

The role of costly commitment signals in assorting cooperators during intergroup conflict

Martin Lang^{1*}, Radim Chvaja^{2,3} and Benjamin G. Purzycki⁴

¹ LEVYNA, Masaryk University, Brno, Czech Republic

² European Research University, Olomouc, Czech Republic

³ Religion Programme, University of Otago, Dunedin, New Zealand

⁴ Religious Studies, Aarhus University, Aarhus, Denmark

* Corresponding author: Martin Lang (martinlang@mail.muni.cz)

Pre-print 13/10/2023

Paper published in Evolution & Human Behavior:

<https://www.sciencedirect.com/science/article/pii/S1090513824000035/>

Abstract

A reliable assortment of committed individuals is crucial for success in intergroup conflict due to the danger of shirking. Theory predicts that reliable communication of commitment is afforded by costly signals that track cooperative intent. Across four pre-registered studies (total N = 1,440, general US population), we used the public goods game where groups competed for resources to investigate whether and how costly signals function to assort cooperators. We found that costly signals assorted more cooperative participants, creating groups that would win most of the between-group clashes. The same effects were not observed when participants were assigned to signal, implying that signaling tracks but does not create cooperative intent. However, contrary to costly signaling theory, we found that low cost signals were more effective in cooperator assortment compared to high cost signals and suggest that future studies need to focus on signaler perception of cost/benefit trade-off of signaling.

1. Introduction

Inter-group conflict over limited resources is thought to be one of the significant drivers of human evolution, shaping human-specific psychology (Bowles, 2008; Choi & Bowles, 2007; Henrich & Muthukrishna, 2021) as well as cultural beliefs and practices that may help outcompete less-cooperative parties (Eckel et al., 2016; Handley & Mathew, 2020; Richerson et al., 2016; Zefferman & Mathew, 2015). Among the key factors predicting success in conflict is the level of intra-group cooperation, where efforts are directed either to increase group resources or to disadvantage competing groups through premeditated acts of aggression (Bowles & Gintis, 2011; De Dreu et al., 2020), which in extreme cases includes even self-sacrificial acts (e.g., suicide terrorism).

Evidence from geographical areas recently perturbed by intergroup conflict lends initial support to this hypothesis: in experimental economic games, participants who experienced violent oppression from other groups play more cooperatively with their ingroup members (Bauer et al., 2014; Gilligan et al., 2014; Voors et al., 2012; albeit not everywhere: Werner & Lampsdorff, 2020), and directly experiencing conflict-related violence predicted later engagement in a community's collective action (Bellows & Miguel, 2009). While these studies were conducted post-conflict and cannot speak to the dynamics of conflict-related cooperation, laboratory studies that manipulated the presence of between-group competition in economic games showed that participants in conflict situations contribute more to a common pool of their group (Majolo & Maréchal, 2017), punish ingroup non-contributors (Sääksvuori et al., 2011), and that cooperative groups have a higher probability of success (Francois et al., 2018).

However, coordinating people to align their interests in order to defeat other parties through increased cooperation is no small feat, given the allure of free-riding that may significantly endanger the whole endeavor. Since intergroup competition is often a numbers game, securing commitment to the joint action among party members is of utmost importance. As illustrated by raiding parties in small-scale societies, people are sensitive to the imbalance of power and are willing to partake in a raid only when having sufficient advantage (Wrangham & Glowacki, 2012), especially when shirking may quickly shift the balance of powers in favor of the opposing party (see Mathew & Boyd, 2014 for consequences of deserting a raiding troop). Scaling the commitment problem from raiding parties to oppressed groups, having the means for the committed members to assort and self-organize similarly predicts the probability of initiation of insurgencies and ethnic conflicts (Ellingsen, 2000; Fearon & Laitin, 2003; Jakobsen & De Soysa, 2009)

While people may verbally commit to helping during intergroup conflict (Glowacki et al., 2016), a verbal commitment is often unreliable and gives individuals with Machiavellian strategies a chance to exploit others (Bereczkei et al., 2015; Számádó, 2010). This problem is amplified in one-shot cooperative dilemmas like conflicts where one side can lose viable resources or risk significant personal harm. A potential solution to communication dishonesty is attaching a cost to communicating commitment such that uncommitted individuals would not be willing to pay the cost if they are not planning to cooperatively partake in the conflict (Sosis et al., 2007). As formalized by costly signaling theory, when both the signaler and receiver may benefit from reliable communication of a signaler's hidden quality (communicating conflict-related cooperative intentions in this case), the high-quality signaler will endure a communication cost to demonstrate signal reliability, and this cost will be disadvantageous for individuals low on the signaled trait, given the purported benefits (Grafen, 1990). In other words,

the hidden quality affects the cost/benefit ratio that the potential signallers face (note that the cost may also be zero for high-quality signallers as long as it is positive for low-quality signallers; Számadó et al., 2022).

The cost/benefit trade-off of signaling was suggested to guarantee the reliability of the human communication of cooperative intent (Bliege Bird & Smith, 2005) and received initial support from mathematical models showing that such signals may evolve under various constraints (Gintis et al., 2001; Roberts, 2020; Salahshour, 2021) and have stable equilibria (Barclay et al., 2021; Lotem et al., 2003; McNamara & Houston, 2002). A laboratory study showed that generosity is associated with cooperative intentions (Fehrler & Przepiorka, 2013), and evidence from communities in Oceania, South America, and South Asia further documented that this generosity is repaid with cooperative opportunities and support from others (Bliege Bird & Power, 2015; Lyle & Smith, 2014; Power & Ready, 2018). Several authors further argued that generosity is not limited to the expectation of reciprocity and may be used as a costly signal of cooperative intention since people increase their generosity when observed (Bereczkei et al., 2010; van Vugt & Hardy, 2010) and when having a chance to be chosen by cooperative others, a phenomenon labeled as competitive altruism (Barclay & Willer, 2007; Sylwester & Roberts, 2010, 2013).

Nevertheless, the boundary between generosity being a costly signal or an investment with the expectation of reciprocal repayment is rather thin and permeable. Although some cultural mechanisms, such as indiscriminate generosity, may *prevent* expectations of reciprocity (Bliege Bird & Power, 2015), the reputation for being generous is often in the eyes of the people with whom an individual frequently interacts (Power & Ready, 2018) and who, therefore, are most likely to reciprocate. Moreover, generosity is a broad and vague quality, and its utility may be dubious in specific collective risky joint actions such as raids or intergroup conflicts. Although people may be generous, it does not guarantee that they are committed to a specific collective action in a particular domain (e.g., a raid). To overcome the vagueness problem, commitment signals to a joint action are often embedded within cultural conventions that prescribe the form and expected costs of the signaled message such that it could be easily decoded by receivers (Barker et al., 2019; Lang & Kundt, 2023; Soler et al., 2014).

For example, the Tsembaga of New Guinea had a complex ritual system used to signal war allegiances with various visual markers, performative dances, and pig sacrifices (Rappaport, 2000). These rituals indicated a willingness to participate in ensuing warfare with a costly signal (pig sacrifices, energy spent), effectively allowing ritual organizers to assess the troop's potential strength (i.e., how many people showed up/danced/sacrificed pigs). Using cross-cultural ethnographic databases, Sosis et al. (2007) investigated the association between costly male rituals (such as teeth-pulling, scarification, piercing, tattooing, and learning secret knowledge) and external warfare in 60 small-scale societies, finding that the number and intensity of required costly rituals were positively associated with the frequency of intergroup conflict. Albeit correlational, this result hints at a causal process where conflict pressures groups to enhance their cooperative efforts, which are bolstered by assorting cooperators through costly signaling. Of course, costly signals would often be embedded within a complex system of cultural/religious beliefs, myths, traditions, and identities that may further fuel inter-group conflict (Akbaba & Taydas, 2011; Brubaker, 2015; Neuberger et al., 2014). Yet, it is the potentially causal role of costly signals in mobilizing a competing troop that we experimentally examine here.

To add validity to our experimental setup, we note that the costly signals associated with warfare differ from the usually studied signals of cooperative intent (e.g., generous giving) in three inter-related ways,

requiring a novel approach to this question: 1) conflict-related signals often have low or non-existent personal value for signal recipients (unproductive signal costs), 2) cooperative dilemmas may be non-iterative due to the potentially dire consequence of inter-group conflict, limiting future repayment of the signal, and 3) if cooperative dilemmas are one-shot, other factors than cooperative reputation are needed to explain signal stability.

Regarding the first aspect, Sosis et al. (2007) showed that conflict-related costly signals often include pain, body modifications, and similar signals that do not benefit recipients (in contrast to a signaler's generous giving). This may be due to the pluripotency of such signals (signaling both a commitment to joint action and specific qualities related to conflict – e.g., bravery, pain tolerance, anxiety management etc.; Barker et al., 2019; Lyle et al., 2009). Nonetheless, using unproductive costs rather than generosity has further advantages, such as limiting reciprocity expectations, thereby effectively increasing signal trustworthiness (i.e., recipients perceive that selfish motives of expected future rewards do not drive the signal; Bliege Bird et al., 2018; Raihani & Power, 2021). Furthermore, in cooperative dilemmas with long return rates (e.g., offspring quality when reaching adulthood), or dilemmas where a potential cooperator may become a competitor (e.g., warfare), signals with unproductive costs limit the temptation of signal recipients to exploit the signaler (Bergstrom et al., 2008; Bolle, 2001). Signaling cooperative intent with generosity may be risky if such signals strengthen a possible opponent, creating a second-order signaling problem (signalers need to trust recipients of their signals). Thus, rather than looking at generosity as a costly signal, it is crucial to investigate signals with unproductive costs that may better capture conflict-related signaling.

The case of inter-group conflict also differs from previous studies of generous giving because conflict carries essential risks of injury and even fatality when betrayed by others, making the cooperative dilemmas potentially one-shot rather than repeated. However, previous models using generosity as a costly signal often relied on the repetitive nature of interactions that secures' signaler benefits (Roberts, 2020), and the same is true of a recent experimental study with unproductive costs (Lang et al., 2022). That is, due to the pre-determined number of interactions, people paying the signal cost and then defecting would be worse off than just plainly defecting. Yet, this is not necessarily the case if defectors could, for instance, desert to the other side during conflict. This caveat calls for a better understanding of how could costly signals work in one-shot interactions.

Importantly, the canonical costly signaling model (Grafen, 1990) postulates that costly signals should be effective in one-shot scenarios (e.g. when handicaps signal genetic quality). The assumption of differential costs has been built into the previous costly signaling models of cooperative intent (Gintis et al., 2001; McNamara & Houston, 2002), but it is unclear why generosity should be differentially costly for people with different intent. While genetic quality may directly affect signal intensity in animal models, this link is more flexible in human intention signaling (Fehrler & Przepiorka, 2013; Sosis, 2003). One possible mechanism facilitating the willingness to pay the signal cost is the perception of the costs and benefits of signaling, which may be biased by the signaler's intention (Sosis, 2003). For instance, blood donors perceive the health risks of blood donations as lower than non-donors, affecting the decision to send the signal (blood donation) or not (Lyle et al., 2009). Yet, this assumption remains largely untested in cooperative signaling (with the exception of Lang et al., 2022), hence this manuscript aims to shed light on this potential mechanism.

