Strength determines coalitional strategies in humans

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Coalitions enhance survival and reproductive success in many social species, yet they generate contradictory impulses. Whereas a coalition increases the probability of successfully obtaining rewards for its members, it typically requires a division of rewards among members, thereby diminishing individual benefits. Non-human primate data indicate that coalition formation is more likely when an individual's probability of success is low when competing alone. No comparable studies exist for humans. Here we show using a computerized competitive game that humans exhibit a systematic, intuitive strategy for coalition formation based on their own and others' levels of perceived strength, a pattern that resembles coalition formation in chimpanzees, \textit{Pan troglodytes}. Despite equal expected pay-offs for all strategies, subjects were more likely to form coalitions as their own level of perceived strength waned. Those chosen as coalition partners tended to be stronger individuals or arbitrarily designated ‘friends’. Results suggest a heuristic for human coalitionary decisions that rests on the perception of relative power rather than on the assessment of pay-offs.

**Keywords:** coalitional strategies; perceived strength; friendship; cooperation

\section{1. Introduction}
Much research in behavioural economics focuses on games in which humans tend not to maximize personal pay-offs, thereby defying rational expectations (Kahneman & Tversky 1979; Camerer & Fehr 2006). Studies of this phenomenon in cooperative games have focused on explaining the occurrence of altruism, because individuals often pay a cost to reward cooperative behaviour or impose sanctions on selfish behaviour (Fehr & Fischbacher 2003). Explanations for such behaviour or impose sanctions on selfish behaviour (Fehr & Fischbacher 2003). Explanations for such bounded rationality range from cultural group selection, where the strategies of a few influence those of a majority (Fehr & Fischbacher 2003), to natural selection for ‘fast and frugal’ heuristics that outperform other strategies in the long term (Trivers 2006; Gigerenzer 2008). Here we extend the study of cooperative behaviour to coalition formation among non-kin. We test the hypothesis that humans exhibit heuristic strategies for deciding when to form coalitions, and for choosing coalition partners. Coalitions previously have been studied with respect to the bargaining strategies between assigned coalition partners (Kalisch \textit{et al.} 1954; Rapoport & Kahan 1976; Zwick & Rapoport 1985). Our study uses a simple economic game, in which all strategies produce equal pay-offs, to ask under what conditions humans tend to form coalitions, and whether they show preferences for particular types of partners. Our main hypothesis, based on the studies of chimpanzee coalitions by Watts (1998), is that the probability of forming a coalition is inversely related to the level of personal strength, defined as the probability of success when competing alone.

Based on the studies of competitive strategies in the closest genetic relatives of humans, we define a coalition as two or more individuals acting cooperatively to compete against a third party (Harcourt \& de Waal 1992). Whereas in many species a shared genetic interest promotes cooperation due to kin selection (Hamilton 1964), cooperation with non-kin is less common and subject to numerous potential influences. Mathematical models indicate that whether an individual joins a non-kin coalition depends on the level of personal strength, affinity between partners, awareness of conflicts, winner and loser effects, fighting costs and the synergy versus antergy of the coalition (Dugatkin 1998; Johnstone \& Dugatkin 2000; Mesterton-Gibbons \& Sherratt 2006; Gavrilets \textit{et al.} 2008). These models further predict thresholds at which individuals facultatively switch from an individual to a coalitional strategy (Mesterton-Gibbons \& Sherratt 2006; Gavrilets \textit{et al.} 2008).

In addition to the theoretical models, predictions about human coalition formation can be generated from naturalistic studies of conflict and cooperation in non-human primates. Empirical tests of these variables with primates are rare, but in a study of coalitionary mate guarding by wild chimpanzees (\textit{Pan troglodytes}), Watts (1998) showed a link between level of personal strength and coalition formation. The number of adult males in a group varied from 1 to more than 20. The highest ranking male present was often successful in monopolizing...
matings with oestrus females, but his probability of success fell as the number of competing males increased. Consistent with the models predicting a threshold effect for coalition formation (Mesterton-Gibbons & Sherratt 2006; Gavrilets et al. 2008), Watts (1998) showed that the highest ranking chimpanzees appeared to follow a decision rule for coalition formation: when their individual mating success declined below 50 per cent, they formed dyads (coalitions with one high-ranking partner) that successfully excluded all other males from mating; when it fell below 33 per cent, they formed triads (coalitions with two partners) that were again successful in excluding other males. Although the division of matings (‘rewards’) within a coalition was not completely equal, males were relatively tolerant of mating efforts by their coalition partners. These strategies enabled members of coalitions to increase their mating access relative to competitors (Watts 1998).

