Sex Differences in Cooperation:
Integrating the Evolutionary and Social Psychological Perspectives

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Abstract

A long line of research has addressed whether there are sex differences in cooperation and other forms of prosocial behavior. Studies of social dilemmas (situations that pose a conflict between individual and collective interests) have yielded particularly contradictory conclusions about whether males or females are more cooperative. This paper presents an evolutionary framework that synthesizes previous results and generates new insights into the sex and cooperation question. Our framework addresses two general bases of sex differences in cooperation. First, we show how variation in the *motivational structure* of social dilemmas generates sex differences in cooperation. We then address two aspects of *social structure* that, according to evolutionary reasoning, generate sex differences in cooperation: the sex composition of the group, and the interpersonal versus intergroup nature of the dilemma. After presenting new hypotheses and reviewing existing research relevant to each hypothesis, we conclude by making suggestions for future research.

Sex Differences in Cooperation: Integrating the Evolutionary and Social Psychological Perspectives

At least since Rapoport and Chammah (1965), researchers have asked whether there are sex differences in cooperation in humans. Four decades later, social scientists still have not developed a clear answer to this seemingly simple question. The primary goal of this paper is to offer a preliminary explanatory framework to make sense of the findings on sex differences -- and similarities -- in cooperation. Our theoretical framework builds on evolutionary reasoning to elucidate how two basic features of social situations, *motivational structures* and *social structures*, can produce sex differences in cooperation and other forms of prosocial behavior. In reviewing the evidence we focus on the experimental game literature on social dilemmas, situations that pit individual against collective interests (Dawes, 1980; Kollock, 1998).

We first address how the *motivational structure* underlying these games affects cooperation. To do so, the section to follow gives a brief overview of the motivational components of *social dilemmas* to explain what motivates non-cooperation. We then build on principles from evolutionary psychology to explain why we should expect human males and females to respond differently to each motivational component (fear and greed) in social dilemmas and review evidence relevant to our hypotheses.

Thereafter, we address two aspects of *social structure* that, according to evolutionary reasoning, should generate sex differences in cooperation: (1) the sex composition of the group (Sell 1997), and (2) the inter-personal versus inter-group nature of the dilemma (Insko et al. 1994; Schopler et al. 1993). We outline a basic evolutionary framework to address each problem and review evidence relevant to each. Finally, we summarize our overall pattern of results and suggest directions for future research and additional tests of the hypotheses.

The literature on sex differences in cooperation is scattered across a number of disciplines without much conversation between them - and surprisingly little within. Thus, our review is necessarily selective. With only a few exceptions, we limit the review to experimental games. Except where they shed light on *behavior*, we ignore research that looks at survey responses to prosocial dilemmas (e.g., Penner et al. 2005). Similarly, we do not address behavioral studies in non-experimental settings (see, e.g., Anthony and Horne 2003). While laboratory studies lack many important nuances of studies in the field, clearer insights can come from controlling for as many factors as possible: laboratory studies - when done properly - are arguably the best means of doing so (Willer and Walker 2007). Furthermore, we do not attempt an exhaustive or representative review of the remaining studies. Instead we selectively review those studies that we consider highly relevant to each of our proposed hypotheses.

Motivations in Social Dilemmas

Social dilemmas are situations that pose a tension between individual and collective interests (Kollock 1998; Komorita and Parks 1995; Messick and Brewer 1983; Weber et al. 2004).[1] Such conflicts arise in a wide range of situations, from the interpersonal (e.g., moving with your partner's new job) to the international (e.g., establishing international arms control agreements, or agreements to reduce greenhouse gas emissions). Because of the breadth of conditions that lead to a divergence of individual and collective interests, the study of social dilemmas has attracted attention from researchers in a wide range of disciplines (Foddy et al. 1999; Komorita and Parks 1994; Suleiman et al. 2004). A common theme of these studies has been to uncover the conditions that make cooperation more likely. Sharper insight into these conditions can help solve real-world social dilemmas.

The most widely studied social dilemma, by far, is the two-person Prisoner's Dilemma (see Kollock 1998). The two-person Prisoner's Dilemma (hereafter PD) confronts each player with two options, to cooperate and to defect. The combinations of these two choices result in four possible outcomes: R (reward) and P (punishment) are the payoffs for mutual cooperation and defection, respectively, while T (temptation) and S (sucker) are the payoffs for unilateral defection and cooperation.