In summary, while previous studies suggest that costly signals may facilitate the reliability of communicating cooperative intent in iterated interactions, it is not clear whether and how costly signals

may help assort cooperators during inter-group conflict. To fill this gap, we conducted four pre-registered studies with a general US population. We used an experimental framework where participants were first scored on their cooperative strategies, randomly divided into high and low cost conditions (cost manipulation), and then asked to choose a group in which they will play a PGG. They could choose between a group requiring a commitment signal (burning resources; we manipulated the amount of resources needed for the signal) and a group without such a signal. After this assortment, participants played one-shot PGG and competed with other groups.

In Study 1, we tested the effects of costly signals in a one-shot PGG with no conflict to get a benchmark result for later studies. In Study 2, we added between-group conflict. We achieved this by awarding the more cooperative group $\frac{1}{4}$ of the earnings from the less cooperative group. This modification allowed us to investigate how the possibility of sending costly commitment signals changes the within- and between-group dynamics during conflict. We also gave participants an opportunity to sacrifice part of their endowment to disadvantage a competing group and tested whether costly signals play a role in the decision to sacrifice for the group. In Study 3, we replicated Study 2 but disassociated the signal cost from resources used during the conflict to avoid disadvantaging signaling groups. Finally, in Study 4, we tested a rival proposition that forced costly signals create commitment in participants rather than signals it. We randomly assigned participants into the signaling and non-signaling groups, testing whether forced signaling would push people to stronger parochial cooperation (including self-sacrifice) despite their preferred strategies.

2. Study 1

2.1. Methods

2.1.1. Participants

Based on the power analysis from our previous study (Lang et al., 2022), we recruited 381 participants from the general US population on the platform Prolific.co, aiming for 320 participants in the final sample. The US population was a convenient sample due to the language of the study and the availability of online participants. After removing participants who did not finish the experiment or did not fit our pre-registered criteria (see SM, section S1), the final sample comprised 337 participants (149 women, 181 men, and seven people selecting another gender; $M_{\text{age}} = 36.0$, $SD = 13.3$). Participants provided informed consent and received 1 USD as a show-up fee plus any amount they earned in the two PGGs ($M_{\text{earning}} = 4.03$ USD, $SD = 0.60$). All studies were approved by the Ethics Committee for Research at Masaryk University.

2.1.2. Design

Participants first filled out a survey on demographic questions and subsequently got acquainted with PGG. Upon demonstrating that they understood the PGG rules, participants were endowed with 1 USD and asked to play a conditional PGG that allowed us to obtain information about participants' cooperative strategies (Fischbacher et al., 2001). That is, we assessed how much are participants' contributions conditional on the mean contribution of other participants: matched contributions

indicate a cooperative strategy and low contributions indicate a selfish strategy. See SM, Section S1.1. for details. After making the conditional decisions, participants were randomly assigned into either the high cost or low cost conditions (see below). Next, they were endowed with 2 USD to play PGG with three other anonymous players (where others' contributions are unknown). All subjects were given a choice of two groups with whom they could play PGG. We call these groups the "revealed" group (revealing intentions through signaling) and the "concealed" group (no signal, hence intention concealed); however, participants decided between groups randomly labeled "X" and "Y." Both groups were defined as trying to maximize the group profit by high contributions from individual members. However, in the revealed group, the willingness to contribute high amounts was explicitly communicated by a sacrifice of part of the endowment (15% in the high cost condition and 2.5% in the low cost condition, based on our randomization), while no such sacrifice was required in the concealed groups (see SM, Section S1.1. for full instructions). That is, participants could choose whether they want to signal their intention of high contribution by burning part of their endowment.

In the next step, participants were informed that they will be randomly paired with three other individuals who chose the same group and asked to allocate any amount from their remaining endowment to the common pool in an interval of 1 USD cents. Participants in the revealed groups could invest only 1.7 (high cost) and 1.95 USD (low cost) after paying the signal cost. After making their allocations, participants were asked why they chose the revealed/concealed group and how much they expected to get back from the group game. After we collected all data, participants were randomly assigned to teams of four based on their choice of the revealed/concealed groups and conditions. Their earnings were calculated and paid through the Prolific app, together with the show-up fee.

2.1.3. Measures

Cooperative strategies were assessed using the conditional PGG, classifying participants into cooperative (matched others' contributions), tempted (matched others' contributions only for low contributions, then selfish), and selfish strategies (generally zero or low contributions). Note that while we pre-registered predictions concerned only the differences between cooperative and selfish strategies, here we report comparisons of cooperative strategies with tempted and selfish strategies collapsed together (this is true for all studies in this paper). The reason for this step is that tempted and selfish both played selfishly in the FGF version of PGG (see Supplementary Results for each study in SM) and by collapsing tempted and selfish strategies into one category, our sample in all studies is divided roughly 50/50 between the cooperative and selfish strategies, increasing the statistical power of planned comparisons (originally planned comparisons between the three types are reported in SM).

Our primary dependent variable assessing whether choosing the revealed group would be associated with intra-group cooperation was the proportion of the remaining endowment contributed to PGG. Participants anonymously allocated any amount from their remaining endowment in an interval of 1 USD cents to the common pool. The sum in the public pool was doubled and then equally redistributed among the four players independent of their allocation. We also asked about age, gender, and financial situations but did not plan to use these variables in the test of our main hypotheses.

2.1.4. Analysis

Analyses were conducted in R (R Core Team, 2020) using the *glmmTMB* package (Brooks et al., 2017) and the *gamlss* package (Stasinopoulos & Rigby, 2007). The probability of selfish individuals present in the revealed group was modeled using logistic regression. Beta regression (with transformed 0s and 1s according to Smithson & Verkuilen, 2006) was used to model the percentage of endowment contributed to the common pool. In the next step, we used Zero-or-one inflated beta regression (ZOIB) to compare specific aspects of contributions, that is, the probability of contributing 0% (denoted as 0), the probability of contributing 100% (denoted as 1), and the percent contributed excluding 0% and 100% contributions. While the probabilities of zero and one are each conditional on the probability of non-zero or one contributions (see Rigby et al., 2019 for technical details), we transformed the estimated probabilities to be interpretable as probabilities of 0% and 100% contributions, which we report in the main text along raw model estimates.

2.1.5. Hypotheses

(H1.1) Cooperators will be more likely to choose the revealed group than selfish individuals, and (H1.2) this difference will be larger in the high cost compared to the low cost condition.

(H1.3) Participants in the revealed group will allocate a larger portion of their remaining endowment to a common pool in PGG compared to participants in the concealed group, and (H1.4) this difference will be larger in the high cost compared to the low cost condition.

2.2. Results

2.2.1. Pre-registered analyses

Participants were equally represented across the high ($n = 169$) and low ($n = 168$) cost conditions. In the high cost condition, 60 participants chose the revealed group, and 109 the concealed group. In the low cost condition, 55 participants chose the revealed group and 113 the concealed group. As predicted (H1.1), participants playing selfish strategies were less likely to choose the revealed group than cooperators ($\beta = -0.71$, 95% CI = [-1.18, -0.25]), demonstrating the functional assortment of costly signals. The estimated probability of joining the revealed group was 42% for cooperative and 26% for selfish strategies. However, contra our prediction (H1.2), this difference was smaller in the high cost compared to the low cost condition ($\beta_{\text{interaction}} = -0.97$, 95% CI = [-1.91, -0.04]). There was no difference in the probability of choosing the revealed group between the cooperative (38%) and selfish (33%) strategies in the high cost condition, and the observed effect was driven by the low cost condition (cooperative = 45%, selfish = 20%).

Regarding cooperative behavior, we observed that participants in the concealed groups contributed, on average, 47% of their endowment, while participants in the revealed groups 60% (H1.3). Using the Beta regression, we found that this difference was well-estimated ($\beta = 0.48$, 95% CI = [0.18, 0.79]). The ZOIB regression further allowed us to infer the probability of contributing nothing (0) or everything (1) to the common pool as well as the size of the mean contribution excluding 0 and 1. We found that revealed groups contributed a larger portion of their remaining endowment compared to concealed groups ($\beta_{\text{excluding 0 or 1}} = 0.36$, 95% CI = [0.10, 0.62]) and had a larger probability of contributing everything ($\beta_{\text{of 1}} = 0.48$, 95% CI = [-0.03, 0.99]). While in the expected direction, the between-group difference in the probability of contributing nothing was not reliably estimated ($\beta_{\text{of 0}} = -0.70$, 95% CI = [-1.71, 0.32]).

However, comparing these between-group differences between the high and low condition revealed no interaction effect in the Beta model (H1.4; $\beta_{\text{interaction}} = 0.11$, 95% CI = [-0.49, 0.72]) and the same was true for the ZOIB model. See Figure 1 for illustrations and Tables S1 and S2 for all model estimates and further details on pre-registered hypotheses.

2.2.2. Exploratory analyses

Since we randomly paired participants to calculate their earnings, we did not explicitly predict the between-group differences in earned amounts (the result would be contingent on a particular random number). Nevertheless, by using 1,000 random pairings of participants, we arrived at results robust to chance (although without the possibility of statistical inference to the general population because the degrees of freedom for this statistical test are affected by the number of simulations). The results of these simulations revealed that while participants in the high cost concealed group earned 2.92 USD on average, participants in the high cost revealed group only 2.69 USD. Contrary, participants in the low cost concealed group earned 2.94 USD, and in the low cost revealed group 3.18 USD.

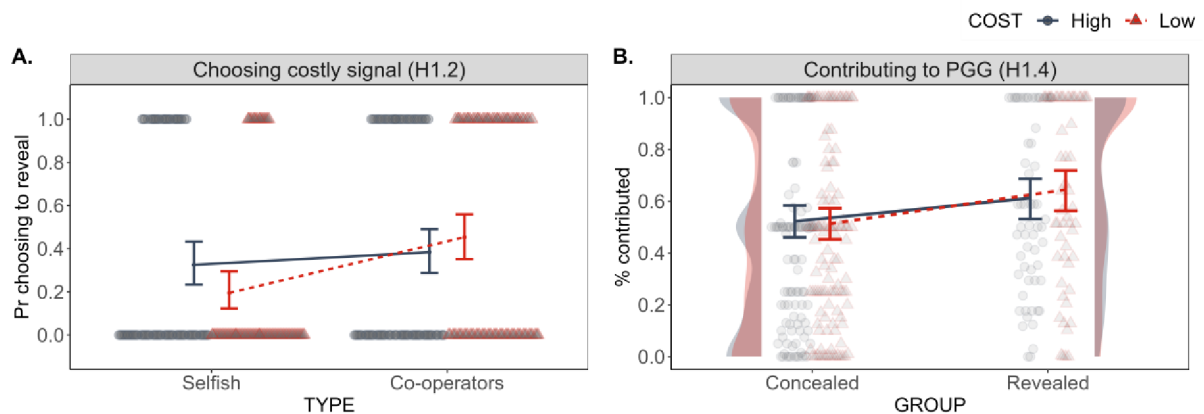


Figure 1 | Results from Study 1. (A.) Signal cost deterred individuals with selfish strategies in the low cost condition but not in the high cost condition. (B.) Both revealed groups contributed higher portions of their remaining endowment, but there was no effect of cost (density plots were added to illustrate the distribution of contribution decisions).

2.3. Discussion of Study 1

In Study 1, our results showed that costly signals, on average, facilitated the assortment of cooperators and led to larger contributions to the common pool in agreement with previous experimental work on costly signaling (Lang et al., 2022). This result suggests that even in one-shot scenarios, costly signaling functions to assort cooperators. However, contra to the previous work and our current predictions, only the low cost signal appeared to be functional in the assortment of cooperators.

