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Original Article

Within-group competition reduces cooperation and payoffs in human groups

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Social organisms in many taxa cooperate to produce resources that are shared among group members. Some cooperatively produced resources may be monopolized by individuals who invest in within-group competition, but these have largely been overlooked in empirical and theoretical research on human cooperation, which has focused on noncontestable public goods. In this study, we allow for the potential of within-group competition over cooperatively produced resources and use a game theoretic "tug-of-war" model and empirical test to show that such competition decreases the degree of cooperation within human groups and hence decreases group members' payoffs. Our study thus sheds light on how cooperative production and equal division of shared resources may have evolved, expands on current models of human cooperation to reflect the many natural conditions with opportunities for within-group competition, and demonstrates unifying principles in cooperation and competition across the animal kingdom. *Key words:* cooperation, humans, public goods, reproductive skew, social groups, tragedy of the commons, tug-of-war, within-group competition. *[Behav Ecol]*

INTRODUCTION

Social organisms from many taxa, from bacteria (Rainey and Rainey 2003) to mammals (Packer and Ruttan 1988), often share cooperatively produced resources. Some such resources are intrinsically nonexcludable (public goods, as strictly defined), whereas others are potentially monopolizable by certain group members, who may then gain direct fitness benefits from obtaining larger shares relative to other individuals in the group (Williams et al. 2002). Studies of cooperation in humans have focused on nonexcludable public goods such as clean air or tax-funded infrastructure, which has led to the implicit assumption that all important group resources are automatically divided equally, even when there is the potential for monopolization (Dawes 1980; Hawkes 1993; Fehr and Gächter 2000; Smith and Bliege Bird 2000; Milinski et al. 2002; Barclay 2004). In this study, we relax the assumption of automatic equal resource division in human groups by applying the principles of "tug-of-war" models used to analyze conflict in nonhuman animals (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and Reeve 2010). Studies of within-group competition on humans have examined competition in other contexts, such as access to relationships (Fehr and Schmidt 1999; Barclay and Willer 2007), but here, we provide an explicit test of how within-group competition over shared resources affects people's payoffs and levels of cooperation.

Competition over cooperatively produced resources

In this study, we concentrate on cooperatively produced, shared resources that are 1) depletable, that is, if one individual takes more, then there is less available for others; 2) contestable, that is, the size of each individual's share is not fixed; and 3) subject to a trade-off, due to limited time and energy budgets, between cooperative resource production and selfish investment in competition to increase the size of one's own share. Such resources are well documented in nonhuman animal societies: for example, an individual's share of cooperatively hunted food may be determined by contest competition (coatis *Nasua narica*: Gompper 1996; chimpanzees *Pan troglodytes*: Watts and Mitani 2002; Williams et al. 2002) or dominance rank (salmonid fish *Oncorhynchus masou macrostomus*: Hakoyama and Iguchi 1997; chimpanzees: Fruth and Hohmann 2002; Williams et al. 2002). However, investing in cooperation to obtain this food for the group may be individually costly (Fruth and Hohmann 2002), reducing an individual's chance of increasing its rank and reproducing in the future, for example, in social wasps (*Polistes dominulus*: Cant and Field 2001; *Liostenogaster flavolineata*: Field et al. 2006). Likewise, reproductive opportunities may be cooperatively produced (Watts 1998), if individuals can only access mates by joining coalitions. This precludes coalition members from investing in other activities (Smith et al. 2010), such as competing for a share of the mating opportunities, which are often distributed unequally among coalition members, for example, in dunnocks *Prunella modularis* (Davies 1992), dolphins *Tursiops aduncus* (Connor et al. 2001), baboons *Papio cynocephalus cynocephalus* (Noë 1990), dwarf mongooses *Helogale parvula* (Rood 1990), and cheetahs *Acinonyx jubatus* (Caro and Collins 1987).