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[1] More precisely, following Liebrand (1986:113-14), they are "situations in which (a) [defection] yields the person the best payoff in at least one configuration of choices made by others; (b) [defection] has a negative impact on the interests of other persons involved; (c) the collective choice of [defection] results in a deficient outcome, that is, a result that is less preferred by all persons than the result which would have occurred if all had [cooperated] instead of [defected]."

In Prisoner's Dilemma, T (unilateral defection) > R (mutual cooperation) > P (mutual defection) > S (unilateral cooperation). This payoff structure is such that, if the game is played only once, defection "dominates" cooperation. That is, no matter what she expects Player B to do, a *rationally self-interested* Player A will defect. If B cooperates, A gains more from defection than cooperation ($T > R$). Similarly A gains more from defection if B defects ($P > S$). Because exactly the same logic applies to Player B, two rationally self-interested actors are doomed to a poorer fate than if they had both cooperated ($P < R$).

The ubiquity of PD in research designs likely stems from the fact that it simultaneously captures two motivations for defection, greed and fear, thus tapping into the complexity of human sociality (see Pruitt and Kimmel 1977). Greed corresponds to the temptation to free-ride on others' cooperation. Formally, the difference between the payoffs for unilateral defection and mutual cooperation captures the greed component in social dilemmas ($greed = T – R$). For the Prisoner's Dilemma game in Table 1a, $greed = 4 – 3$. Fear, on the other hand, denotes the prospect that one's cooperation may be exploited (that is, that one may be "suckered"). The fear component is given by the difference between the payoff for mutual defection and S unilateral cooperation (fear = P – S). For the Prisoner's Dilemma game in Table 1a, $fear = 2 – 1$. An uncooperative response to the fear component in social dilemmas may be thought of as social risk avoidance.

In short, the greed component relates to the trustworthiness of ego, while the fear component relates to whether ego trusts alter. Both components can motivate non-cooperation, but for different reasons. The person who responds to the greed component asks "given the best-case scenario (the other cooperates), how should I respond?" whereas the person who responds to fear asks "given the worst-case scenario (the other defects), how should I respond?"

Different levels of fear and greed generate different types of social dilemmas. For instance, the Chicken Dilemma of Figure 2 reverses the two lowest payoffs in PD (P and S) such that $T > R > S > P$. As in PD, because $T > R$, greed motivates defection. However, because $S > P$, fear does not. Another well-known dilemma called "Assurance," shown in Figure 3, reverses the two *highest* payoffs in PD, such that $R > T > P > S$. This game therefore presents precisely the opposite problem of that posed by Chicken. In Assurance, because $R > T$, defection cannot result from greed. Rather, defection results from the fear that others will defect (because $P > S$).[2]

Sex Differences in Responses to Motivational Structures

We now outline a preliminary explanatory framework to address sex differences in responses to the fear and greed components of social dilemmas. The framework builds on basic principles from evolutionary psychology about hypothesized sex differences in risk seeking and risk avoidance, cooperation and competition.

The starting point for contemporary evolutionary approaches is that human social behavior is a product of natural selection for traits that enabled our ancestors to solve important adaptive problems such as finding a mate, parenting, and group living (Tooby and Cosmides 1992). Over the course of human evolution males and females have faced different adaptive problems, particularly in the area of parental investment (Trivers 1972), with implications for modern day sex differences in social behavior (Buss and Schmitt 1993). Like any other mammal, human females typically invest vastly greater amounts of time and energy in nurturing and raising offspring than human males and therefore benefit (reproductively) by being more selective in their mate choices. Females should therefore have evolved to be careful in choosing partners and avoid taking too many risks to avoid being exploited in social interactions, particularly with strangers.

Female choice intensifies sexual competition among males, which increases the variance in male “fitness” or reproductive success (e.g., some men get more mating opportunities than others while some get none at all). This tends to select for psychological mechanisms that generate more risk-seeking and competitive behaviors in males to show off their qualities and resourcefulness (Wilson and Daly 1985). Relative to females, males have evolved a “high-risk-high stakes” game strategy to attract mates with repercussions for a wide range of social behaviors (Miller 2000).

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[2] The relative values of fear and greed can also be affected by other situational factors. For instance, in PD situations in which the interactants make their decisions sequentially (rather than simultaneously), the first mover faces a “fear” component whereas the second mover faces only a greed component. See, e.g., Simpson (2006).