Why would a low cost signal work better than the high cost signal in this case? We hazard that participants with selfish strategies did not expect the low cost signal to assort cooperators as it would in the high cost condition; hence, paying the signal cost would not guarantee an opportunity to free-ride cooperators in the low cost condition but would in the high cost condition. Importantly, we expected that this perception will differ under inter-group conflict where free-riding on the signaling group is much less profitable because free-riders also have 'skin in the game'. Indeed, in real life, paying the signal cost and then shirking in conflict might mean negative fitness consequences for the free-rider

if the whole group loses. Thus, we expected that adding intergroup competition to the current design would increase the efficiency of the high cost signal by better repelling selfish individuals. Furthermore, we investigated whether the commitment to cooperation communicated through costly signals indicates only the willingness to work together with team members or also helping one's team by harming the opponent team.

3. Study 2

3.1. Methods

3.1.1. Participants

We used the same recruitment protocol as in Study 1. We recruited 330 participants, and after removing participants based on pre-registered criteria (see SM, section S2.1), the final sample comprised 317 participants (151 women, 161 men, and five people selecting another gender; $M_{\text{age}} = 37.7$, $SD = 12.7$). Participants again received 1 USD show-up fee plus their game earnings ($M_{\text{earning}} = 3.21$ USD, $SD = 0.91$).

3.1.2. Differences from Study 1

The structure of this study copied Study 1 with two crucial additions. When choosing the group for playing PGG, participants were informed that their earnings will partially depend on the behavior of another competing team (Bornstein, 1992), simulating parochial competition (De Dreu et al., 2020). Specifically, participants played PGG against another randomly chosen team, and the team who had a higher sum in the common pool took $\frac{1}{4}$ of the other team's pool. If the two teams had the same amount in the common pool, no one would win, and both teams would retain their pools.

Moreover, after making their allocation decisions, participants were informed that a randomly selected person from each team would be endowed with an additional 1 USD. This additional endowment could be either kept by the chosen participant or used to decrease the sum in the common pool of the competing team by 2 USD, effectively increasing the chance to win for their team. Note that the sacrifice decision should not be driven by the prospect of earning more money because sacrifice would lead to a maximal earning of 0.95 USD for the person who paid the extra 1 USD. All participants were asked to make this hypothetical choice. After the game play, we randomly paired participants into teams based on their choice of group and condition assignment, calculated the size of their common pool, and matched them with another randomly chosen team from the same condition. We randomly selected one participant from each team for whom the sacrifice decision was valid, selected the winning team, and calculated individual earnings. All participants were paid through the Prolific app.

Apart from measures used in Study 1, we additionally collected data on the decision to sacrifice the extra endowment to increase the team's probability of success. We also additionally modeled the difference between the revealed and concealed groups in their willingness to sacrifice the extra endowment to harm the outgroup using binomial regression.

3.1.3. Hypotheses

(H2.1) Cooperators will be more likely to choose the revealed group than selfish individuals, and (H2.2) this difference will be larger in the high cost compared to the low cost condition.

(H2.3) Participants in the revealed group will allocate a larger portion of their remaining endowment to the common pool than participants in the concealed group, and (H2.4) this difference will be larger in the high cost compared to the low cost condition.

(H2.5) Participants in the revealed group will have a higher probability of using the extra endowment to harm the other competing group compared to participants in the concealed group, and (H2.6) this difference will be larger in the high cost compared to the low cost condition.

3.2. Results

3.2.1. Pre-registered analyses

Our sample for Study 2 comprised 156 participants in the high cost and 161 participants in the low cost condition. Compared to Study 1, fewer participants selected the revealed group in the high cost condition (n revealed = 29, n concealed = 127), but the distribution of participants was comparable to Study 1 in the low cost condition (n revealed = 50, n concealed = 111). As in Study 1, participants with selfish strategies were less likely to choose the revealed groups compared to cooperators, providing further support for the functional role of costs in assortment, although 95% CIs of this effect included 0 ($\beta = -0.47$, 95% CI = [-0.99, 0.05]). Contrary to our prediction (H2.2), there was no between-condition difference ($\beta_{\text{interaction}} = -0.06$, 95% CI = [-1.14, 1.02]).

We found that revealed groups contributed on average 68% of their remaining endowment while concealed groups contributed 50%. Modeling these differences with a Beta regression supported our hypothesis that participants in the revealed groups will contribute higher portions of their endowment—an effect that was well estimated (H2.3; $\beta = 0.57$, 95% CI = [0.22, 0.92]). Using the ZOIB regression further showed that revealed groups contributed a larger portion of their endowment ($\beta_{\text{excluding 0 or 1}} = 0.32$, 95% CI = [-0.01, 0.65]), and had a larger probability of contributing everything ($\beta_{\text{of 1}} = 0.88$, 95% CI = [0.33, 1.44]).

Importantly, these between-group differences were larger in the high cost condition (H2.4). We observed that the high cost revealed group contributed the largest percent of their endowment (83%), followed by the low cost revealed group (59%), high cost concealed group (53%), and low cost concealed group (46%). However, note that while these differences are substantial and in the direction predicted, they were unreliably estimated due to the low number of participants in the high cost revealed group. Beta regression of the interaction between the COST and GROUP factor showed the predicted (but poorly estimated) negative effect ($\beta_{\text{interaction}} = -0.48$, 95% CI = [-1.24, 0.28]). Similarly, the ZOIB regression estimated the difference between revealed and concealed groups of the probability of contributing everything as lower in the low cost condition ($\beta_{\text{interaction of 1}} = -1.02$, 95% CI = [-2.22, 0.18]) and while most of the probability mass is below zero, the true effect may be smaller (see the density plots at Fig. 2B).

Finally, the probability of choosing to sacrifice the extra 1 USD to hurt the other competitive team (H2.5) was higher in the revealed (probability = 44%) compared to the concealed (probability = 31%) groups

($\beta = 0.57$, 95% CI = [0.05, 1.09]), supporting the idea that pro-group behavior in revealed groups may also take the form of hurting other competing groups. There was no between-condition difference (H2.6; $\beta_{\text{interaction}} = -0.15$, 95% CI = [-1.22, 0.92]). See Fig. 2 for illustrations and Tables S3 and S4 for all model estimates and further test of pre-registered hypotheses.

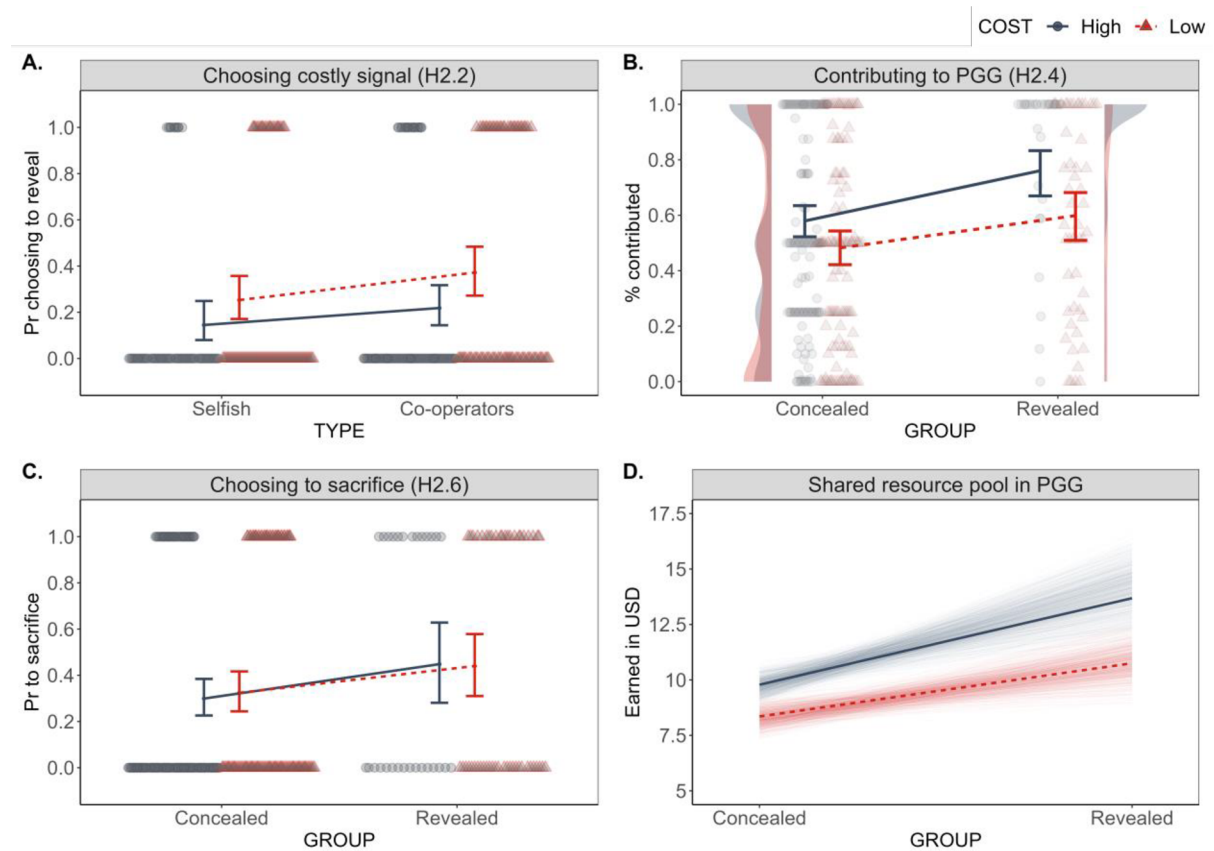


Figure 2 | Results from Study 2. (A.) While cooperators were more likely to choose the revealed groups than participants with selfish strategies (H2.1.), most cooperators did not choose the revealed group in the high cost condition. (B.) High cost revealed group contributed the largest portion of their endowment to the common pool (H2.4.). (C.) Revealed groups had a higher probability of sacrificing the extra endowment (H2.5), but there was no between-condition effect. (D.) Simulations of the Group*Condition interaction effects over 1000 random pairing of participants show that teams formed of the high cost revealed groups would redistribute the largest pool of money.

3.2.2. Exploratory analyses

Our simulations generated 1000 random pairings of participants into teams based on their group choice and condition assignment, random pairings of teams to compete, and random choices of participants for whom the decision to sacrifice an extra endowment was activated (one in each team). The results of these simulations showed that participants in the high cost revealed group would, on average, earn the most (3.71 USD), followed by participants in the low cost revealed group (3.49 USD), participants in the high cost concealed group (3.38 USD) and, finally, participants in the low cost concealed group (3.16 USD).

Looking at the data aggregated at the team level, teams in the high cost revealed group had the highest probability of winning a competition with another team (probability = 78%) despite the cost they had to pay, followed by low cost revealed teams (probability = 58%), high cost concealed teams (probability

= 50%), and low cost concealed teams (probability = 39%). Likewise, high cost revealed teams would, on average, had the largest pool of shared resources to redistribute (13.69 USD), followed by low cost revealed teams (10.75 USD), high cost concealed teams (9.78 USD), and low cost concealed teams (8.35 USD). See Fig. 2D. Importantly, the standard deviation of individual earnings within a team was the lowest in the high cost revealed groups (0.43 USD cents vs 0.69-0.71 in the other groups), indicating that high earnings were evenly distributed in these groups (rather than monopolized by a single free-riding individual).