Although the balance between cooperation and conflict, and how this balance affects the degree of equal sharing, has been a major research focus in the field of behavioral ecology (Vehrencamp 1983; Keller and Reeve 1994; Sherman et al. 1995), within-group competition over cooperative group production has largely been overlooked in studies of human cooperation. In the classic "public goods" economic games typically used to investigate human cooperation in the laboratory, equitable division of resource production is usually forced on the players, so there is no opportunity for within-group

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competition (e.g., Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Puurtinen and Mappes 2009; Kümmerli et al. 2010). Many potentially contestable resources are indeed divided relatively equitably within human groups, for example, food in hunter-gatherer societies (Kaplan and Hill 1985; Smith and Bliege Bird 2000; Hawkes et al. 2001). However, in these cases, equal sharing is not automatic and often results from costly enforcement of social institutions (Boehm 1993; Bowles et al. 2003; Gurven 2004) or because there are diminishing returns from investment in defending a share that is too large for oneself (Blurton Jones 1984). In other cases, there is competition over depletable and nonmonopolizable resources: male competition over females occurs in hunter-gatherer societies (Knauft 1991), and in industrialized nations, there is high competition over possession of resources to produce fuel and food (Hardin 1968, 1998; Penn 2003). Many types of social competition have been described as "arms races" (Axelrod 1984; Frank 2007), a term which connotes costly investment by multiple parties in escalated competition that reduces individuals' ability to invest in cooperation (or indeed anything else) and that is detrimental to all. There is therefore a need to test explicitly the effect of within-group competition on cooperation.

Modeling within-group competition over group resources

Within-group competition and variation in resource division can be quantified using game theoretic analysis: for example, tug-of-war models predict evolutionarily stable energy investments in costly competition (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and Reeve 2010). In a simple tug-of-war, resources are divided according to the relative investments individuals make in competition and the asymmetry in their competitive efficiency. For example, if individual A invests twice as much as individual B in competition over shared resources and if the 2 individuals have an equal competitive efficiency, then A obtains twice as large a fraction of the resources. Tug-of-war models successfully predict both the degree of equitable division of resources according to the values of the efficiency parameters and relative competitive investments, and how much resource is used up in competition. These models have been applied to both small and large societies of invertebrates and vertebrates, such as allodapine bees *Exoneura nigrescens* (Langer et al. 2004), meerkats *Suricata suricatta* (Clutton-Brock et al. 2001), lions *Panthera leo* (Packer et al. 2001), and wood mice *Apodemus sylvaticus* (Gerlach and Bartmann 2002), but tug-of-war theory has not yet been applied explicitly to humans. However, because depletable and contestable resources are shared among humans living in groups and because human and nonhuman coalitionary behaviors are similar (Harcourt and de Waal 1992), we expect humans to engage in within-group tug-of-war competition over shared resources, as do other animals.

We hypothesize that when faced with choosing how much of one's own personal resources to 1) keep for oneself, 2) cooperatively contribute toward producing group goods, or 3) selfishly invest in competing for a larger share of the group goods, people may increase their payoffs by investing more in competition relative to the other 2 options. Given that there is a trade-off between cooperatively contributing to the shared resource and competing for it, we predict that when people have the option to engage in within-group competition, 1) people will invest less in cooperatively producing the shared resource and 2) the size of the shared resource will be smaller. We tested these predictions both mathematically, in a game theoretic model, and empirically, in a laboratory economic game.

MODEL

We first develop a simple model that inserts a tug-of-war into a basic public goods game. Each of n group members begins with an amount of personal resource t. Of this resource, individuals keep an optimal amount s^*, invest an optimal amount z^* in competition, and contribute $t - s^* - z^*$ to the group. Contributions are summed and multiplied by k, so there is a collective benefit to contributing. This "group productivity" is then divided among all group members according to their relative investments in competition (the tug-of-war): if any given focal individual invests z in competition and the $n - 1$ other group members invest z^*, then the fraction f of group productivity that the focal individual obtains is:

$$f = \frac{z}{z + (n-1)z^*}. \tag{1}$$

It is stipulated that if all investments in competition are zero (z and $z^* = 0$), the resource is shared equally, as is typically assumed in most human cooperation experiments.