In short we should expect that, particularly in interactions with strangers and potential mates, males will take more risks than females. Results from the broader literature on risk-taking support this basic conclusion. For instance, in a meta-analysis of 150 studies of sex differences in risk-taking, Byrnes et al. (1999) found that males were more risk-taking than females in fourteen out of the sixteen behaviors studied, including drug abuse, sexual activity, placing oneself in physical danger, and taking financial and intellectual risks.

When applied to social dilemmas, sex differences in responses to risk and competition suggest the following hypotheses. (1) Because it contains both fear and greed, *we will* not *find sex differences in PD;* (2) *to avoid being exploited, females will respond more strongly (non-cooperatively) to the fear component in social dilemmas*; (3) *males, on the other hand, will respond more strongly (non-cooperatively) to the greed component*.

Motivational Structures Expected to Produce Sex Similarities

The vast literature on PD, along with its public goods and commons dilemma variants, provides the most relevant evidence for the predicted *absence* of sex differences in cooperation in situations containing both fear and greed. Thousands of studies have employed the PD (Kollock 1998). Even if researchers checked for sex differences in only a fraction of these, we should reasonably expect *some* studies to find sex differences by mere chance. But our hypothesis suggests these differences should not be systematic and they are not. While some prior studies report that males are more cooperative (e.g., Brown-Kruse and Hummels 1993; Sell and Wilson 1991), others find that females are (e.g., Bonacich 1972; Dawes et al. 1977). The majority of PD studies reporting controls for participant sex seem to find no sex differences in behavior in PD (see, e.g., Caldwell 1976; Kuwabara 2006; Sell 1997; Simpson 2003). In short, we believe the evidence clearly points to an absence of sex differences in behavior in decision structures such as the PD.

Motivational Structures Expected to Produce Sex Differences

While the absence of sex differences in PD is instructive, the hypotheses that predict the presence of differences based on changes in motivational structures provide a stronger test of our explanatory framework. A number of recent studies provide evidence relevant to these hypotheses. These studies use other types of social dilemmas that explicitly manipulate the presence of fear and greed in simultaneous decision dilemmas (Kuwabara 2005; Simpson 2003) or "trust" dilemmas (see Buchan et al. 2008 and references therein).

Consider first the hypothesis that females will respond more strongly to the fear component in social dilemmas. This hypothesis can be assessed using evidence from decision-structures that contain fear, but not greed. In a series of experiments by Kuwabara (2005) males and females made a series of one-shot decisions in various games, without knowledge of their partner's sex. In the "Fear of Greed" Dilemma shown in Figure 4, the participant (the row player) had no incentive to free-ride on the partner's cooperation. However, the other (column player) *did* have an incentive to exploit or free-ride on the participant's cooperation. Thus, for the focal participant, there was a fear component ($P > S$). As predicted by the framework outlined above, females' cooperation rates (.26) were substantially lower than those of males (.43). Thus, females responded more strongly to the fear component than did males, as our hypothesis predicts.[3]

The findings on sex differences in trust dilemmas (also called "investment games" see especially Buchan et al. 2008) echo results from the Fear of Greed Dilemma. In a typical trust dilemma, each of two players (a truster and a trustee) is given an endowment. The truster can send (invest) any amount of his or her endowment to the trustee and any transferred amount is tripled. In turn, the trustee may return any portion of the tripled amount to the truster. However, unlike transfers, returns are not subject to a multiplier. Thus, the truster faces a fear component but no greed component: his or her cooperation can be exploited by the trustee, but he or she cannot exploit the trustee. On the other hand, the trustee faces a greed component but no fear component.

In a review of prior work using the trust dilemma, Buchan et al. (2008) note that, while there are some exceptions (presumably due to various procedural differences),

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[3] Simpson (2003) also provided a test of the "fear hypothesis," but Kuwabara (2005) points to problems with the test. We therefore do not review it here.

females tend to be less trusting than males in the dilemma. Furthermore, Buchan and associates replicated this general trend: When participants in their experiment had no information about the sex of the trustee, female trusters entrusted less. This is consistent with our argument that females respond more strongly to the fear component in social dilemmas.

Now consider how males and females respond to the greed component of social dilemmas. One source of evidence comes from the Greed Dilemma (Figure 5), which contains greed, but not fear. Four studies – two by Simpson (2003) and two by Kuwabara (2005) – show that males cooperate less than females in the dilemma. For instance, Simpson found that females' cooperation rates ranged from .47 (Study 1) to.57 (Study 2). Males' cooperation rates were much lower, from .22 (Study 1) to.33 (Study 2). Kuwabara found similar sex differences in cooperation in the Greed Dilemma. All in all, these findings strongly support the hypothesis that males respond more non-cooperatively than females to the greed component of social dilemmas.