Other research with primates demonstrates that high-rank individuals tend to be the most attractive coalition partners, presumably because they maximize the combined strength of a coalition (Duffy et al. 2007). For example, when low-ranking animals intervene in conflicts, they tend to support the higher ranking of two contestants (Perry 1996; Chapais & St.-Pierre 1997; Silk et al. 2004). A partner’s level of strength therefore also influences coalition formation.

Furthermore, while coalitions with non-kin occur both opportunistically and with long-standing social partners, preferential coalitions with ‘friends’ occur in both male and female chimpanzees as well as other primates (de Waal 1982; Boesch & Boesch-Achermann 2000; Mitani 2006), such as vervets (Cercopithecus aethiops sabaeus) (Hunte & Horrocks 1987) and Japanese macaques (Macaca fuscata) (Chapais & St.-Pierre 1997). This influence of relationship quality can be owing to close associates having high mutual tolerance. In laboratory studies, chimpanzees chose to cooperate more often with social partners who were more likely to share their rewards from collaborating (Melis et al. 2006). Male chimpanzees also engage in inter-group boundary patrols and form intra-group coalitions more frequently with those with whom they groom and maintain close proximity (Watts & Mitani 2001). Thus preference to form coalitions with those of high rank and with friends occurs in both sexes and across a variety of species.

Given the importance of level of personal strength, partner’s level of strength and relationship quality to coalitions found in a number of species of monkeys and apes, we tested the hypothesis that these factors would affect coalition formation in humans. We also examined explicitly whether a threshold effect emerges for coalition formation following a rule similar to the one proposed by Watts (1998) for chimpanzees: after probabilities of individual gain dip below 50 per cent, switch to a coalition strategy and divide rewards with one partner. To this end, we designed a computerized game to examine under what conditions a subject chooses to form a coalition.

2. EXPERIMENT 1

(a) Method

Sixty-one male and sixty-three female subjects individually competed for money (maximum $5 per game) against two fictional same-sex opponents (labelled ‘friend’ or ‘non-friend’) in 28 rounds of a computerized game. On each round, the player competed against the two opponents for 100 points (for a total of 2800 points distributed among the player and two opponents over the entire game). Personal strength (probability of winning all 100 points in a round when competing alone) varied randomly between rounds from 20 to 80 per cent (in 10% increments). Over the whole game, every player experienced four instances of each level of personal strength. On every round, the sum of the player’s level of personal strength and the levels of strength of the two opponents (each opponent’s probability of winning all 100 points in the round) equaled 100 per cent, with the levels of the two opponents’ strengths unequally apportioned. In two of the rounds at each level of personal strength, the stronger opponent was labelled the friend, whereas on the other two the stronger opponent was the non-friend. Half of the subjects played under competitive instructions, such that the player earning the highest number of points won all the money. The other half played under non-competitive instructions in which all earned points were converted to money. The players were told how much they had won only after the game had ended.

On each round, the player was informed of his/her own level of personal strength and the levels of each of the two opponents’ strengths, and was given three choices: (i) compete alone, with level of personal strength indicating probability of winning the 100 points, (ii) form a coalition with either one of the two opponents, with levels of personal strength and opponents’ strength summed to generate their coalitional strength (combined probability of winning the 100 points on that round by competing together), and if the coalition won, divide the points proportionally according to personal strength versus opponents’ strength, or (iii) avoid competing (i.e. ally with both opponents) by dividing the 100 points on that round among the player and the two opponents according to the levels of strengths of each, thereby guaranteeing a pay-off for everyone. While summing the levels of strength of the players is not the only potential algorithm for generating coalitional strength, little empirical data exist regarding the precise advantage that accrues to a coalition relative to that of individuals, and theoretical models reach differing conclusions (Adams & Mesterton-Gibbons 2003; Mesterton-Gibbons & Sherratt 2006). Consequently, we chose a simple additive model.