This focal individual keeps a fraction s of its personal resource t. Its total payoff (i.e., the sum of resources kept for itself plus the share of group productivity obtained through the tug-of-war) is therefore:

$$s + fk[(t - s - z) + (n-1)(t - s^* - z^*)]. \tag{2}$$

To find the strategies s and z that maximize an individual's payoff, we partially differentiate Equation 2 with respect to s and to z and set each partial derivative equal to zero. We use the second derivative test to verify that these are fitness maxima. The evolutionarily stable solutions (Nash equilibria) occur when the fitness-maximizing values of s and z are the same as s^* and z^*. The evolutionarily stable solutions to this tug-of-war game depend on the group's productivity relative to its size. If $k > n$, a group member should invest

$$z^* = \frac{t(n-1)}{n} \tag{3}$$

in competition and contribute all the rest to the group's shared resources. However, if $k < n$, the individual should keep all its resources for itself ($s^* = t$; no competition and no contribution).

We then substitute these fitness-maximizing values for s^* and z^* into Equation 2 to find an individual's payoff at equilibrium. If $k > n$, a group member obtains a payoff of value kt/n and if $k < n$, a group member obtains t.

We can now compare this tug-of-war game with a game where individuals cannot invest in competition (z and $z^* = 0$), that is, where group resources are automatically divided equally (a classic public goods game). In the automatic equal division game, the optimal solutions are 1) if $k > n$, contribute everything ($s^* = 0$) and obtain a payoff of value kt; 2) if $k < n$, keep everything ($s^* = t$) and therefore obtain a payoff t.

Thus, the effect of including a possible tug-of-war in a classic public goods game, that is, of players having the option to compete over shares of group productivity, is that individuals will 1) be less cooperative and 2) obtain lower payoffs than when the resource is automatically equally divided. This yields a kind of tragedy of the commons (Hardin 1968) where the evolutionarily stable strategies leave all players worse off (i.e., cannot be invaded by more cooperative strategies). Because there is a possibility of a tug-of-war whenever resources are contestable, the actual levels of cooperation in nature in such cases are expected to be significantly lower than as described by public goods models with automatic resource division.

Importantly, note that although it is never strictly rational to cooperate in our experiment because the multiplier k is less than the group size n ($k = 2$ and $n = 4$), we nevertheless predict some nonzero level of cooperation in both conditions. This is because many empirical studies demonstrate that people regularly contribute to group productivity even when $k < n$ and in experimental conditions where there is no incentive to cooperate (Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). As such, the relevant predictions for our experiment are the relative differences between the tug-of-war and the equal division games, not the absolute contributions or payoffs (Kümmerli et al. 2010).

MATERIALS AND METHODS

Empirical test

We recruited 48 voluntary participants from the Cornell University community (27 females and 21 males; mean [±standard error, SE] age: 20.73 ± 1.64 years) to play an economic game, programmed using z-Tree software (Fischbacher 2007). Participants played the game in groups of 4 and sat at computer terminals visually isolated from other group members; they did not know how many rounds of the game they would play. All decisions were confidential and only associated with code numbers; all methods were approved by the Institutional Review Board for Human Participants. Players read an instruction program and completed a quiz to test their understanding of the game before they could begin the experiment itself. Participants earned "lab dollars" (L$), which were exchangeable to US dollars at a rate of 300:1, plus a baseline payment of US$2. Mean (±SE) earnings were 9.70 ± 1.11 US dollars, depending on participants' decisions during the game. Each game consisted of 2 experimental conditions.

Equal division condition

Each round, each player received L$100 and decided how much to invest in a "personal fund" versus cooperatively contribute to a "group fund" (standard public goods game, e.g., Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). Contributions to the group fund were doubled and redistributed equally among all participants. Therefore, each player's payoff at the end of each round was equal to her investment in the personal fund plus one quarter of the doubled group fund. Each player saw a screen at the end of each round displaying her payoff and the overall contribution to the group fund that round.