3.3. Discussion of Study 2

In Study 2, we investigated the effectiveness of costly signaling in the assortment of cooperators during intergroup competition. While we found that most participants (with both cooperative and selfish strategies) chose the concealed groups, cooperators were still more likely to choose the revealed group compared to participants with selfish strategies. Moreover, participants who paid the signal cost were more dedicated to the common cause, especially in the high cost condition. We observed the highest percentage of the remaining endowment contributed to the common pool in the high cost revealed group as well as the highest probability of contributing everything.

The prosociality in the revealed groups was not limited to benefiting other members through mutual cooperation. Participants in the revealed groups were also more likely to sacrifice extra money to harm an opponent team. Our simulations showed that the combination of large contributions to the common pool and willingness to use resources to disadvantage competing teams would make teams in the high cost revealed group the most likely winners of the competition. These teams would also have the largest pool of shared spoils (1.5x the pool of teams in the low cost concealed group; see Fig. 2D). This result suggests that in situations demanding absolute commitment, highly costly signals might give groups a competitive edge over other groups due to committed investments into the group effort. The lowest variance in individual earnings within the teams of the high cost revealed groups further suggest that the group benefits are not restricted only to some individuals at the cost of others but impartially distributed. In the following study, we aimed to mitigate the problem of low number of people choosing the revealed groups by disassociating the signal cost and the amount participants have available to invest in PGG.

4. Study 3

4.1. Methods

4.1.1. Participants

We used the same recruitment protocol as in Study 2. We recruited 345 participants, and after removing participants based on pre-registered criteria (see SM, section S2.1), the final sample comprised 328 participants (161 women, 163 men, and four people selecting another gender; $M_{\text{age}} = 41.9$, $SD = 13.1$). Participants again received 1 USD show-up fee plus their game earnings ($M_{\text{earning}} = 3.66$ USD, $SD = 0.87$).

4.1.2. Differences from Study 2

The structure of this study copied Study 2 with one crucial modification: the signal cost in the revealed group did not decrease the amount participants could invest in PGG. That is, participants received an endowment of 2.3 USD and were told that 0.3 USD is their personal bonus while 2 USD could be used for investments in PGG. When choosing the groups to play PGG with, participants in the high cost condition were offered to give up their personal bonus of 0.3 USD to join the revealed group while in the low cost condition the signal fee was 0.05 USD (and participants would keep 0.25 USD).

Apart from measures used in Study 2, we additionally collected data on personality characteristics that could help explain the choice between the revealed/concealed groups (Trust Propensity scale: Frazier et al., 2013; Forgiveness, Sincerity, and Fairness facets of the HEXACO scale Ashton & Lee, 2009; The General Risk Question: Dohmen et al., 2011.) We reasoned that participants with cooperative strategies may not see the need for costly signals because they operate in contexts where the costs of indiscriminate cooperation are smaller than signaling costs (as shown in the models of Gintis et al., 2001; McNamara & Houston, 2002) and where forgiveness therefore pays off. We also asked participants about their expectations of others' behavior in the concealed and revealed groups.

4.1.3. Hypotheses

(H3.1) Cooperators will be more likely to choose the revealed group than selfish individuals, and (H3.2) this difference will be larger in the high cost compared to the low cost condition.

(H3.3) Participants in the revealed group will allocate a larger portion of their remaining endowment to the common pool than participants in the concealed group, and (H3.4) this difference will be larger in the high cost compared to the low cost condition.

(H3.5) Participants in the revealed group will have a higher probability of using the extra endowment to harm the other competing group compared to participants in the concealed group, and (H3.6) this difference will be larger in the high cost compared to the low cost condition.

(H3.7) Scores on the Trust Propensity scale will be negatively correlated with the probability of choosing a costly signal in cooperators and (H3.8) this effect will be stronger than in selfish individuals

(H3.9) Scores on the HEXACO Forgiveness facet will be negatively correlated with the probability of choosing a costly signal in cooperators (H3.10) this effect will be stronger than in selfish individuals

4.2. Results

4.2.1. Pre-registered analyses

Our sample for Study 3 comprised 164 participants in the high cost and 164 participants in the low cost condition. Compared to Study 2, we saw 59% increase in participants choosing the revealed group in the high cost condition (n revealed = 46, n concealed = 118), although the preference for the concealed group was still dominant. Participants choices in the low cost condition were similar to those in Study 2 (n revealed = 56, n concealed = 108).

Testing H3.1, we again observed that participants with selfish strategies were less likely to choose to signal than participants with cooperative strategies ($\beta = -0.58$, 95% CI = [-1.06, -0.11]). Similar to Study 1, this effect was stronger in the low cost compared to the high cost condition ($\beta_{\text{interaction}} = -1.26$, 95% CI = [-2.23, -0.29]). See Fig. 3 for illustrations and Table S5 for all model estimates. We further tested hypotheses that trust propensity and a willingness to forgive others may cause cooperative participants to perceive the signal cost as unnecessary (because people are cooperative even without signals or can be forgiven for not cooperating). However, the trusting and forgiving cooperators were not less likely to choose the signal (trust: $\beta = 0.89$, 95% CI = [-0.48, 2.26]; forgiveness: $\beta = 0.01$, 95% CI = [-0.32, 0.33]) and interacting these psychological measures with cooperative strategies likewise yielded no reliably estimated differences (trust propensity: $\beta_{\text{interaction}} = -0.32$, 95% CI = [-2.11, 1.47]; forgiveness: $\beta_{\text{interaction}} = -0.18$, 95% CI = [-0.61, 0.24]).

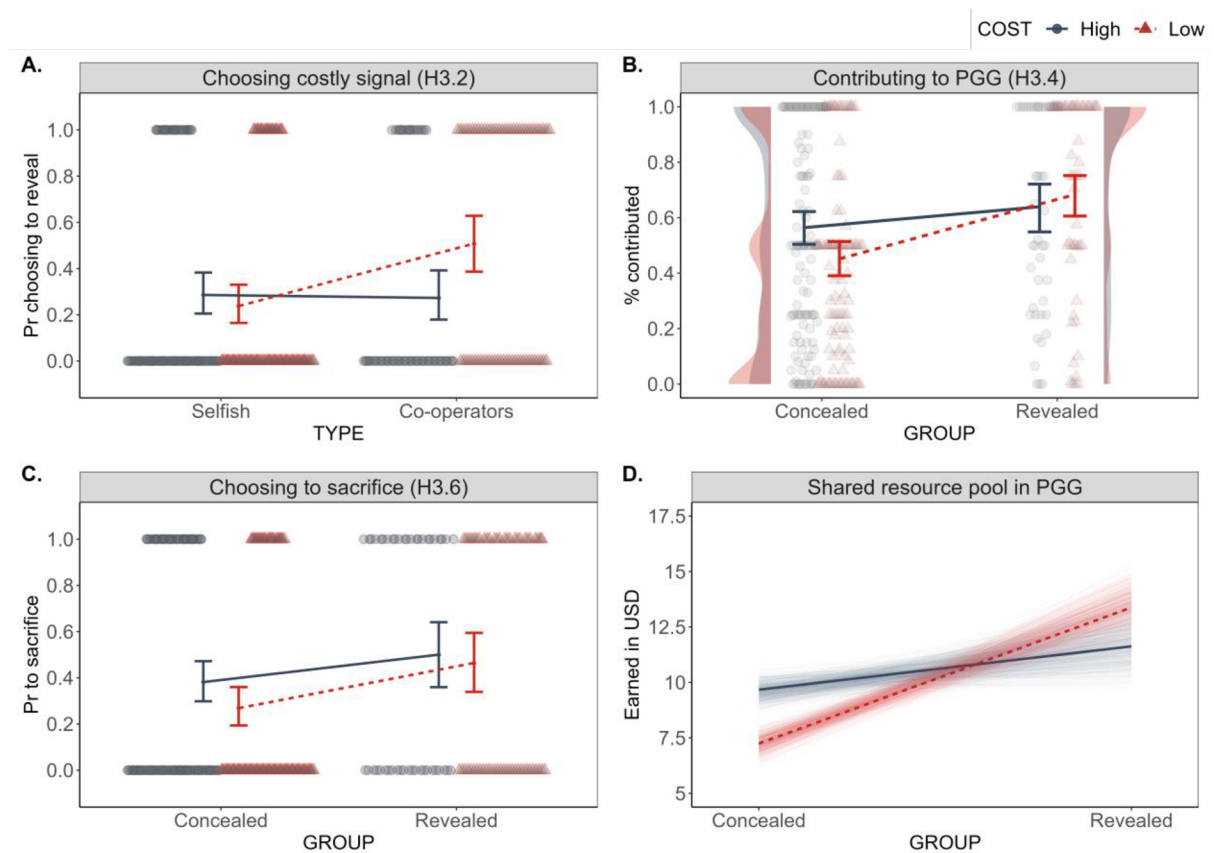


Figure 3 | Results from Study 3. (A.) Signal cost assorted cooperators only in the low cost conditions. (B.) Revealed groups contributed the larger portion of their endowment to the common pool, and predominantly contributed everything. (C.) Revealed groups had a higher probability of sacrificing the extra endowment. (D.) Simulations of the Group*Condition interaction effects over 1000 random pairing of participants show that teams formed of the low cost revealed groups would redistribute the largest pool of money.

Looking at the average contributions, we again observed that the functional assortment of cooperators resulted in higher contributions in the revealed groups (67% vs 47% in concealed groups), and this difference was well estimated in the Beta regression (H3.1; $\beta = 0.65$, 95% CI = [0.33, 0.97]). Analogically to Study 2, the ZOIB regression further showed that revealed groups had a larger probability of contributing everything ($\beta_{\text{of } 1} = 0.89$, 95% CI = [0.38, 1.40]). However, contrary to Study 2, these between-group differences were larger in the low cost condition, albeit the 95% CIs from the Beta regression contained 0 ($\beta_{\text{interaction}} = 0.63$, 95% CI = [-0.02, 1.28]). The results of the ZOIB regression

further showed that this difference was not particular to any of the four parameters that ZOIB estimates.

Regarding the choice to sacrifice an extra endowment to disadvantage the other group, the revealed groups had again a higher probability of sacrifice compared to the concealed groups (48% vs 33%) and this difference was well-estimated ($\beta = 0.64$, 95% CI = [0.16, 1.12]). The between-condition difference was unreliably estimated ($\beta_{\text{interaction}} = 0.38$, 95% CI = [-0.59, 1.34]). See Fig. 3 for illustrations and Table S6 for all model estimates.

4.2.2. Exploratory analyses

We further tested whether the differences between the low and high cost condition in the effective assortment of cooperators stem from different expectations of others' contributions. Subtracting the perception of contributions in the concealed group from the revealed group, the perceived advantage of signaling was on average 3% increase in perceived contributions and this expectation did not differ between the high and low cost conditions for cooperators ($\beta = -0.64$, 95% CI = [-7.14, 5.87]). Selfish participants did not differ from this null finding ($\beta_{\text{interaction}} = -0.88$, 95% CI = [-9.23, 7.47]). Expected probability that the other group will sacrifice the extra endowment to hurt the ingroup predicted individual willingness to sacrifice ($\beta = 1.82$, 95% CI = [0.82, 2.81]), but this motivation did not moderate the larger sacrifice probability in the revealed compared to concealed groups ($\beta_{\text{interaction}} = -1.28$, 95% CI = [-3.44, 0.88]).