Levels of personal strength were clearly demonstrated before the game began. Although each choice in a given round produced identical expected pay-offs, players were not told this explicitly. Instead, after describing the three choices a player confronted, we illustrated the expected pay-offs for each choice using a concrete example in which the player had a personal strength of 60 and one opponent’s strength was 30 and the other opponent’s strength equalled 10. In the illustration, the player therefore had a 60 per cent probability of winning the 100 points alone, and the two opponents had 30 and 10 per cent probabilities of winning the 100 points alone, respectively. If the player chose to play alone, the player would have a 60 per cent chance of winning 100 points. If the player formed a coalition with the opponent with the 30 per cent probability of winning,
their coalitional strength or combined probability of winning the 100 points increased to 90 per cent. Should they win the 100 points, the points would be divided proportionally according to their individual strengths or probabilities of winning (60 : 30), thereby yielding twice as many points for the player as for the coalition partner, in this case 67 : 33. Finally, if the player chose a guaranteed pay-off of points by allying with both opponents, then the player and the two opponents received the number of points that corresponded to their individual levels of strength or probabilities of winning alone, in this instance 60 points for the player with the two opponents receiving 30 and 10 points, respectively. Therefore, although unstated, the player’s expected pay-off equalled 60 for each choice (60% of winning 100 by playing alone; 90% of winning 100 with pay-offs divided 67 : 33 in a coalition; or 60 guaranteed points). To facilitate understanding and increase the ecological validity of the game, on each round, the player and two opponents were depicted by three identical same-sex cartoon faces with the words ‘Me’, ‘Friend’ and ‘Non-Friend’ displayed beneath one of each of the faces (with the friend and non-friend alternating directional positions on each round and the player’s face always centred), and the strengths or probabilities of winning indicated above the faces.

(b) Results
(i) The influence of level of personal strength (probability of winning alone)

We conducted an initial repeated-measures analysis of variance (ANOVA) on the percentage of choices to compete alone at each level of personal strength, with sex and instruction (competitive or non-competitive) as independent variables. An individual could choose to compete alone from 0 to 4 times per level of personal strength. A linear contrast analysis demonstrated that personal strength influenced the choice of competing alone with stronger players competing alone more frequently, \( F_{1,120} = 202.8, p < 0.0001 \) (figure 1).

Players who chose not to compete alone could either form a coalition and increase their probability of winning something, or accept a guaranteed pay-off of points that corresponded to their level of personal strength on that round. Again, an individual could choose to form a coalition or select a guaranteed pay-off from zero to four times per the level of personal strength, so the percentage of coalition formation decisions and guaranteed pay-offs was computed for each individual at every level of personal strength. To examine the percentages of coalitional choices and guaranteed pay-offs, we conducted a repeated-measures ANOVA with two repeated factors, type of choice (percentage of coalitions versus percentage of guaranteed pay-offs) and level of personal strength, with sex and instruction as independent variables. A linear contrast best explained the effect of personal strength: weaker players both formed more coalitions and chose more guaranteed pay-offs, \( F_{1,120} = 228.3, p < 0.0001 \) (figure 1). At all levels of personal strength, however, players preferred to form a coalition with one opponent (\( X = 54.5, \text{s.d.} \pm 24.2, N = 124 \)) over guaranteed pay-offs of points for everyone (\( X = 10.5, \text{s.d.} \pm 18.4, N = 124, F_{1,120} = 198.3, p < 0.0001 \)).

