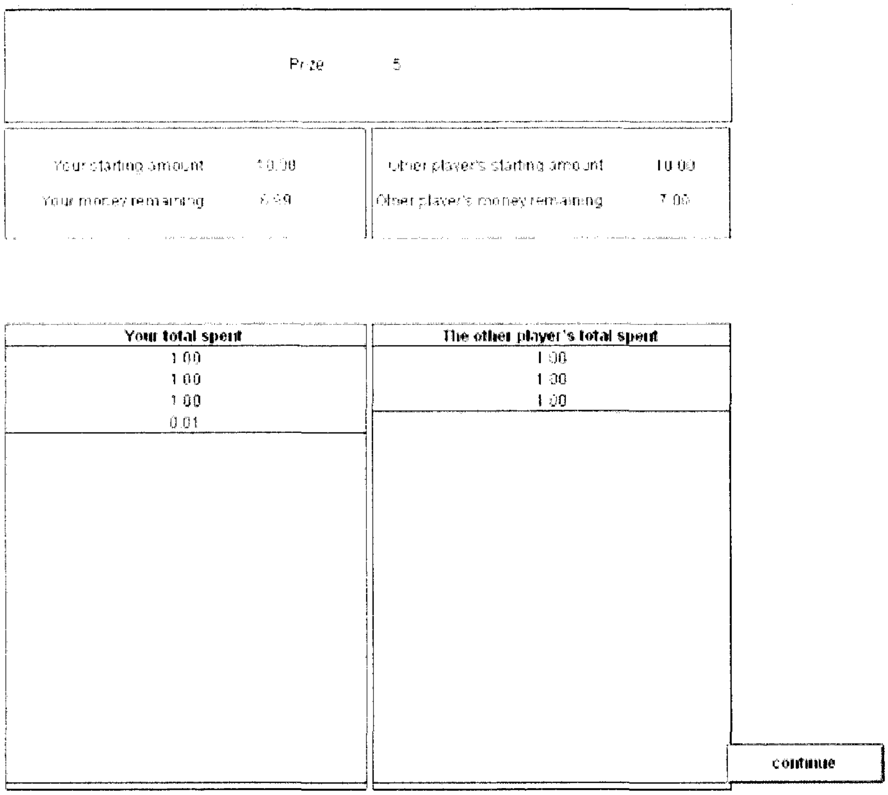
After the questionnaire, you will be called out of the room individually to receive your payment. **Your payment will be equal to your average total payoff over all rounds of the game**. Once you have your cash, you can walk out the door!

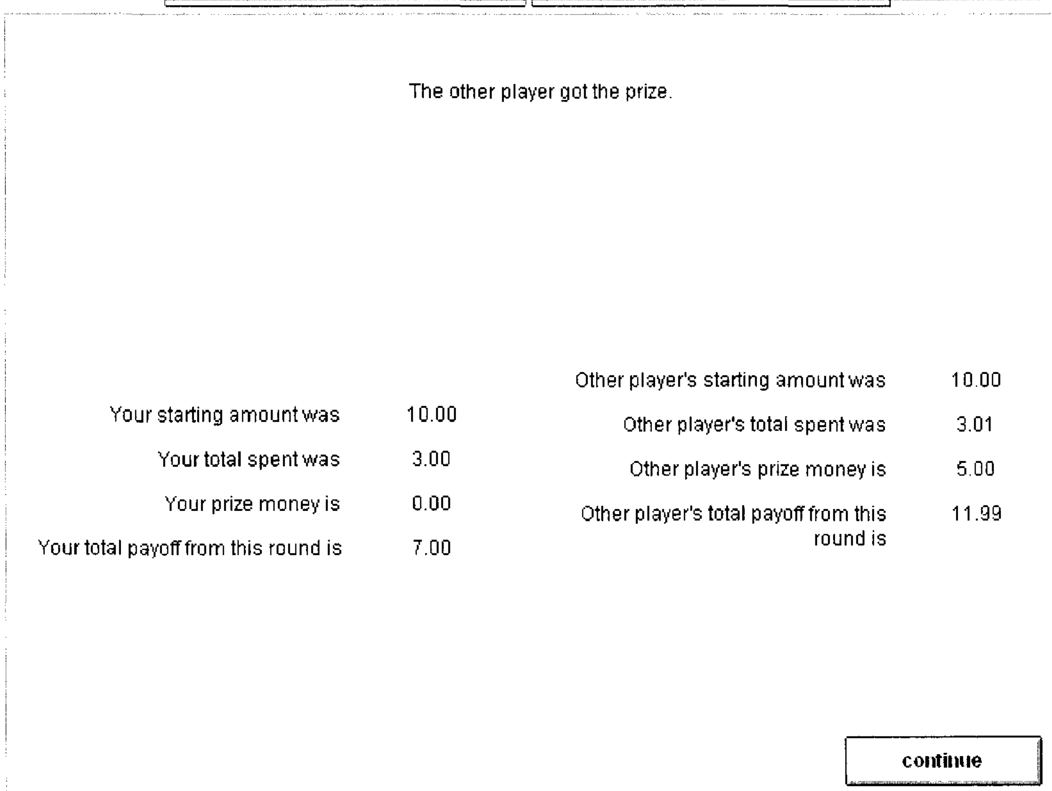
Screenshots for "War of Attrition with ownership framing"