Looking at the average earning using the same simulations as in Study 2, we observed participants in the low cost revealed group would earn the most (4.19 USD), followed by participants in the high cost concealed group (3.66 USD), participants in the high cost revealed group (3.57 USD) and, finally, participants in the low cost concealed group (3.29 USD). These earnings were disproportionate to the probability of winning a between-group competition and the amount of shared resources, respectively (low cost revealed: 73%, 13.38 USD; high cost revealed: 63%, 11.62 USD; high cost concealed: 49%, 9.67 USD; low cost concealed: 32%, 7.24 USD). This result reflects the fact that the high cost revealed groups had a mixture of cooperating and selfish participants, leading to a large common pool but low average earnings.

4.3. Discussion of Study 3

Study 3 replicated the general findings of Study 2 (cooperators are more likely to choose a costly signal, contribute more, and win more) with some important qualifications regarding the size of the signal cost. While the design change in Study 3 increased the number of people self-selecting into the revealed group in the high cost condition, this increase included people with cooperative as well as selfish strategies and translated into worse performance of the high cost revealed teams compared to Study 2. In contrast, the low cost signal was efficient in assorting cooperators and as a result the low cost revealed group had the largest investments, probability of winning and earnings. The absence of the difference in expected advantage of signaling between the high cost and low cost conditions suggests that the signaling cost was acceptable in the low cost condition regarding the expected earnings but this would not be the case in the high cost condition where larger contributions need to be expected in order for the signal to appear profitable. Interestingly, summarizing Studies 1-3 in Figure 4A suggests that these trends may be opposite for cooperative and selfish strategies: while increasing signal cost

attracts more participants with selfish strategies (with the exception of Study 2), the opposite is true for participants with cooperative strategies, suggesting an optimal threshold at which costly signals may work.

Another potential explanation of our findings in Studies 1-3 is that our classification of cooperative strategies does not correspond perfectly with actual behavior in PGG. While, on average, the classified strategies corresponded to the behavior (as expected by the signaling theory), in some notable cases (especially in Study 2), participants who were classified as playing the selfish strategy contributed their full endowment in the high cost revealed group (contrary to the signaling theory; compare Fig. 4A and 4B).

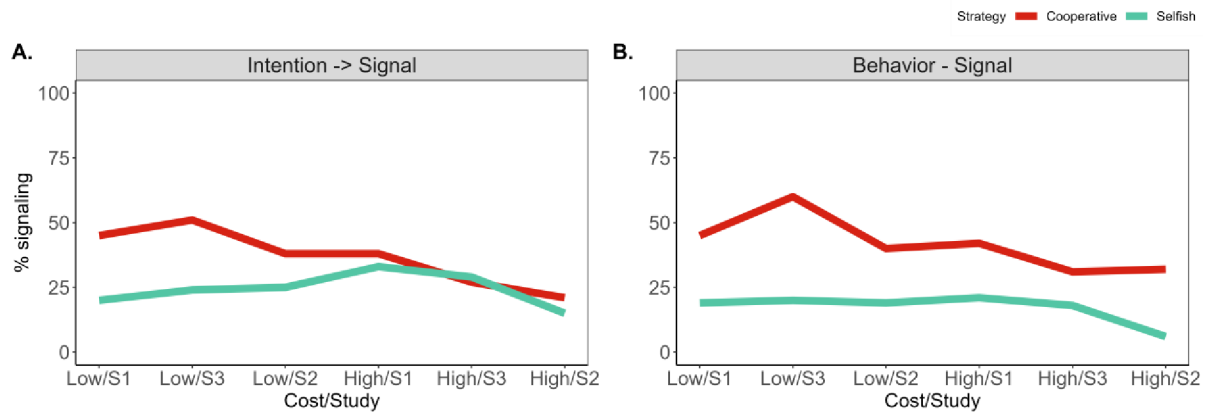


Figure 4 | Summary of signaling probability across Studies 1-3. The x-axis display studies sorted by the costliness of the signal and study type (no competition, competition, competition with signal cost taken from game resources). We first plot (A.) the probabilities based on the detected cooperative and selfish strategies from the unconditional PGG. In figure (B.), cooperative and selfish strategies are categorized based on their actual PGG behavior, with cooperators defined as contributed at least 75% of their endowment and selfish as giving less than 25% of their endowment (i.e., comparing just the extreme ends of cooperative strategies). Note that in contrast to plot (A.) where causality is inferred based on the logical sequence of our study, we remain agnostic about the causal flow in plot (B.).

A possible explanation for the last finding is that undergoing a costly signal actually creates a quality in the signaler (or, at least, forces a cooperative strategy). Indeed, the effort-justification hypothesis proposed by Aaronson and Mills (1959) suggests that involuntarily undergoing embarrassing or painful initiation is associated with a higher self-reported value of group membership due to cognitive dissonance. In their study, Aaronson and Mills (1959) found that women undergoing severe initiation in order to join a discussion group (reading aloud sex-related swear words) valued this group more than women undergoing mild initiation, and subsequent studies replicated this effect with electric shocks, discomfort, and other forms of hazing (Gerard & Mathewson, 1966; Keating et al., 2005).

Contrary to costly signaling theory, which predicts that forcing low-quality individuals to signal is detrimental for those individuals (Searcy & Nowicki, 2005), the effort-justification hypothesis suggests that forcing individuals to send costly signals of commitment may simultaneously re-enforce and invigorate their commitment. Thus, in Study 4, we investigated whether forcing participants to send costly signals would make the signaling teams more cooperative and win more competitive encounters.

5. Study 4

4.1. Methods

4.1.1. Participants

Using the same recruitment protocol as in Study 2, we expected that our manipulation would have smaller effects when testing H4.2 compared to H2.4 in Study 2 (because the revealed group will contain more participants with selfish strategies). Thus, we recruited 401 participants to have sufficient statistical power to detect these smaller effects (see SM, S4.1 for details on the power analysis). After removing participants based on pre-registered criteria, the final sample comprised 381 participants (189 women, 187 men, and five people selecting another gender; $M_{\text{age}} = 38.8$, $SD = 11.8$). There were 95 participants in each combination of group and condition except for low cost revealed group that comprised 96 participants. Participants again received 1 USD show up fee plus their game earnings ($M_{\text{earning}} = 3.61$ USD, $SD = 0.93$).

4.1.2. Differences from Study 2

The structure of this study copied Study 2 with one crucial modification: participants did not select between revealed and concealed groups but were randomly assigned to them.

4.1.3. Hypotheses

(H4.1) Participants in the revealed group will allocate a larger portion of their remaining endowment to the common pool than participants in the concealed group, and (H4.2) this difference will be larger in the high cost compared to the low cost condition.

(H4.3) Participants in the revealed group will have a higher probability of using the extra endowment to harm the other competing group compared to participants in the concealed group, and (H4.4) this difference will be larger in the high cost compared to the low cost condition.

4.2. Results

5.2.2. Pre-registered analyses

Testing H4.1, we observed only a negligible between-group difference in the average percentage of the remaining endowment invested into the common pool (55% in the concealed and 58% in the revealed group). Using the Beta regression as in previous studies, we did not detect a well estimated effect, suggesting that the between-group difference is unstable or too small to be detected with our sample size ($\beta = 0.19$, 95% CI = [-0.08, 0.46]). Modeling these differences with the ZOIB regression showed that while the 95% CI of the effect included zero, the probability of contributing nothing to the common pool was smaller in the revealed groups ($\beta_{\text{of } 0} = -0.71$, 95% CI = [-1.51, 0.09]). Specifically, while there was an 11% probability of contributing nothing in the concealed groups, this probability dropped to 5% in the revealed groups.

Interacting group and condition (H4.2) revealed that the highest invested percentage was observed in the high cost revealed group (62% vs. 52-58% in other groups). This difference was not reflected in the Beta regression ($\beta_{\text{interaction}} = -0.37$, 95% CI = [-0.91, 0.18]) but was reflected in the μ parameter of the

ZOIB regression modeling mean contributions ($\beta_{\text{interaction excluding 0 or 1}} = -0.62$, 95% CI = [-1.13, -0.10]). Nevertheless, despite being well estimated, the size of this effect is below the threshold of interest set by our a priori power analysis. Future studies considering this effect to be of importance would need to increase the sample size to assess this effect reliably. There was no interaction effect for the probability of contributing nothing or everything. In contrast to Study 2 and the prediction of effort justification model (H4.3 and H4.4), we did not observe a higher probability of sacrifice in the revealed groups ($\beta = -0.17$, 95% CI = [-0.60, 0.25]), nor a Condition*Group interaction ($\beta_{\text{interaction}} = -0.35$, 95% CI = [-1.20, 0.50]). See Table S7 for all estimates and 95% CI and Figure 5 for illustration.

5.2.3. Exploratory analyses

We further pre-registered an exploratory investigation of how group assignment would interact with participants' cooperative strategies as assessed by the conditional PGG. As expected, compared to cooperators, participants playing the selfish strategy contributed lower amounts to the common pool—an effect well estimated by the Beta regression ($\beta = -0.96$, 95% CI = [-1.23, -0.68]). Average estimated contributions were 70% for cooperators and 42% for participants playing a selfish strategy.

When preparing Study 4, we reasoned that if forced signaling should be group-beneficial, we should observe an increase in the common pool allocations among participants playing a selfish strategy. Indeed, we observed an increase from 39% mean allocation in the concealed groups to 45% mean allocation in the revealed groups. Nonetheless, this difference was not systematically detected in the Beta regression ($\beta = 0.29$, 95% CI = [-0.08, 0.67]) and the same applies to the results of the ZOIB regression (see Table S8).

As in Study 2, we simulated random pairings of participants into teams to calculate average earnings. We found that participants in the high cost revealed group would, on average, earn the least (3.06 USD), followed by participants in the low cost revealed group (3.30 USD), participants in the high cost concealed group (3.35 USD) and, finally, participants in the low cost concealed group (3.55 USD). Team-shared resources to be distributed showed a similar pattern where the low cost concealed group earned the most (10.8 USD), and the three remaining groups had comparable earnings (9.52-9.66 USD). These patterns are exactly opposite to what we found in Study 2 and to some extent Study 3. See also SM, Section 4 for additional analyses.

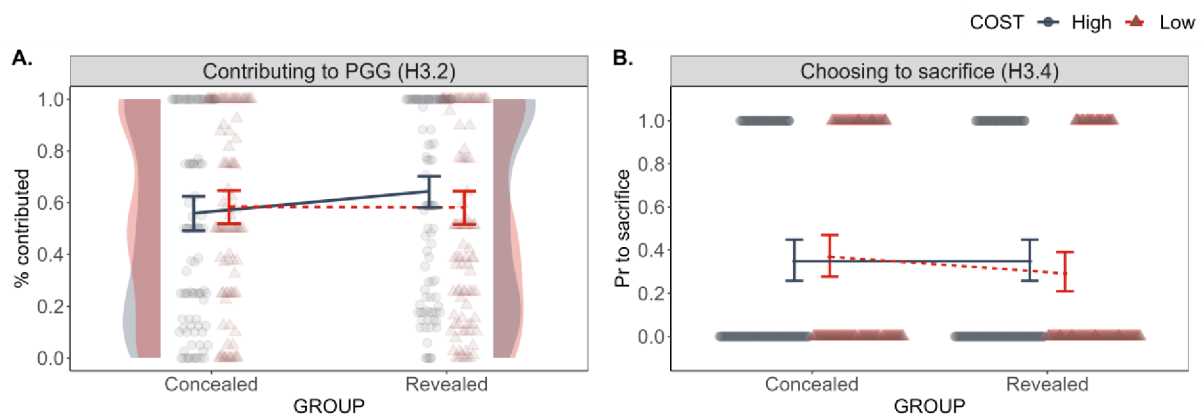


Figure 5 | Results from Study 4. (A.) High cost revealed group contributed the largest portion of their endowment to the common pool. (B.) No between-group difference in the probability of sacrificing the extra endowment.