Additionally, three interactions: level of personal strength \( \times \) type of choice \( F_{6,720} = 22.3, p < 0.0001 \); level of personal strength \( \times \) instructions, \( F_{6,720} = 3.6, p = 0.002 \); and type of choice \( \times \) instructions, \( F_{1,120} = 5.4, p = 0.02 \), were significant, but were qualified by a three-way interaction between type of choice \( \times \) level of personal strength \( \times \) instructions interaction, \( F_{6,720} = 4.0, p = 0.001 \). Follow-up Tukey’s tests \( (p < 0.05) \) showed that players accepted guaranteed pay-offs more often under non-competitive than competitive instructions at their three lowest levels of personal strength: 40; 30; and 20.

(ii) Threshold of level of personal strength for ceasing to compete alone

We next examined whether players exhibited thresholds of personal strength at which they ceased to compete alone. Of 124 subjects, 106 (85.5%) ceased competing alone at a specific level of personal strength (probability of winning alone) and never competed alone beneath that level of personal strength. By contrast, five (4.0%) competed alone on every round and 13 (10.5%) displayed

Figure 1. Percentage of choices competing alone, in a coalition, or with a guaranteed pay-off at each level of personal strength (black bars, alone; grey bars, coalition with one; white bars, guaranteed pay-off).

Figure 2. Number of individuals at each level of personal strength, who ceased competing alone at that level of personal strength and at all lower levels and henceforth only chose coalitional strategies or guaranteed pay-offs.
no clear strategy. Figure 2 displays the percentage of individuals of the total (124), who ceased competing alone at each level of personal strength. As shown in figure 2, the majority of individuals ceased competing alone when their probability of winning alone declined to 50 per cent or below. In other words, 85 per cent of individuals decided to risk competing alone to win all the points only above a specific probability of winning and never below that level. These thresholds of personal strength for competing alone emerged despite the random distribution of levels of personal strength that the players confronted across rounds.

Furthermore, the distribution of the number of individuals who ceased competing alone at each level of personal strength differed from randomness ($\chi^2(6) = 24.5$, $p = 0.0004$, two-tailed). The levels of personal strength at which players switched from an individualistic to a coalitional strategy, or to guaranteed pay-offs, tended to be intermediate. This indicates that a large proportion of individuals found it aversive to compete alone when their own personal strength diminished below a set point. They therefore switched either to forming a coalition or accepting guaranteed pay-offs for themselves and their opponents.

(iii) The effect of level of opponent's strength and friendship on coalition formation

We then examined coalitional choices to determine the effects of the level of opponent's strength (opponent's probability of winning alone) and friendship with the player. Omitting those who competed alone on a round or chose guaranteed pay-offs, the percentage of individuals who made coalitional choices for the stronger versus weaker opponent, and friend versus non-friend, were compared in an ANOVA with sex and instructions as independent variables and level of opponent's strength (strong versus weak) and friendship (friend versus non-friend) as repeated factors. Players formed coalitions more often with strong opponents ($X = 33.2$, s.d. $\pm 12.4$, $N = 117$) than weak ones ($X = 16.8$, s.d. $\pm 12.4$, $N = 117$, $F_{1,115} = 51.3$, $p < 0.0001$). Despite the fact that the designation of friend was completely arbitrary, players were more likely to form coalitions with a player labelled friend ($X = 33.5$, s.d. $\pm 11.4$, $N = 117$) than non-friend ($X = 16.4$, s.d. $\pm 11.4$, $N = 117$, $F_{1,115} = 64.8$, $p < 0.0001$). Level of opponent's strength (opponent's probability of winning alone) and friendship formed an additive model: strong friend ($X = 42.5$, s.d. $\pm 17.2$, $N = 117$); weak friend ($X = 24.6$, s.d. $\pm 18.7$, $N = 117$); strong non-friend ($X = 23.9$, s.d. $\pm 20.5$, $N = 117$); and weak non-friend ($X = 9.0$, s.d. $\pm 13.1$, $N = 117$). Tukey's honestly significant differences test on the interaction between levels of opponent's strength $\times$ friendship $\times$ sex, $F_{1,115} = 4.9$, $p = 0.029$, did not yield any significant differences.

To determine whether the decision rules used were consciously available, we conducted a second study.