The results of trustees' decisions in trust dilemmas are remarkably consistent with the findings from the Greed Dilemma. For instance, Snijders and Keren (1999) found that male trustees returned less – a matter of greed -- than female trustees when the truster's gender was unknown (see also Buchan et al. 2008). Furthermore, Croson and Buchan (1999) replicated this difference in the U.S., Japan, China and South Korea. Overall, then, existing evidence is in line with the hypothesis that males respond more strongly than females to the greed component in social dilemmas.

Our discussion thus far has focused on minimally social situations in which decision-makers have no information about fellow interactants (or their genders), and there is no shadow of the future, possibilities of reputation building, etc. As a result, differences - and similarities - between the behaviors of males and females can be straightforwardly attributed to motivational structures. The results from these studies are strongly consistent with the preliminary evolutionary-based theoretical framework linking sex differences in mating strategies to differences in social cooperation. In a later section, we suggest some additional ways of addressing how motivational structure influences sex differences and similarities in cooperation. For now, we turn to the impact of social structures.

Social Structures and Sex Differences

We address two types of social structure: the sex composition of the group, and whether decisions occur in an intergroup context. For each type we outline a set of hypotheses that can be preliminarily tested using results from prior work.

Sex Composition and Costly Signaling

The theoretical framework for sex composition effects we offer here is based on *costly signaling theory*, an evolutionary theory explaining trait differences between individuals (Grafen 1990; Zahavi 1975). Signaling approaches assume that individuals engage in costly personal acts such as prosocial displays as a means to signal important information about themselves (such as wealth or generosity) to others (Iredale, Van Vugt, & Dunbar 2008). In order for a given behavior, prosocial or otherwise, to be classified as a costly signal it must *i*) be costly to the sender, *ii*) easily observable by others, *iii*) make the audience behave preferentially toward the sender, and *iv*) be associated with some underlying positively valued trait (fitness, group-motivation, etc.) of the sender (Smith and Bird 2000). Because of the underlying association between signal cost and signaler quality, it is difficult (or prohibitively costly) for those who do not possess the quality to fake the signal. We consider each of these requirements, as they relate to cooperation, briefly in turn.

First, cooperation is typically costly to the signaler, by definition. This is true of the various forms of prosocial behavior we consider below. These costs will be born discriminately. As Wright (1998) has argued, because of the costs associated with cooperative signals, we should not expect these signals to be transmitted between competitors. This is because acting prosocially toward a potential competitor reduces the fitness differential between signaler and signaled: the very information the signal is intended to transmit. Thus, prosocial costly signals should be strongest when directed at coalition partners or members of the opposite sex (as targets or observers).

Second, when considered independently of other evolutionary theorizing, costly signaling approaches predict low levels of cooperation in one shot interactions, or in interactions where others' contributions are unknown. This is because fleeting one-shot interactions do not allow signalers to reap returns from onlookers, as discussed below.

However, because anonymous interactions were rare in our ancestral past, some theorists argue that people nevertheless cooperate in one-shot interactions because they cannot really grasp this evolutionary novel situation and assume that they are in fact being observed (Haley and Fessler 2005). In addition, a number of studies show that, although prosociality occurs "in private" (see Simpson and Willer 2008) there are strong effects of observability on cooperation. Following Sell (1997), we argue that observability should moderate the impact of sex composition on cooperation.[4]

Third we know from both fieldwork (Smith and Bird 2000) and experiments on indirect reciprocity (Milinski et al. 2001; Roberts 1998) that prosocial behaviors lead audiences to act preferentially toward senders. For instance, Milinski et al. (2002) found that donors to charity were treated more generously than non-donors in subsequent interactions.

Iredale, Van Vugt and Dunbar (2008) have shown that costly signaling accounts can be used to shed light on how the sex composition of groups or audiences influences prosociality (see also Zahavi and Zahavi 1997). To apply costly signaling theory to sex composition effects, we need to know what females and males look for in mates: these should be the qualities signaled by the opposite sex.

Whereas males preferences tend to focus on proximal indicators of fecundity (e.g., youth and attractiveness), females show a greater preference for indicators of a willingness to share resources, status, and leadership (Kenrick and Keefe 1992). Previous work shows that prosocial behaviors such as cooperation signal motivation to share resources, as well as status and leadership skills (Hardy and Van Vugt 2006; Willer 2008).