Tug-of-war condition

In addition to the options in the equal division game, players could invest any of their L$100 in competition over shares of the group fund (termed "extraction" to avoid framing problems). In this experimental condition, each individual's share of the doubled group fund was determined by her relative investment in competition: for example, if players A, B, C, and D invested L$10, L$20, L$30, and L$40, respectively, in competition, then player A got $10/(10 + 20 + 30 + 40) = 1/10$ of the group fund. If a player invested nothing in competition when others did do so, she did not benefit from the group fund; if no players invested in competition, the group fund was split equally. In sum, each player's payoff each round was equal to her investment in her personal fund plus her share of the doubled group fund, with shares being determined by relative investments in competition (Equation 1). At the end of each round, each player saw a screen displaying her payoff, the overall contribution to the group fund, and the fraction of the group fund she obtained that round.

Statistical analyses

We used a within-subjects design: participants played 10 rounds of each condition, with order of conditions counterbalanced between groups. To control for interdependence within groups, we treated each group of 4 as an N of 1. We analyzed group contributions using a general linear model (SPSS 17.0) with experimental condition (tug-of-war vs. equal division) and round (10 rounds per condition) as within-subjects variables and with the order of conditions as a between-subjects variable.

RESULTS

Cooperative contributions to group productivity

Contributions were lower in the tug-of-war than in the equal division condition ($F_{1,10} = 20.83$, $P = 0.001$), supporting our prediction. The difference in contributions between the tug-of-war and the equal division conditions was so robust that it was independently significant in both orders of experimental condition (equal division first: $F_{1,5} = 15.4$, $P = 0.011$; tug-of-war first: $F_{1,5} = 7.26$, $P = 0.043$; Figure 1), and order did not interact with other variables (all Fs < 1.1), such that the 2 orders could even be considered independent replications of each other.

Consistent with past research in public goods games (e.g., Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004), contributions fell over time ($F_{9,90} = 12.88$, $P < 0.001$) in both experimental conditions (equal division: $F_{9,90} = 10.73$, $P < 0.001$; tug-of-war: $F_{9,90} = 5.38$, $P < 0.001$). There was a significant round by condition interaction ($F_{9,90} = 2.63$, $P = 0.010$): contributions fell more under equal division than under tug-of-war most likely because they had further to fall from.

Controlling for investments in competition

One might argue that contributions were lower in the tug-of-war simply because participants had an extra option for investment (i.e., competition), in addition to contribution. To control for participants' having less money available to contribute in the tug-of-war, we analyzed contributions as a percentage of the money remaining after investment in competition: we divided all contributions by the quantity "100 minus competition." Under this new analysis, contributions (as a proportion of the amount available) were still lower under tug-of-war than under equal division ($F_{1,10} = 5.92$, $P = 0.035$; Figure 2). This further supports our argument that competition decreases cooperation within social groups. Contributions decreased across rounds in this new analysis also ($F_{9,90} = 9.90$, $P < 0.001$), but the round by condition interaction was no longer significant ($F < 1$).

Amount kept

An alternative hypothesis for the decreased contribution in the tug-of-war condition is that participants were confused by more options being available: for example, participants may have experimented with both options (keeping and competition) and responded by keeping money instead of contributing it. If this is true, we should see participants keeping more money for themselves in the tug-of-war condition than under equal division. Instead, the opposite was true: participants actually kept more money for themselves in the equal division