5.3. *Discussion of Study 4*

In Study 4, we investigated whether forced signaling would increase within-group cooperation and willingness to sacrifice extra funds for the group's welfare. The results revealed a small effect of this manipulation, manifested mainly as a lower probability of contributing nothing to the common pool in the revealed groups. An exploratory analysis suggested that our manipulation might have had a small effect on participants with selfish strategies, but this effect was unreliably estimated and if real would require a large sample of such participants to reliably assess this effect. Our manipulation did not affect the willingness to sacrifice for the group.

Importantly, the results of our simulations showed that neither individual earnings nor the shared common pool would be the largest in the revealed groups. In contrast to Study 2, where we observed that team earnings in the high cost revealed group were 1.5 the size of earnings in the low cost concealed group, the differences in team earnings were only small in Study 4, with the low cost concealed group earning the most. Together, these results suggest that while forced signaling may push people away from extreme selfishness (contributing nothing), this effect would not be sufficient to offset the cost of the forced signal.

6. **General discussion**

We assessed whether costly signals assort cooperators during one-shot intergroup conflict and whether this assortment would help signaling teams to win in competition against other teams. We used a public goods paradigm where participants chose between groups with costly entry requirements and groups without such requirements. The results of our studies summarized in Fig. 6 (collapsed estimates) show support for the basic hypotheses, namely that cooperators are more likely to choose a signaling group and that signaling groups contribute more to the common pool and sacrifice an extra-endowment to increase the winning chances of their group. Our simulations also showed that cooperator assortment through costly signaling increases the probability of winning an intergroup competition and garnering largest benefits. In Study 4, we directly compared costly signaling hypothesis with its rival theory of effort justification, finding only little support for the latter theory. Forcing participants to undergo costly signals did not increase their average contributions, although we observed minor negative effects on contributing zero to the common pool.

Our results also revealed that increasing signal cost is not linearly associated with better cooperator assortment as would be predicted by costly signaling theory (Fig. 6 high/low cost estimates), at least in its original form developed to explain animal communication (Grafen, 1990; Johnstone & Grafen, 1993). In the absence of conflict and when signal cost was not taken from money invested into the common pool during a conflict (Studies 1 and 3), the low cost signals were the most profitable, assorting cooperators that contributed large amounts of their endowment to the common pool. This effect is likely caused by the fact that participants estimated the advantage of signaling to be rather low (3% higher contributions) and similar across cost size; hence, the advantage of signaling might offset the low but not the high cost. Paradoxically, this effect was reversed for some players with selfish strategies who anticipated better free-riding opportunities in the high cost revealed groups (compared to low cost revealed groups).

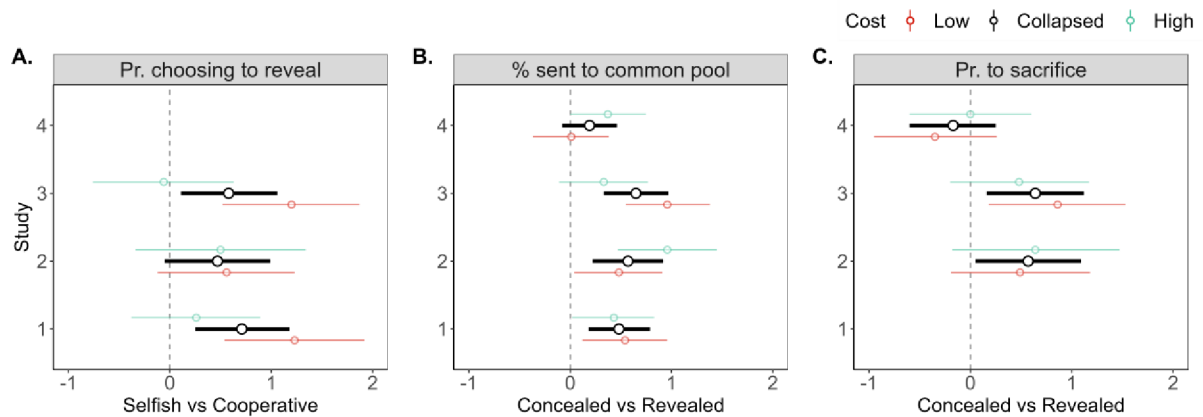


Figure 6 | Summary of main results from Studies 1-4. The plot displays model estimates with 95% CIs, providing support for costly signals (albeit not necessarily highly costly signals) effectively assorting cooperators. Model estimates are displayed across the low/high cost conditions (collapsed) as well as separately for each condition. On the x-axes are plotted differences between participants with selfish and cooperative strategies estimated by a logistic regression (A.), differences between concealed and revealed groups estimated by a Beta regression (B.), and differences between concealed and revealed groups estimated by a logistic regression (C.).

However, this dynamic significantly changed in Study 2 where signal costs directly decreased how much money one can invest into the common pool during intergroup conflict. We observed that mostly deeply committed individuals chose the high cost revealed group in this case, contributing on average 83% of their remaining endowment. In combination with their willingness to sacrifice to hurt the other groups, teams in the high cost revealed groups were the most successful in our simulated, randomized intergroup clashes. In this sense, unproductive costs directly handicapping the group as in Study 2 may function similar to commitment devices (Aimone et al., 2013; Frank, 1988).

An important caveat to the success of the high cost signals in Study 2 is that most cooperators were unwilling to pay the signaling costs. We set up our artificial intergroup conflict such that there was no imbalance of power and groups were of the same size, but in real life, the small-sized ultra-cooperative groups could be beaten by larger, albeit less cooperative groups. One factor possibly giving an edge to these small ultra-cooperative groups may be the will to sacrifice for the common cause (Atran et al., 2014). We show that cooperators who assort in signaling groups are also more willing to hurt the outgroup at own cost if this would help the ingroup. This finding is in line with a study of the conflict between Israel and Palestine where Ginges et al. (2009) showed that for both nationalities, participation in communal rituals positively predicted self-reported support for suicide attacks. Our findings suggest that cooperation in this case is not driven by generalized morality or altruism but is strictly parochial (Choi & Bowles, 2007). We further found that the willingness to sacrifice was predicted by the fear that the other group will do the same, a result in accord with previous studies (Böhm et al., 2016; Mifune et al., 2017). Yet, this motivation did not explain the larger willingness to sacrifice in the revealed groups, suggesting heightened parochial cooperation of signalers rather than fear as the driving factor.

To further the understanding of the dynamics between cost size and effective cooperator assortment, future studies should investigate the factors that affect the cost and benefit estimation. One such factor may be adding further cost and benefits to (non)signaling (Fehrer & Przepiorka, 2013). For example, in religious rituals, believers may perceive that failure to perform a ritual increases the probability of eternal punishment if these rituals are mandated by a moralizing deity (Lang et al., 2019; Purzycki et al., 2016) or that they may gain further benefits from ritual participation such as boosting their well-being (Xygalatas et al., 2019). Such added costs and benefits could stabilize even highly costly religious

signals because the trade-off of signaling would be much lower for non-believers. Of course, this solution begs the question of where such a biased perception comes from, and we point to the important role of socialization and internalization that again extends the canonical costly signaling model (Berger & Luckmann, 1991; Sosis, 2003).

The decision to signal may be further affected by the perceived need for signaling. As previous models showed, the benefits of costly signals are dependent on the proportion of cooperators in the population (Gintis et al., 2001; McNamara & Houston, 2002). If the proportion is high, there is no need to pay the signaling cost because assorting with other cooperators is highly likely. We reasoned that this might be the case in our studies since participants were sampled from a rather trustworthy population in the USA. To this effect, we included the measure of trust propensity in Study 3 but found that this measure did not explain why cooperators failed to signal. This discrepancy might be partially explained by the fact the cost of being suckered was relatively low in our experiment, at least compared to real-life intergroup conflict. While previous studies found that small stakes in economic games track real-life behavior relatively well (Amir et al., 2012; Kröll & Rustagi, 2016), increasing the stakes in future experiments could lead to increased signaling because the perceived cost of being suckered would be larger than the perceived cost of signaling.

Similarly, the frequency of signaling might be increased by including positive costs that avoid loss aversion such that participants choosing the concealed groups would get a monetary bonus while this bonus would not be awarded to participants choosing the revealed groups. These opportunity costs (Iannaccone, 1994; Sosis, 2003) model situations when the signaler forgoes a potential benefit and, by missing these opportunities, communicates their intention (e.g., to demonstrate their commitment to a vegan diet, a vegan would not eat all rather than eat an animal product in a restaurant that does not offer vegan meals). These opportunity costs often serve as costs associated with ultra-cooperative groups (Iannaccone, 1992), yet it is unclear whether they may also reliably assort cooperators during one-shot intergroup conflict. From the game-theoretical perspective, including positive rather than negative costs should not affect the between- and within-group dynamics (Számadó et al., 2022), but we wager that such a change might significantly impact signaler and receiver psychology (Lang et al., 2022; Soler, 2012). If these positive and negative costs would indeed differently motivate participants' gameplay and, especially, the decision to sacrifice and hurt the outgroup, these results could help us better understand how some ultra-cooperative groups may motivate their members to commit self-sacrificial violent acts (Iannaccone & Berman, 2006).

In a similar vein, the results of Study 4 provide important insights into cultural practices such as rites of passage and hazing that mandate wasteful displays, suffering pain, or various forms of shaming. It has long been argued that these practices forge social bonds between initiates/hazees (Aronson & Mills, 1959; Van Gennep, 1909). While we do not deny that these practices may have such effects, the results of Study 4 suggest that these effects are probably quite limited or not driven by signals with unproductive costs. This interpretation is in line with recent findings from a study of university fraternities (Cimino & Thomas, 2022) that failed to show a reliable link between the severity of hazing practices and the following commitment to other hazees or the fraternity chapter (see also Lodewijckx & Syroit, 1997; Shaver et al., 2018).

Nevertheless, it is important to point out that our study instigated a somewhat artificial conflict scenario and strictly focused on rational cost/benefit calculations. Joint participation in costly dysphoric rituals (often involving sensory pageantry) likely acts on various affective processes that may produce powerful

shared memories amplified through post-hoc ritual exegesis (Konvalinka et al., 2011; Whitehouse, 1996; Xygalatas et al., 2019). These events may be often recalled and used to build a group identity (Xygalatas, 2012) and inform ritual participants about their commitment (Lang & Kundt, 2023; Sosis, 2003). Thus, while we argue that burning resources is first and foremost a communicative act amplified by pressures on cooperation such as intergroup conflict, performing costly acts may also have further downstream effects modifying commitment to the group. Future studies should thus assess the interplay between cognitive trade-off computations and embodied affective processes related to costly signaling and their longitudinal dynamics.