The forgoing suggests the following preliminary hypothesis: *cooperative signaling will be higher in the presence of an opposite sex audience than a same-sex audience and males should engage in higher rates of cooperative signaling than females with an opposite sex audience.*

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[4] Sell (1997) outlines a status and influence account of sex composition effects. Briefly, she argues that we should expect the most cooperation from males paired with females because males' higher relative status allows them to influence females' subsequent contributions. For this reason, Sell argues that we should only observe sex composition effects when group members know each other's genders.

Before turning to the evidence relevant to this hypothesis, we note two ancillary hypotheses. First, we might reasonably expect stronger tendencies for females, compared to males, to signal certain qualities to potential mates. For instance, whereas males are generally expected to provide resources, there are stronger expectations for females to provide time and emotional support, particularly to friends and relatives (Gabriel and Gardner 1999). Although we know of no existing evidence relevant to this ancillary hypothesis, in a later section we describe how the hypothesis can be tested via a straightforward extension of existing methods.

Second, note that our hypothesis deals primarily with simple cases in which audiences are either mostly male or mostly female. In groups in which other members are mixed-sex, we might expect to observe "competitive altruism" among males to be perceived as the most generous or as the best leader (Barclay and Willer 2007; Hardy and Van Vugt 2006; Roberts 1998). We review some evidence relevant to this ancillary prediction and propose additional tests later in the paper.

Social Structures Expected to Produce Signaling

A number of studies provide evidence relevant to the costly signaling hypothesis. First, consistent with the hypothesis, Sell and colleagues (1993; Sell 1997) have shown that sex composition affects contributions only when contributions (signals) are observable by others. When participants were given no information about others' contributions, Sell et al. (1993) found that neither sex, nor sex composition affected contribution rates in repeated public goods games.[5] But in a study where contributions were known, males who were ostensibly paired with females cooperated at higher levels than participants in any other condition (including males paired with males, and females paired with males or females). This is consistent with the costly signaling account presented earlier, as well as Sell's (1997) status/influence account (see note 4).

A reasonable criticism of our costly signaling explanation of Sell's findings is that participants did not meet each other. Thus, there may have been little incentive for males to signal various qualities to females. However, in classic cases of costly signaling, such

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[5] Like most empirical investigations of public goods games, the structure of incentives in Sell and colleagues' study was equivalent to an N-Person Prisoners' Dilemma, with equal parts fear and greed. Thus, it isn't surprising that sex of the participant had no independent effect on contributions.

as peacock's tails or stotting by gazelles, there is no conscious effort to signal the qualities connected to larger, more colorful, plumes or the ability to waste time while being pursued by a predator. Likewise, we do not assume that males paired with females consciously assumed they would meet the females and that higher contributions would pay off. Instead, we suggest that the costly signaling process operates automatically (Iredale et al. 2008). That said, a more convincing case for the costly signaling account would entail direct contact between the signaler and intended target of the signal. Besides providing different types of settings in which to evaluate the costly signaling account, the two studies reviewed next do just that.

The signaling account suggests that we should observe the predicted sex composition effects in other types of domains, such as those involving physical exertion. Evidence for this comes from Kerr and MacCoun (1985) who paired male and female participants with a same- or opposite sex interaction partner (actually a confederate whom the participant met in person) on a motor production task. The task involved each person squeezing a bulb to produce airflow: if one person's performance met a threshold the team was awarded a bonus, but a high performance from the second person did not add to the bonus.[6]

The procedure generated substantial sex composition effects, such that male participants were substantially less likely to free-ride on female compared to male partners. Conversely, female participants were substantially *more* likely to free-ride on male compared to female partners. Both male and female participants were less willing to shoulder a free-riding male, compared to a female free-rider.

In public goods studies, like those of Sell and colleagues and Kerr and MacCoun, the potential beneficiary of cooperation and signaled audience member are the same. However, people may use generosity toward one party to signal others (Smith and Bird 2000). An experiment by Iredale et al. (2008) showed that males made larger monetary donations to charity when in the presence of an attractive female observer, compared to an attractive male observer. Female participants, on the other hand, were unaffected by

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[6] The incentive structure of the motor production task is similar to the Chicken Game discussed earlier. Sex composition effects aside, if feedback indicates the partner is free-riding, the participant is better off exerting effort to gain the bonus. On the other hand, if feedback indicates that one's partner is exerting sufficient effort to reach the goal each trial, the participant is better off not expending effort, since he or she will receive his or her share of the bonus regardless.

the sex of the observer. This is perhaps the strongest evidence for our costly signaling hypothesis, since the targets of the cooperation and signal were distinct.