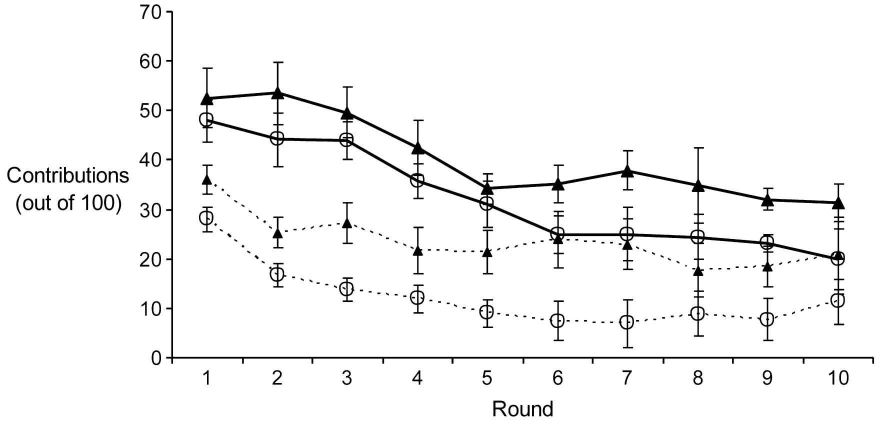

Figure 1
Mean contributions to the group fund of 100 (±SE) when the group fund was divided equally (equal division: solid lines) versus divided according to investment in within-group competition (tug-of-war: dotted lines). Open circles represent groups where the equal division condition came first and closed triangles represent groups where the tug-of-war condition came first. Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

condition than under tug-of-war (means [±, SE] for equal division: 63.8 ± 6.5; for tug-of-war: 55.9 ± 6.9, $F_{1,11}$ = 6.54, P = 0.027), which falsifies this hypothesis. In addition to testing participants' understanding before they started the experiment, we asked participants in an anonymous postexperiment questionnaire whether the instructions had been clear and what strategies they adopted during the game; 91% of players indicated that they completely understood the instructions. Thus, the lower contributions in the tug-of-war condition are better explained as being a result of the competition rather than being due to confusion.

Payoffs

Players' payoffs (i.e., total earnings in the game from investment in the personal fund plus shares of the group fund) were higher in the equal division condition than in the tug-of-war (mean earnings [±SE] in L$: equal division: 1362.79 ± 65.29; tug-of-war: 916.54 ± 16.00; paired t_{11} = 6.71, $P <$ 0.001; Figure 3), as predicted. If all participants had contributed everything in every round of a given condition, each participant would have earned L$2000 (US$6.67, excluding US$2 baseline payment); if all players kept all their money, each player would have earned $1000 (US$3.33, excluding US$2 baseline payment). In the tug-of-war, people expended resources in competition rather than contributing toward production of the shared group resource and thus players did worse overall than if they had simply kept all their money (one-sample t_{11} = 5.28, $P <$ 0.001).

DISCUSSION

The tug-of-war model predicted that the option to invest in competition over group productivity leads to people 1) contributing less and 2) obtaining lower payoffs. The results of the experimental game support both of these predictions. The decrease in cooperation in the tug-of-war condition could not be explained by participants simply withholding more money or having less available to contribute but instead arose from participants contributing a smaller relative amount to group productivity. These experimental results reflect many situations outside the laboratory where competition over real-life resources may reduce cooperative production and hence individuals' payoffs. For example, parties in dispute over land may spend money in a military arms race instead of spending money on using the land to produce resources that can then be shared; rivals for the leadership of a political party may harm their party's chances of electoral success by engaging in fierce

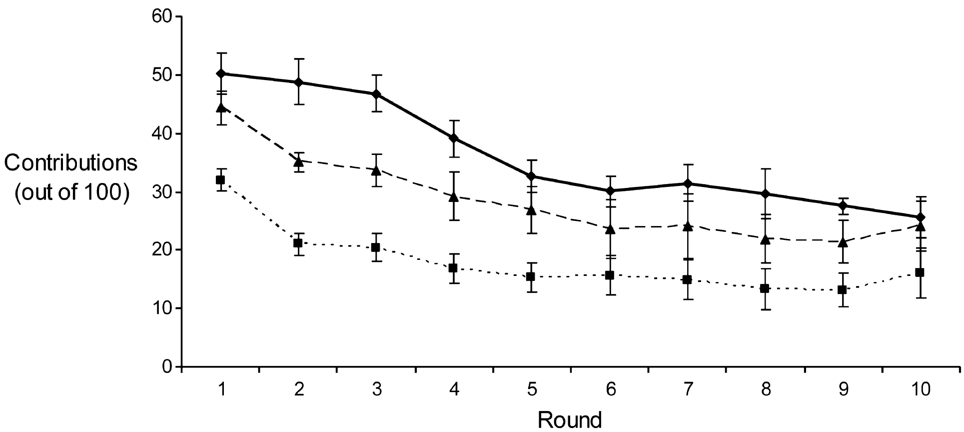

Figure 2
Mean contributions to the group fund of 100 (±SE) when the group fund was divided equally (equal division: solid line) versus divided according to investment in within-group competition (tug-of-war: dotted line). The dashed line represents contributions in the tug-of-war as a percentage of the amount remaining after investing in within-group competition. All 3 lines display data both from groups where the equal division condition came first and from those where the tug-of-war came first. Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