4. DISCUSSION

Subjects followed a consistent strategy. When individuals were strong (had a high probability of winning all the points alone), they mostly competed alone. At intermediate strength, they would form a coalition with a stronger and/or friendlier opponent. When they were the weakest, they tended to opt for a guaranteed reward. Individuals playing under the competitive condition switched to a guaranteed reward at a lower probability of winning than individuals playing under non-competitive conditions. Thus the same strategy for forming coalitions applied across conditions, with small compensations for changes in the ecology.

Furthermore, 85 per cent of individuals exhibited a threshold for ceasing to compete alone and permanently switching to a coalitional strategy or guaranteed pay-offs. In most cases, individuals competed alone only above an intermediate probability of winning, centred around 40–50%. At lower probabilities of winning alone, they always formed coalitions or chose guaranteed pay-offs with the other two players. The threshold effect occurred despite random fluctuations in the probabilities of winning alone. Thus, individuals followed a powerful rule predicated on personal strength (probability of winning alone) that guided their decision-making process.

Finally, when individuals formed coalitions, they tended to select as their partners stronger players and arbitrarily designated friends. These preferences occurred under both the competitive and non-competitive conditions even though they did not affect the probability of winning the reward.
The coalition-forming strategy that we observed resembled decision-making by male chimpanzees competing to monopolize mating access to attractive females. First, individual chimpanzees switched from competing alone to forming a coalition when their probability of success declined to approximately 50 per cent (Watts 1998). Second, chimpanzees exhibited a threshold effect such that when high-ranked individuals experienced a probability of success at or below 50 per cent, their tendency to form coalitions was consistent (Watts 1998). Third, high-ranked chimpanzees’ choice of partner was the next strongest individual (Watts 1998). Finally, several studies demonstrate that chimpanzees were more likely to form coalitions or cooperate with opponents whose affiliative behaviour allowed them to be operationalized as friends (de Waal 1982; Boesch & Boesch-Achermann 2000; Melis et al. 2006; Mitani 2006; Duffy et al. 2007).

Expected pay-offs in our game were identical for each choice, so on any given round no rationale existed for selecting one strategy over another. The consistency of our results therefore strongly implies the operation of a heuristic governing coalitionary decisions, comparable with other types of heuristics observed in studies of behavioural decision-making (Kahneman & Tversky 1979; Gigerenzer 2008). That the current results resemble so closely chimpanzees’ coalitional strategies for mate guarding suggests an evolved heuristic, possibly with phylogenetic roots to 5–6 million years ago (Mesterton-Gibbons & Sherratt 2006).

Choices of partners are understandable in relation to benefits and costs. Stronger individuals provide the greatest increase in the probability of obtaining rewards. For instance, among male chimpanzees, the two highest ranking males can sometimes monopolize females, but a coalition of a strong and weak male will probably be vulnerable to disruption by a high-ranking male. Thus, high-ranked individuals should be more popular as coalition partners. Low-ranked individuals therefore probably find coalition building more difficult than higher ranked individuals, simply because they are less popular as partners. Weaker individuals also will suffer higher costs from conflicts, thereby inducing them to accept any reward no matter how small (Mesterton-Gibbons & Sherratt 2006; Gavrilets et al. 2008). Both the probability of coalition formation and the costs of competition require consideration in future games.

Friends also probably make good coalition partners because of the mutual trust established between them, thereby reducing the risks of coalition failure (Melis et al. 2006; Gavrilets et al. 2008). Popularity of an individual then may depend both on an individual’s capacity to obtain a reward within a given ecology and on that individual’s history of building trust with other individuals by reliably sharing rewards.

Individual differences also probably influence perceptions of strength and hence coalition formation (Mesterton-Gibbons & Sherratt 2006; Gavrilets et al. 2008). In humans, dominance rank (Sapolsky 2005) and inhibition (Schwartz et al. 2003) probably influence perceptions of personal strength and subsequent decisions about coalition formation and potential partners. Interestingly, we found no sex differences in our analyses. This suggests that human males and females use similar decision rules for forming coalitions, although sex differences in social structures, including size and rigidity of the status hierarchy, could affect the use of coalitions in practice.