Finally, results from a study by Andreoni and Petrie (2008) are relevant to the ancillary "competitive altruism" hypothesis presented earlier. The study, designed to address the impact of sex- and beauty-composition on contributions to public goods, displayed photos of all group members on participants' computer screens during the public goods task. In a condition in which individuals knew each others' contributions, males contributed more as the proportion of males in their group increased. In fact, the authors draw on costly signaling theory to explain this result, suggesting that males may have been competing to be perceived by females in the group as more cooperative or group-oriented. Thus, although more systematic evidence is clearly needed, the results are in line with the ancillary costly signaling hypothesis. Later, we address the need to more systematically tease apart the opposing effects of larger female audiences (which makes the signal more efficient) and larger male audiences (which creates the need for a stronger, or more cooperative, signal).

Results from Trust Games Do Not Contradict the Signaling Account.

Before moving on to our next hypothesis, we note that studies of one-shot trust games in which participants know each others' genders tend to find no effect of sex-composition on trust or trustworthiness (see studies reviewed in Buchan et al 2008). Although important, we do not believe the absence of sex-composition effects is inconsistent with the costly signaling account for the following reasons. Briefly, high levels of trust (as indicated by the truster's behavior) do not point to any of the underlying qualities that male-generosity in the presence of females is assumed to signal (e.g., status, leadership, willingness to share resources). This is because there is at least an implicit assumption that the sender should return some amount of the transfer (see Coleman 1990). Thus, the only underlying quality that the truster's behavior clearly signals is *trust*. And we know of no reason to expect sex composition effects with respect to trust (see also Buchan et al. 2008).

In addition, the costly signaling hypothesis does not suggest we should expect sex composition effects for a trustee's behavior. This is because the resources that might be returned by the trustee originate with the truster. Thus, the trustee cannot use return amounts to signal generosity with his or her *own* resources. Instead, other factors (e.g., norms of reciprocity, or the sex of the trustee, as discussed earlier) should be the primary determinant of a trustee's behavior. This is exactly what prior research has shown (see Buchan et al. 2008).

Summing up, the results of prior work are consistent with the costly signaling account, with males showing high levels of cooperation and prosocial behavior in the presence of a female audience. Furthermore, this seems to hold whether the beneficiary of the prosocial behavior and the intended target are the same (as in public goods games) or whether prosocial behavior is used to signal an observer who does not benefit from the prosociality per se (as in the public contributions to charities). Finally, we do not find sex composition effects in those types of decisions that do not lend themselves to costly signals (as in trust games). We now turn to a second aspect of social structure expected to effect sex differences in cooperation.

Intergroup versus Interpersonal Cooperation Problems

While most research has focused on the effects of sex differences in cooperation in *interpersonal* social dilemmas, evolutionary theorizing suggests we should also expect sex differences in cooperation (and competition) to vary with interpersonal versus intergroup contexts.

Researchers have long noted differences in male- and female-approaches to group versus interpersonal interactions (e.g., Baumeister and Sommer 1997; Benenson 1993; Gabriel and Gardner 1999). Furthermore these differences appear at a very early age. For instance, experiments show that, among children as young as three years old, females show a greater preference for interpersonal interaction whereas males show a preference for group interaction (Beneson 1993). These differences continue into adolescence and adulthood (Baumeister and Sommer 1997) and have a number of important consequences. For instance, whereas females tend to define themselves in terms of interpersonal relationships, males tend to define themselves in terms of group memberships (Gabriel and Gardner 1999).

We build on an evolutionary framework to suggest that a sex difference in group versus interpersonal orientations should manifest itself in differential responses to intergroup versus interpersonal contexts. Males in ancestral environments engaged in substantially more intergroup conflict than females (Keeley 1996). And prior research shows that, despite the risks, there are also benefits to males who engage in warfare. For instance, in traditional societies, male warriors are granted higher status and have more mates than non-warriors (Chagnon 1988).

Following Van Vugt et al. (2007), we suggest that the males' evolutionary legacy with intergroup conflict and the consequent intergroup orientation will lead them to respond more competitively or non-cooperatively to intergroup contexts, compared to interpersonal contexts. As a result, we should expect *higher ingroup cooperation and greater between-group competition from males, compared to females. Females on the other hand are expected to respond more strongly to interpersonal contexts, directing their cooperation or self-sacrifice towards close others***.** We now turn to existing experimental evidence relevant to these hypotheses.