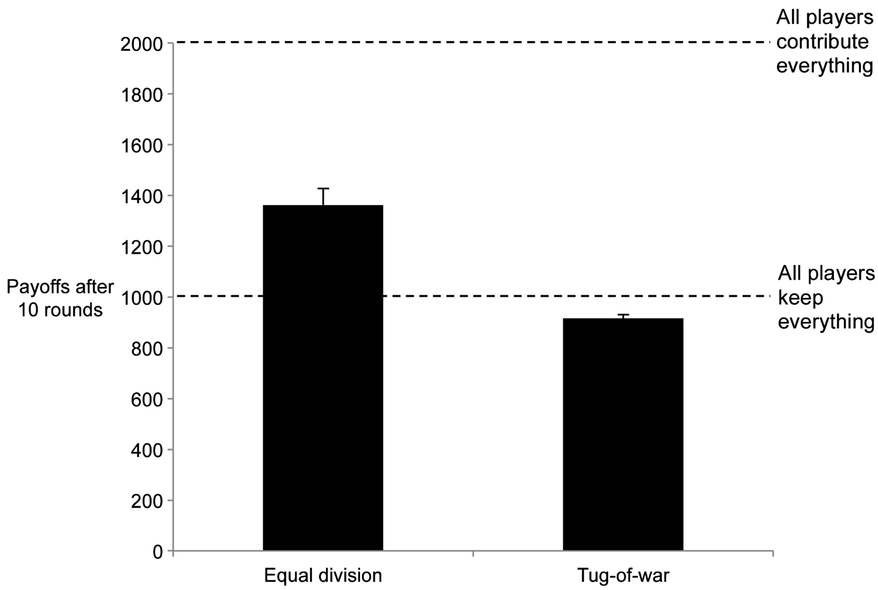

Figure 3
Mean payoffs (±SE) in lab dollars at the end of each experimental treatment (i.e., after 10 rounds). Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

within-party competition; and if academic collaborators put time and energy into contesting first authorship, they may produce a lower quality collaborative project than if they devoted all their resources to the project itself. In some nonhuman primates, the mere potential for resource monopolizability, regardless of whether it is realized, can reduce cooperation in laboratory tasks (brown capuchins *Cebus apella*: de Waal and Davis 2003; chimpanzees: Melis et al. 2006).

Given the parameters in our experiment, notably with $k < n$, the model predicted that the optimal decision is to keep all of one's own resources, regardless of the potential for competition. However, people still contributed in both experimental conditions in our laboratory game, despite not having any incentive for cooperation, such as between-group competition (Bornstein and Ben-Yossef 1994; Puurtinen and Mappes 2009) or reputation (Yamagishi 1986; Nowak and Sigmund 1998). Classic "public goods games," which by default have equal division, have yielded the same results in this regard (e.g., Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). Players' suboptimal decisions may simply be because people avoid extreme options in laboratory games, regardless of whether they are optimal (Kümmerli et al. 2010) or due to unconscious concerns about reputation (Haley and Fessler 2005; Burnham and Hare 2007). In order to control for this, each participant in our experiment played both experimental conditions: the relevant results are therefore contributions in one condition relative to the other, and the absolute values are not important.