Acknowledgements

We would like to thank our colleagues at the Department for the Study of Religion and Laboratory for the Experimental Study of Religion (LEVYNA) at Masaryk University for the useful discussion of this paper. We are particularly grateful to Jan Krátký, Radek Kundt, Eva Kundtová Klocová, and Peter Maňo. M.L. acknowledges the generous support from the MSCAfellow3@MUNI project [CZ.02.2.69/0.0/0.0/19_074/0012727]. The research infrastructure HUME Lab Experimental Humanities Laboratory, Faculty of Arts, Masaryk University supported part of the work. During the preparation of this manuscript, Radim Chvaja was supported by the Templeton Religion Trust (Grant ID: TRT-2022-30378). The funders have/had no role in the study design, data collection and analysis, decision to publish or preparation of the manuscript.

Author contributions

M.L. and R.C. developed the idea for the three studies, and B.G.P. provided comments. M.L. and R.C. collected data, and M.L. analyzed them. ML drafted the paper, and all authors provided comments.

Data and code availability

Data and code from all studies are publicly available at OSF: <https://osf.io/ahy2b/>.

Competing interests

The authors declare no competing interests.

References

- Aimone, J. A., Iannaccone, L. R., Makowsky, M. D., & Rubin, J. (2013). Endogenous group formation via unproductive costs. *Review of Economic Studies*, *80*(4), 1215–1236.
<https://doi.org/10.1093/restud/rdt017>
- Akbaba, Y., & Taydas, Z. (2011). Does religious discrimination promote dissent? A quantitative analysis. *Ethnopolitics*, *10*(3–4), 271–295. <https://doi.org/10.1080/17449057.2011.561988>
- Amir, O., Rand, D. G., & Gal, Y. K. (2012). Economic Games on the Internet: The Effect of \$1 Stakes. *PLoS ONE*, *7*(2), e31461. <https://doi.org/10.1371/journal.pone.0031461>
- Aronson, E., & Mills, J. (1959). The effect of severity of initiation on liking for a group. *The Journal of Abnormal and Social Behavior*, *59*(2), 177–181. <https://doi.org/10.1037/h0047195>
- Ashton, M. C., & Lee, K. (2009). The HEXACO-60: A short measure of the major dimensions of personality. *Journal of Personality Assessment*, *91*(4), 340–345.
<https://doi.org/10.1080/00223890902935878>
- Atran, S., Sheikh, H., & Gomez, A. (2014). Devoted actors sacrifice for close comrades and sacred cause. *Proceedings of the National Academy of Sciences*, *111*(50), 17702–17703.
<https://doi.org/10.1073/pnas.1420474111>
- Barclay, P., Bliege Bird, R., Roberts, G., & Számadó, S. (2021). Cooperating to show that you care: Costly helping as an honest signal of fitness interdependence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1838), 20200292.
<https://doi.org/10.1098/rstb.2020.0292>
- Barclay, P., & Willer, R. (2007). Partner choice creates competitive altruism in humans. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1610), 749–753.
<https://doi.org/10.1098/rspb.2006.0209>

- Barker, J. L., Power, E. A., Heap, S., Puurtinen, M., & Sosis, R. (2019). Content, cost, and context: A framework for understanding human signaling systems. *Evolutionary Anthropology*, 28(2), 86–99. <https://doi.org/10.1002/evan.21768>
- Bauer, M., Cassar, A., Chytilová, J., & Henrich, J. (2014). War's enduring effects on the development of egalitarian motivations and in-group biases. *Psychological Science*, 25(1), 47–57. <https://doi.org/10.1177/0956797613493444>
- Bellows, J., & Miguel, E. (2009). War and local collective action in Sierra Leone. *Journal of Public Economics*, 93, 1144–1157. <https://doi.org/10.1016/j.jpubeco.2009.07.012>
- Berezkei, T., Birkas, B., & Kerekes, Z. (2010). Altruism towards strangers in need: Costly signaling in an industrial society. *Evolution and Human Behavior*, 31(2), 95–103. <https://doi.org/10.1016/j.evolhumbehav.2009.07.004>
- Berezkei, T., Szabo, Z. P., & Czibor, A. (2015). Abusing Good Intentions: Machiavellians Strive for Exploiting Cooperators. *SAGE Open*, 5(2), 215824401559311. <https://doi.org/10.1177/2158244015593119>
- Berger, P. L., & Luckmann, T. (1991). *The Social Construction of Reality: A Treatise in the Sociology of Knowledge*. Penguin Books. <https://doi.org/10.2307/323448>
- Bergstrom, C., Kerr, B., & Lachmann, M. (2008). Building trust by wasting time. In *Moral Markets: The Critical Role of Values in the Economy* (pp. 142–156). Princeton University Press.
- Bliege Bird, R., & Power, E. A. (2015). Prosocial signaling and cooperation among Martu hunters. *Evolution and Human Behavior*, 36(5), 389–397. <https://doi.org/10.1016/j.evolhumbehav.2015.02.003>
- Bliege Bird, R., Ready, E., & Power, E. A. (2018). The social significance of subtle signals. *Nature Human Behaviour*, 1. <https://doi.org/10.1038/s41562-018-0298-3>
- Bliege Bird, R., & Smith, E. A. (2005). Signaling theory, strategic interaction, and symbolic capital. *Current Anthropology*, 46(2), 221–248. <https://doi.org/10.1086/427115>

- Böhm, R., Rusch, H., & Gülerk, Ö. (2016). What makes people go to war? Defensive intentions motivate retaliatory and preemptive intergroup aggression. *Evolution and Human Behavior*, 37(1), 29–34. <https://doi.org/10.1016/j.evolhumbehav.2015.06.005>
- Bolle, F. (2001). Why to Buy Your Darling Flowers: On Cooperation and Exploitation. *Theory and Decision*, 50, 1–28.
- Bornstein, G. (1992). The free-rider problem in intergroup conflicts over step-level and continuous public goods. *Journal of Personality and Social Psychology*, 62(4), 597–606. <https://doi.org/10.1037/0022-3514.62.4.597>
- Bowles, S. (2008). Conflict: Altruism's midwife. *Nature*, 456(20), 326–327. <https://doi.org/10.1038/456326a>
- Bowles, S., & Gintis, H. (2011). *A Cooperative Species: Human Reciprocity and Its Evolution*. Princeton University Press.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), 378–400.
- Brubaker, R. (2015). Religious dimensions of political conflict and violence. *Sociological Theory*, 33(1), 1–19. <https://doi.org/10.1177/0735275115572153>
- Choi, J. K., & Bowles, S. (2007). The coevolution of parochial altruism and war. *Science*, 318(5850), 636–640. <https://doi.org/10.1126/science.1144237>
- Cimino, A., & Thomas, B. J. (2022). Does hazing actually increase group solidarity? Re-examining a classic theory with a modern fraternity. *Evolution and Human Behavior*, 43(5), 408–417. <https://doi.org/10.1016/j.evolhumbehav.2022.07.001>
- De Dreu, C. K. W., Gross, J., Fariña, A., & Ma, Y. (2020). Group Cooperation, Carrying-Capacity Stress, and Intergroup Conflict. *Trends in Cognitive Sciences*, 24(9), 760–776. <https://doi.org/10.1016/j.tics.2020.06.005>

- Dohmen, T., Falk, A., Huffman, D., Sunde, U., Schupp, J., & Wagner, G. G. (2011). Individual risk attitudes: Measurement, determinants, and behavioral consequences. *Journal of the European Economic Association*, *9*(3), 522–550. <https://doi.org/10.1111/j.1542-4774.2011.01015.x>
- Eckel, C. C., Fatas, E., Godoy, S., & Wilson, R. K. (2016). Group-level selection increases cooperation in the public goods game. *PLoS ONE*, *11*(8), 1–13. <https://doi.org/10.1371/journal.pone.0157840>
- Ellingsen, T. (2000). Colorful community or ethnic witches' brew? Multiethnicity and domestic conflict during and after the Cold War. *The Journal of Conflict Resolution*, *44*(2), 228–249.
- Fearon, J. D., & Laitin, D. D. (2003). Ethnicity, insurgency, and civil war. *The American Political Science Review*, *97*(1), 75–90.
- Fehrler, S., & Przepiorka, W. (2013). Charitable giving as a signal of trustworthiness: Disentangling the signaling benefits of altruistic acts. *Evolution and Human Behavior*, *34*(2), 139–145. <https://doi.org/10.1016/j.evolhumbehav.2012.11.005>
- Fischbacher, U., Gächter, S., & Fehr, E. (2001). Are people conditionally cooperative? Evidence from a public goods experiment. *Economics Letters*, *71*(3), 397–404. [https://doi.org/10.1016/S0165-1765\(01\)00394-9](https://doi.org/10.1016/S0165-1765(01)00394-9)
- Francois, P., Fujiwara, T., & Ypersele, T. Van. (2018). The origins of human prosociality: Cultural group selection in the workplace and the laboratory. *Science Advances*, *4*(eaat2201), 1–9. <https://doi.org/10.1126/sciadv.aat2201>
- Frank, R. H. (1988). *Passions with reason: The strategic role of emotions*. W. W. Norton & Company.
- Frazier, M. L., Johnson, P. D., & Fainshmidt, S. (2013). Development and validation of a propensity to trust scale. *Journal of Trust Research*, *3*(2), 76–97. <https://doi.org/10.1080/21515581.2013.820026>

- Gilligan, M. J., Pasquale, B. J., & Samii, C. (2014). Civil war and social cohesion: Lab-in-the-field evidence from Nepal. *American Journal of Political Science*, *58*(3), 604–619.
<https://doi.org/10.1111/ajps.12067>
- Ginges, J., Hansen, I., & Norenzayan, A. (2009). Religion and support for suicide attacks. *Psychological Science*, *20*(2), 224–230. <https://doi.org/10.1111/j.1467-9280.2009.02270.x>
- Gintis, H., Smith, E. A., & Bowles, S. (2001). Costly Signaling and Cooperation. *Journal of Theoretical Biology*, *213*(1), 103–119. <https://doi.org/10.1006/jtbi.2001.2406>
- Glowacki, L., Isakov, A., Wrangham, R. W., McDermott, R., Fowler, J. H., & Christakis, N. A. (2016). Formation of raiding parties for intergroup violence is mediated by social network structure. *Proceedings of the National Academy of Sciences*, *113*(43), 12114–12119.
<https://doi.org/10.1073/pnas.1610961113>
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*(4), 517–546.
[https://doi.org/10.1016/S0022-5193\(05\)80088-8](https://doi.org/10.1016/S0022-5193(05)80088-8)
- Handley, C., & Mathew, S. (2020). Human large-scale cooperation as a product of competition between cultural groups. *Nature Communications*, *11*(1), 1–9.
<https://doi.org/10.1038/s41467-020-14416-8>
- Henrich, J., & Muthukrishna, M. (2021). The Origins and Psychology of Human Cooperation. *Annual Review of Psychology*, *72*(1), 1–34. <https://doi.org/10.1146/annurev-psych-081920-042106>
- Iannaccone, L. R. (1992). Sacrifice and stigma: Reducing free-riding in cults, communes, and other collectives. *Journal of Political Economy*, *100*(2), 271–291. <https://doi.org/10.1086/261818>
- Iannaccone, L. R. (1994). Why Strict Churches Are Strong. *American Journal of Sociology*, *99*(5), 1180–1211.
- Iannaccone, L. R., & Berman, E. (2006). Religious extremism: The good, the bad, and the deadly. *Public Choice*, *128*(1–2), 109–129. <https://doi.org/10.1007/s11127-006-9047-7>