A vignette experiment by Gabriel and Gardner (1999) assessed participants' willingness to sacrifice their own self-interest for the benefit of a friend (in the interpersonal condition) or for a group's benefit (in the collective case). Consistent with above reasoning, females were more likely than males to forgo their own self-interest in the interpersonal case, whereas the sex difference was reversed in the collective case, with males showing greater self-sacrifice for the group.

Our hypothesis also predicts that males will respond more strongly to intergroup comparisons and interactions than females. Van Vugt et al. (2007) compared the contributions of males versus females to public goods. Participants were led to believe that the study was being conducted at several universities in addition to their own. Those in the *intergroup* condition were told that the goal of the research was to compare performance across universities (thus establishing an intergroup comparison context), while those in the *individual* condition were told that the goal was to compare the performances of individuals. Across three different experiments, including one-shot and repeated public goods games, males responded strongly to the manipulation, contributing at higher levels in the intergroup than the individual condition. Females, on the other hand, were unaffected by the intergroup manipulation.

Some studies find that females respond as strongly as males to intergroup manipulations. For instance, in a study of common pool resources, Kramer and Brewer (1984) found that while males responded more strongly than females to one basis of intergroup comparison (age), females responded just as a strongly as males to an intergroup manipulation based on college major. Thus, while there is some evidence that intergroup manipulations positively impact both males' and females' cooperation with ingroups, the bulk of the evidence suggests that this tendency is stronger among males than females.

We should expect sex differences to emerge not only for cooperation with an ingroup, but also for competition with outgroups. A meta-analysis (Wildschut et al. 2003) of findings on the individual/group discontinuity effect (the tendency for groups to be more competitive than individuals) revealed a greater discontinuity for males than for females. Thus, when considered in light of the above findings, these results suggest that males' stronger responses to intergroup contexts can have two distinct but related consequences: greater cooperation within groups and greater competition between groups.

Summing up, we believe the bulk of evidence provides support for the preliminary hypothesis that males will respond more strongly than females to intergroup contexts. Compared to females, males tend to cooperate at higher levels with ingroup members composed of strangers, and to be more competitive in intergroup interactions. Females' orientation, on the other hand, leads them to be more prosocial toward close relations. The section to follow outlines some suggestions for future work on the intergroup hypothesis and the two other sets of hypotheses presented above.

Direction for Future Research

Although the findings outlined above point to the plausibility of our preliminary framework, most of the studies were not designed specifically to test these hypotheses. Thus, this section fleshes out some additional implications of our framework and briefly points to some possibilities for future work.

The motivational structure hypotheses could be straightforwardly extended to other types of dilemmas (e.g., the Chicken and Assurance Dilemmas given in Figures 2 and 3), as well as to sequential decision collective action problems. In real-world public goods, people often make their decisions sequentially, with knowledge about the number of others who have already contributed (e.g., Erev and Rapoport 1990). In such situations, the motivational structure changes over time (Heckathorn 1993; Marwell and Oliver 1993). Initial stages of collective action, *fear* that others will not contribute motivates non-cooperation. The collective action problem then is transformed into Prisoner's Dilemma, where both fear that further contributions will not be forthcoming, *and* a desire to free-ride on others' past (and potential future) contributions motivate non-cooperation. The latter stages of mobilization primarily confront potential contributors with greed, i.e., an incentive to free-ride on the already-successful efforts of others. Our earlier arguments about motivational structures suggests that, all other things equal, we should expect higher contributions from males and females in the earlier and latter stages of collective action, respectively. Future research should assess these predictions using data on contributions to real world collective actions, or by modeling sequential-decision collective actions in laboratory experiments.

Contributions to real world collective actions may also provide an interesting venue for additional tests of the costly signaling account presented earlier. A number of previous researchers have interpreted participation in protests and social movements in light of costly signaling arguments (Miller 1996; for a review, see Kanazawa 2001). However, a systematic test awaits future work. The research outlined earlier suggests that the costly signaling account may prove useful in illuminating sex differences in participation in various forms of social movements.

Our application of costly signaling theory provides a springboard for a number of additional studies. For instance, the suggestive evidence from Andreoni and Petrie (2008) that males engage in competitive prosociality in mixed-sex groups needs to be explored more systematically. One particularly important question for future work relates to optimum sex-composition. On the one hand, according to the signaling account, a greater proportion of females means a larger audience for males' signals, but fewer males with whom to compete for the status of best leader or "most generous" group member. On the other hand, a greater proportion of males means more competitors (and thus a greater incentive to act more prosocially) for a smaller audience. It isn't clear how signalers strike a balance between these competing motives. But future research should address these issues through a more systematic investigation of sex composition and signaling processes.