Effects of competition on cooperation and productivity

In a tug-of-war model, the amount of group resources that each individual obtains is a product of 1) the total pool of resources produced by the group and 2) the fraction of this total that each individual obtains relative to other group members; these are determined by within-group cooperation and between-group competition (West et al. 2006; Reeve and Hölldobler 2007) and within-group competition (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and Reeve 2010), respectively. An individual can maximize its payoff by free-riding on others' contributions to group productivity and, if there is the potential for competition, by investing more in competition relative to other group members at the expense of contributing. This is likely to result in an arms race of escalating competitive investments (Axelrod 1984; Frank 2007), the intensity of which may vary depending on the abundance and monopolizability of group resources, such as cooperatively hunted meat (Blurton Jones 1984; Bliege Bird and Bird 1997). Due to the trade-off between competition and cooperation, this reduces group productivity and thus may lead to a "tragedy of the commons" (Hardin 1968; Rankin et al. 2007), leaving all group members worse off than if none had invested in competition. Individuals in these competitive groups will have lower fitness than individuals in groups with higher cooperation (Reeve and Hölldobler 2007; Wilson and Wilson 2007), such that each individual would individually benefit from suppression of competition (West et al. 2006).

Given the significant reduction in people's payoffs in the tug-of-war condition in our experiment, we predict selection for mechanisms to reduce within-group competitive conflict and increase the relative benefit of within-group cooperation (Ratnieks and Reeve 1992; Bowles et al. 2003; Bowles 2006; West et al. 2006). This prediction may explain the fact that many contestable and depletable resources outside the laboratory are, in practice, usually shared equally, for example, big game in hunter-gatherer societies (Knauft 1991; Hawkes 1993; Smith and Bliege Bird 2000). However, this egalitarianism is not necessarily cost-free and automatic but may be enforced (Boehm 1999). Allowing for within-group competition may thus provide insight into why there was selection for equitable division of potentially contestable resources. We suggest that 1) equitable division was preceded by high within-group competition because individuals benefit by escalating their competitive investments relative to other group members and 2) the detrimental effect of this competition allowed selection for "individually costly group beneficial" (Bowles et al. 2003) suppression mechanisms, via genetic selection or via cultural evolution and the differential survival of cultural norms (Boyd and Richerson 2009).

These mechanisms may include policing (Frank 1995, 2003; El Mouden et al. 2010) or social institutions such as monogamy and food sharing norms (Bowles et al. 2003) and self-government (Ostrom et al. 1992) but will likely differ in different societies and for different resources. Across cultures, one might predict 1) less investment in and reliance on cooperatively produced resources if those shared resources are contestable or need to be competed over because they are in short supply; 2) higher cooperation in experimental economic games in cultural groups habitually exposed to contestable shared resources than in groups exposed to noncontestable resources; and 3) greater investment and reliance on cooperative resources in species or cultural groups that have mechanisms for equal sharing. Future research should investigate the variation in resource competition and suppression mechanisms both among and within cultures. In addition, because payoffs may be more inequitable when there is more within-group competition, our results suggest that there may be selection for reproductive leveling mechanisms to reduce fitness differences among group members, an idea which has not been explicitly tested in humans (Bowles 2006).

SUMMARY

This study demonstrated mathematically and empirically the detrimental effect of within-group competition on individuals' cooperation and therefore their payoffs. The novel result that a within-group tug-of-war can lead to a tragedy of the commons may explain why many human groups have evolved mechanisms to ensure contestable resources are shared equally (Knauft 1991; Boehm 1999; Bowles 2006). Allowing for the potential of within-group competition in laboratory games lets us model a broader range of natural situations more accurately, an important goal in the study of human cooperation (Janssen et al. 2010). Additionally, acknowledging competition within human groups helps us draw parallels with the dynamics of cooperation and conflict in nonhuman social animals (Harcourt and de Waal 1992) and suggests that the trade-off between competition and cooperation is likely a universal principle across the animal kingdom (de Waal and Davis 2003). Finally, given that human competition (and hence lack of cooperation) over depletable resources such as oil, cod stocks, and clean water from irrigation systems (Hardin 1968, 1998; Ostrom et al. 1999; Dietz et al. 2003; Penn 2003) has led to many current environmental problems, we suggest that recognizing the need to reduce this competition will allow more effective management of these issues.

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