Differing ecologies also probably affect perceptions of strength. Under conditions of scarcity, including food shortages or population increases, individuals of all ranks may be more prone to attempt to form coalitions or to accept small but certain rewards. Only those with past high rank and trusted relationships however may be successful at coalition formation. Support for the importance of the ecology stems from the finding in the current game that individuals in the competitive condition chose guaranteed pay-offs at lower probabilities of winning compared with individuals in the non-competitive condition. Intuitively, individuals in the explicitly competitive condition probably believed that not providing rewards to the second opponent increased their own advantage. Critically, however, individuals in the competitive condition were more likely than those in the non-competitive condition neither to compete alone at the lowest probabilities of winning to at least attempt to beat stronger opponents, nor to select guaranteed pay-offs at the highest probabilities of winning to ensure beating their opponents. Thus, the heuristic was powerful enough to apply across differing conditions albeit with a shift in the absolute level of strength that produced choices of guaranteed pay-offs.

The observed heuristic can also be viewed partially within the general framework of risk aversion. The current heuristic cannot be predicated solely on avoiding risk, because otherwise individuals would always select guaranteed pay-offs by sharing the points with the two opponents. Understanding the components of risk aversion and how this affects decision-making constitutes a complex problem (Davies & Satchell 2007). An often-used index of risk is the ‘risk premium’, the amount by which the expected value (EV) of a gamble exceeds a guaranteed pay-off. In the present study, the risk premium is 0, since, in all cases, the EV and the amount that can be obtained with certainty are identical. For example, when an individual’s level of strength is 20, EV equals 20. By allying with the two other players, they can gain 20 with certainty. By this definition, risk aversion cannot explain the current findings.

However, if we simply equate risk with uncertainty, then our results can be described as consistent with a model of uncertainty aversion. When individuals have a high probability of winning alone (and thus low uncertainty), they will choose to risk competing alone to gain all the rewards rather than ensuring a high certain pay-off. When their probability of winning alone decreases sufficiently, they can maintain a low level of uncertainty by preferentially forming a coalition with one other, even though their rewards must now be divided with the coallitional partner. It is only when their uncertainty is particularly high, i.e. when their probability of winning alone becomes extremely small, that subjects opt for a total reduction of uncertainty and accept a small, but guaranteed reward. A potential explanation of this pattern consistent with Kahneman & Tversky’s (1979) prospect theory is that individuals who have a high probability of winning underestimate their subjective risk, whereas those with a lower probability of winning...
This suggestion is consistent however with the recent data on humans demonstrating that individuals made to feel powerful process information differently than individuals made to feel less powerful (Smith et al. 2008). How powerful versus weak individuals make decisions regarding competition for resources without the potential for either coalition formation or guaranteed pay-offs merits examination in future studies.

The heuristic we have identified could not have not been predicted on general principles, since different species have different strategies. For example, in savannah baboons (Papio cynocephalus), low- or middle-ranked males form coalitions with others of similar rank against a high-ranking male (Bercovitch 1988). This may result from the highest ranking baboon male’s vastly superior fighting ability, precluding the need for coalition formation (Noe & Sluijter 1995). In our study, by contrast, subjects did not tend to form a coalition with a weaker player against the strongest player. Variation among species in coalition-forming strategies is not well understood, but should provide insight into the reasons humans’ coalition-building decisions have been shaped in particular ways.

In summary, our results indicate the presence of a simple heuristic rule guiding the context of coalition formation and the choice of particular partners. In particular, an individual’s willingness to form coalitions is influenced by the perceived probability of winning alone. Similarities in decisions about coalition formation between humans and our closest genetic relatives support the hypothesis that the principles of human cooperation constitute an evolved strategy. Our paradigm offers opportunities to examine heuristics for coalition formation in humans under varying physical and social conditions, and with individuals varying in relevant personal characteristics.

We followed all ethical guidelines for collection of data with human subjects as provided by the Department of Health and Human Services of the United States.

REFERENCES