We also need an empirical test of whether sex differences in the tendency to engage in costly signaling reverse for other types of pro-social behavior. For instance, Iredale and colleagues (2008) found the costliest signals (larger charitable donations) by males in the presence of attractive females. But our ancillary hypothesis predicts greater amounts of volunteering by females than by males in the presence of a potential mate. Additionally, we should note that prior research suggests that females place less emphasis on mate attractiveness than other characteristics. Thus, future replications of Iredale et al. (2008) may also manipulate characteristics of the observer that may be more relevant to female signaling strategies. For instance, the relative status of an opposite-sex observer should have a greater impact on females' tendencies to engage in costly signaling.

In addition to testing direct implications of our arguments, a careful integration of our hypotheses should generate new testable insights. For instance, prior research (Insko et al. 1990; Schopler et al. 2003; Wildschut and Insko 2007) interprets the individual-group discontinuity effect in terms of how groups' versus individuals' respond to the fear and greed components of social dilemmas. Given that males show more discontinuity and respond more strongly to the greed component (and less strongly to the fear component), these two lines of reasoning can be usefully integrated to address how the sex composition of groups interacts with the motivational structure of group interactions (whether they are primarily driven by greed or distrust) to develop a more nuanced understanding of discontinuity processes.

Conclusion

The problem of sex differences in cooperation has been a long-standing issue in the social sciences. Researchers in a range of disciplines have offered varied arguments about whether and why we should expect sex differences in cooperation and, if so, whether we should see more cooperation by males or females. The evolutionary framework presented in this paper points to a key reason for the contradictory conclusions from previous work: with some important exceptions (e.g., Buchan et al. 2008; Kerr and MacCoun 1985; Sell 1997), previous research has tended to focus on *main effects* of sex. But the evolutionary framework suggests that the impact of sex on cooperation will be highly contingent on the situation. For instance, we have shown that whether males or females are more cooperative depends in predictable ways on the situation's motivational structure. Similarly, the evolutionary framework offers specific predictions about how social structural features of the situation, including sex composition effects and group vs. individual decision contexts, do or do not lead to sex differences in cooperation. In short, the framework provides a clear account of why we should not expect sex differences in cooperation independent of context.

Although the bulk of findings reviewed herein are consistent with our evolutionary framework, a number of important caveats are in order. First, as noted earlier, our goal was not to offer a comprehensive review of the literature on sex differences in cooperation. Thus, future research should more thoroughly weigh the evidence relevant to our framework. Perhaps more importantly, future research should conduct new tests of various implications of our arguments. Some implications for which no relevant data currently exist were outlined in the previous section.

At a theoretical level, the most important limitation of the current work is that, for simplicity, we focused almost exclusively on evolutionary bases of sex differences in cooperation. As a result, we ignored many important social and cultural factors that undoubtedly play a role as well. For instance, females sometimes respond more strongly than males to intergroup contexts. In short, we are not suggesting that situation-dependent sex differences anticipated by our framework are immune to cultural and socialization forces. The evolved social psychology of human behavior is decidedly malleable. Explicitly incorporating social and cultural processes into the evolutionary framework would almost certainly take us much further in advancing coherent answers to the question of sex and cooperation that has long puzzled social scientists and laypeople.

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Figure 1: Prisoner's Dilemma

	C	D
C	3, 3	1, 4
D	4, 1	2, 2

$T = 4 > R = 3 > P = 2 > S = 1$

Figure 2: Chicken Dilemma

	C	D
C	3, 3	2, 4
D	4, 2	1, 1

$T = 4 > R = 3 > S = 2 > P = 1$

Figure 3: Assurance Dilemma

	C	D
C	4, 4	1, 3
D	3, 1	2, 2

$R = 4 > T = 3 > P = 2 > S = 1$

Figure 4: Fear of Greed Dilemma

	C	D
C	4, 2	1, 4
D	4, 1	3, 1

Focal (Row) *Player:* $T = R = 4 > P = 3 > S = 1$
Other (Column) *Player:* $T = 4 > R = 2 > P = S = 1$

Figure 5: Greed Dilemma

	C	D
C	2, 2	1, 4
D	4, 1	1, 1

$T = 4 > R = 2 > P = S = 1$