8


Prize 5
Your starting amount 10.00
Your money remaining 6.99
Other player's starting amount 10.00
Other player's money remaining 7.00
Your total spent
1.00
1.00
1.00
0.01
The other player's total spent
1.00
1.00
1.00
continue


The other player got the prize.
Your starting amount was 10.00
Your total spent was 3.00
Your prize money is 0.00
Your total payoff from this round is 7.00
Other player's starting amount was 10.00
Other player's total spent was 3.01
Other player's prize money is 5.00
Other player's total payoff from this round is 11.99
continue

Post experiment questionnaire and results. All questions, except the last three, were answered with a 5 point Likert scale ranging from strongly disagree to strongly agree.

description	min	ave	max	sdev	n
I understood how the experiment worked after reading the instructions.	1	3.54	5	1.03	50
How many people do you know that have participated in this experiment?	0	1.06	6	1.56	50
I would have played differently if the game wasn't played for money.	1	2.87	5	1.24	52
I would have played differently if the game was played for more money (e.g., all quantities were multiplied by 10).	1	3.23	5	1.34	52
The money made me take the game more seriously.	1	3.63	5	1.09	52
The money made me take the game less seriously.	1	1.90	3	0.69	52
During the game, I believed I would get my money at the end of the experiment in accordance with the rules in the instructions.	1	3.90	5	0.98	52
I would do another experiment of this type.	3	4.31	5	0.67	52
I understood how the experiment worked after going through the first round.	1	3.86	5	1.06	51
My play improved over the rounds of the game.	1	3.98	5	0.96	50
I thought I was playing against a computer programmed strategy.	2	3.33	5	1.15	12
I thought I was playing against the other people in the room.	1	3.17	4	0.94	12
I thought I was playing against people at another place.	1	2.33	4	0.98	12
I felt the game was competitive.	1	3.50	5	1.08	52
I felt the game was cooperative.	1	2.71	5	0.96	52
In playing the game, I tried to win the prize.	1	3.90	5	1.32	52
In playing the game, I tried to maximize my average payoff.	3	4.13	5	0.99	8
In making my decisions, I tried to think about what had worked for me in previous rounds.	1	4.42	5	0.89	52
In making my decisions, I tried to think about what the other player would do.	1	4.13	5	0.95	52
When the other player spent a small amount, I felt friendly towards the other player.	1	3.21	5	1.05	52
When the other player spent a small amount, I felt hostile towards the other player.	1	2.13	4	0.93	52
When the other player spent a large amount, I felt friendly towards the other player.	1	2.39	4	0.92	51
When the other player spent a large amount, I felt hostile towards the other player.	1	3.17	5	1.15	52
I tried to punish the other player by spending more.	1	2.80	5	1.31	51
I tried to be nice to the other player by spending less.	1	2.10	5	1.05	52

I felt I could trust the other player not to escalate.	1	2.21	5	1.11	52
I tried to tie with the other player.	1	2.08	5	1.13	52
I followed a strategy in my decisions.	1	3.96	5	1.10	52
I chose randomly in my decisions.	1	1.88	4	0.86	52
This game reminded me of other games I have played.	1	2.79	5	1.07	52
I feel like I earned the money I got in the rounds of the game.	1	3.39	5	0.98	51
I think I know the best way to play this game.	1	3.19	5	1.21	52
I realized that if I spent $0 every time, I would at least get an average total payoff of $10.	1	3.40	5	1.43	48
For how many years have you spoken English?	2	14.75	28	6.01	51
Are you male or female? (0=female, 1=male)	0	0.46	1	0.50	52
How old are you?	16	19.29	30	3.00	52