- Jakobsen, T. G., & De Soysa, I. (2009). Give me liberty, or give me death! State repression, ethnic grievance and civil war, 1981–2004. *Civil Wars*, *11*(2), 137–157.
<https://doi.org/10.1080/13698240802631061>
- Johnstone, R. A., & Grafen, A. (1993). Dishonesty and the handicap principle. *Animal Behaviour*, *46*(4), 759–764. <https://doi.org/10.1006/anbe.1993.1253>
- Konvalinka, I., Xygalatas, D., Bulbulia, J., Schjoedt, U., Jegindö, E.-M., Wallot, S., Van Orden, G., & Roepstorff, A. (2011). Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proceedings of the National Academy of Sciences*, *108*(20), 8514–8519.
<https://doi.org/10.1073/pnas.1016955108>
- Kröll, M., & Rustagi, D. (2016). Shades of dishonesty and cheating in informal milk markets in India. *SAFE Working Paper No. 134*.
- Lang, M., Chvaja, R., Purzycki, B. G., Václavík, D., & Staněk, R. (2022). Advertising cooperative phenotype through costly signals facilitates collective action. *Royal Society Open Science*, *9*, 202202. <https://doi.org/10.1098/rsos.202202>
- Lang, M., & Kundt, R. (2023). The evolution of human ritual behavior as a cooperative signaling platform. *Religion, Brain & Behavior*, *e-print before press*.
<https://doi.org/10.1080/2153599X.2023.2197977>
- Lang, M., Purzycki, B. G., Apicella, C. L., Atkinson, Q. D., Bolyanatz, A., Cohen, E., Handley, C., Klocová, E. K., Lesorogol, C., Mathew, S., McNamara, R. A., Moya, C., Placek, C. D., Soler, M., Vardy, T., Weigel, J. L., Willard, A. K., Xygalatas, D., Norenzayan, A., & Henrich, J. (2019). Moralizing gods, impartiality, and religious parochialism across 15 societies. *Proceedings of the Royal Society B*, *286*(1898), 1–10. <https://doi.org/doi.org/10.1098/rspb.2019.0202>
- Lodewijkx, H. F. M., & Syroit, J. E. M. M. (1997). Severity of initiation revisited: Does severity of initiation increase attractiveness in real groups? *European Journal of Social Psychology*, *27*(3), 275–300. [https://doi.org/10.1002/\(SICI\)1099-0992\(199705\)27:3<275::AID-EJSP822>3.0.CO;2-S](https://doi.org/10.1002/(SICI)1099-0992(199705)27:3<275::AID-EJSP822>3.0.CO;2-S)

- Lotem, A., Fishman, M. A., & Stone, L. (2003). From reciprocity to unconditional altruism through signalling benefits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1511), 199–205. <https://doi.org/10.1098/rspb.2002.2225>
- Lyle, H. F., & Smith, E. A. (2014). The reputational and social network benefits of prosociality in an Andean community. *Proceedings of the National Academy of Sciences of the United States of America*, 111(13), 4820–4825. <https://doi.org/10.1073/pnas.1318372111>
- Lyle, H. F., Smith, E. A., & Sullivan, R. J. (2009). Blood donations as costly signals of donor quality. *Journal of Evolutionary Psychology*, 7(4), 263–286. <https://doi.org/10.1556/JEP.7.2009.4.1>
- Majolo, B., & Maréchal, L. (2017). Between-group competition elicits within-group cooperation in children. *Scientific Reports*, 7(srep43277), 1–9. <https://doi.org/10.1038/srep43277>
- Mathew, S., & Boyd, R. (2014). The cost of cowardice: Punitive sentiments towards free riders in turkana raids. *Evolution and Human Behavior*, 35(1), 58–64. <https://doi.org/10.1016/j.evolhumbehav.2013.10.001>
- McNamara, J. M., & Houston, A. I. (2002). Credible threats and promises. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357(1427), 1607–1616. <https://doi.org/10.1098/rstb.2002.1069>
- Mifune, N., Simunovic, D., & Yamagishi, T. (2017). Intergroup biases in fear-induced aggression. *Frontiers in Psychology*, 8. <https://doi.org/10.3389/fpsyg.2017.00049>
- Neuberg, S. L., Warner, C. M., Mistler, S. A., Berlin, A., Hill, E. D., Johnson, J. D., Filip-Crawford, G., Millsap, R. E., Thomas, G., Winkelman, M., Broome, B. J., Taylor, T. J., & Schober, J. (2014). Religion and intergroup conflict. *Psychological Science*, 25(1), 198–206. <https://doi.org/10.1177/0956797613504303>
- Power, E. A., & Ready, E. (2018). Building bigness: Reputation, prominence, and social capital in rural south India. *American Anthropologist*, 120(3), 444–459. <https://doi.org/10.1111/aman.13100>

- Purzycki, B. G., Apicella, C., Atkinson, Q. D., Cohen, E., McNamara, R. A., Willard, A. K., Xygalatas, D., Norenzayan, A., & Henrich, J. (2016). Moralistic gods, supernatural punishment and the expansion of human sociality. *Nature*, *530*(7590), 327–330.
<https://doi.org/10.1038/nature16980>
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Raihani, N. J., & Power, E. A. (2021). No good deed goes unpunished: The social costs of prosocial behaviour. *Evolutionary Human Sciences*, *3*, 1–21. <https://doi.org/10.1017/ehs.2021.35>
- Rappaport, R. (2000). *Pigs for the Ancestors: Ritual in the Ecology of a New Guinea People*. Waveland Press.
- Richerson, P., Baldini, R., Bell, A. V., Demps, K., Frost, K., Hillis, V., Mathew, S., Newton, E. K., Naar, N., Newson, L., Ross, C., Smaldino, P. E., Waring, T. M., & Zefferman, M. (2016). Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behavioral and Brain Sciences*, *39*(2016), e30.
<https://doi.org/10.1017/S0140525X1400106X>
- Rigby, R., Stasinopoulos, M., Heller, G., & De Bastiani, F. (2019). *Distributions for Modelling Location, Scale and Shape: Using GAMLSS in R*. CRC Press.
- Roberts, G. (2020). Honest signaling of cooperative intentions. *Behavioral Ecology*, *31*(4), 922–932.
<https://doi.org/10.1093/beheco/araa035>
- Sääksvuori, L., Mappes, T., & Puurtinen, M. (2011). Costly punishment prevails in intergroup conflict. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3428–3436.
<https://doi.org/10.1098/rspb.2011.0252>
- Salahshour, M. (2021). Evolution of cooperation in costly institutions exhibits Red Queen and Black Queen dynamics in heterogeneous public goods. *Communications Biology*, *4*(1), 1340.
<https://doi.org/10.1038/s42003-021-02865-w>

- Searcy, W., & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press.
- Shaver, J. H., DiVietro, S., Lang, M., & Sosis, R. (2018). Costs do not explain variance in trust among secular groups. *Journal of Cognition & Culture*, *18*(1–2), 180–204.
<https://doi.org/10.1163/15685373-12340025>
- Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods*, *11*(1), 54–71.
<https://doi.org/10.1037/1082-989X.11.1.54>
- Soler, M. (2012). Costly signaling, ritual and cooperation: Evidence from Candomblé, an Afro-Brazilian religion. *Evolution and Human Behavior*, *33*(4), 346–356.
<https://doi.org/10.1016/j.evolhumbehav.2011.11.004>
- Soler, M., Batiste, F., & Cronk, L. (2014). In the eye (and ears) of the beholder: Receiver psychology and human signal design. *Evolutionary Anthropology*, *23*(4), 136–145.
<https://doi.org/10.1002/evan.21413>
- Sosis, R. (2003). Why aren't we all hutterites? Costly signaling theory and religious behavior. *Human Nature*, *14*(2), 91–127.
- Sosis, R., Kress, H. C., & Boster, J. S. (2007). Scars for war: Evaluating alternative signaling explanations for cross-cultural variance in ritual costs. *Evolution and Human Behavior*, *28*(4), 234–247. <https://doi.org/10.1016/j.evolhumbehav.2007.02.007>
- Stasinopoulos, D. M., & Rigby, R. A. (2007). Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software*, *23*(7), 1–46.
- Sylwester, K., & Roberts, G. (2010). Cooperators benefit through reputation-based partner choice in economic games. *Biology Letters*, *6*(5), 659–662. <https://doi.org/10.1098/rsbl.2010.0209>
- Sylwester, K., & Roberts, G. (2013). Reputation-based partner choice is an effective alternative to indirect reciprocity in solving social dilemmas. *Evolution and Human Behavior*, *34*(3), 201–206. <https://doi.org/10.1016/j.evolhumbehav.2012.11.009>

- Számadó, S. (2010). Pre-Hunt Communication Provides Context for the Evolution of Early Human Language. *Biological Theory*, 5(4), 366–382. https://doi.org/10.1162/biot_a_00064
- Számadó, S., Samu, F., & Takács, K. (2022). Condition-dependent trade-offs maintain honest signalling. *Royal Society Open Science*, 9(10), 220335. <https://doi.org/10.1098/rsos.220335>
- Van Gennep, A. (1909). *The Rites of Passage* (1954th ed.). Routledge.
<https://doi.org/10.1080/135762702317447768>
- van Vugt, M., & Hardy, C. L. (2010). Cooperation for reputation: Wasteful contributions as costly signals in public goods. *Group Processes and Intergroup Relations*, 13(1), 101–111.
<https://doi.org/10.1177/1368430209342258>
- Voors, M., Nillesen, E., Verwimp, P., Bulte, E., Lensink, R., & Soest, D. Van. (2012). Violent conflict and behavior: A field experiment in Burundi. *American Economic Review*, 102(452), 941–964.
- Werner, K., & Lambsdorff, J. G. (2020). Emotional numbing and lessons learned after a violent conflict – Experimental evidence from Ambon, Indonesia. *Journal of Development Studies*, 56(5), 859–873. <https://doi.org/10.1080/00220388.2019.1590550>
- Whitehouse, H. (1996). Rites of terror: Emotion, metaphor and memory in Melanesian initiation cults. *The Journal of the Royal Anthropological Institute*, 2(4), 703–715.
<https://doi.org/10.2307/3034304>
- Whitehouse, H., & Lanman, J. A. (2014). The ties that bind us. *Current Anthropology*, 55(6), 1–23.
<https://doi.org/10.1086/678698>
- Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model. *Human Nature*, 23(1), 5–29.
<https://doi.org/10.1007/s12110-012-9132-1>
- Xygalatas, D. (2012). *The Burning Saints: Cognition and Culture in the Fire-walking Rituals of the Anastenaria*. Equinox.

Xygalatas, D., Khan, S., Lang, M., Kundt, R., Kundtová Klocová, E., Krátký, J., & Shaver, J. H. (2019).

Effects of extreme ritual practices on psychophysiological well-being. *Current Anthropology*, 60(5), 699–707. <https://doi.org/10.1086/705665>

Zefferman, M. R., & Mathew, S. (2015). An evolutionary theory of large-scale human warfare: Group-structured cultural selection. *Evolutionary Anthropology*, 24(2), 50–61.

<https://doi.org/10.1002/evan.21439>