

cannot be allocated to growth or reproduction. The ecological costs of herbivory resistance are more long-term and indirect; examples are decreased attractiveness to pollinators or decreased competitive ability. The costs associated with punishment mechanisms such as ostracism may be distinguishable in a similar way. We agree with Guala that the direct short-term costs associated with ostracizing free-riders will often be low. However, on the longer term, there can be strong negative implications. Ostracized individuals may become desperados, causing a lot of trouble. They may resort to antisocial or criminal behavior, affecting the feeling of safety in their former group and necessitating protection measures. In the worst case, trust and cooperation break down. This way, the presence of ostracized individuals in the environment can lead to a new equilibrium with lower payoff levels than in the original state. Although there have been some experiments that include ostracism as an option (e.g., Maier-Rigaud et al. 2009; Masclet 2003), they do not accommodate those “ecological” costs.

Punishment in one type of interaction may have implications for different types of interaction. Economic experiments typically focus on a single type of interaction, such as a public goods game. If punishment is incorporated in these experiments, it can only affect behavior in that specific context. This is not in line with how behavior is structured in humans (and other animals). There is ample evidence that behavioral tendencies in one type of interaction are closely correlated with the behavior in quite different contexts. As shown by evolutionary models from the biological literature (e.g., Wolf et al. 2007; 2008), such correlation structures (called “behavioral syndromes” or “personalities”) can be adaptive, even if the behavior in a particular type of situation may appear maladapted. For example, the tendency to show antisocial behavior in a public goods context may – for good reasons – be correlated with the tendency to actively participate in group defense when the group is facing an external challenge. Ostracizing individuals because of their behavior in a public goods context may therefore have harmful effects later.

Punishment may destroy established hierarchies and role patterns and lead to social unrest. The participants of a typical economic experiment do not know each other well and interact anonymously. In real life, many interactions take place in small communities where individuals do know each other, and are well aware of their place in the group. Individuals differ in relevant aspects (like age, expertise, or authority), and relationships between individuals (like leadership and social rank) have been settled in the past. Such patterning of a group due to well-established relationships between its members is important, because it reduces conflict and facilitates division of labor. Punishing an individual by social exclusion can break down such group structures, leading to social unrest. The re-establishment of stable social relationships can take a long time, and some individuals may end up in a worse position than they had before. Guala himself refers repeatedly to the work of Ostrom (1990), who has shown that stable group membership is one of the key predicting features making institutions for collective actions viable.

Punishment may have asymmetric effects, thus leading to tension between group members. Interactions in economic experiments are usually random. In contrast, real-world interactions take place in interaction networks that are often highly structured. This can be important, because group members may differ considerably in the way they are connected to a punished individual. Individuals will differ not only in the degree they suffer from the free-riding behavior of a specific individual, but also in the implications that punishment of that individual may have for them. Ostracizing an individual may have a small effect on group member A,

while it severely affects the social network of group member B. The costs and benefits of punishing a particular free-rider can therefore be highly asymmetrical, leading to contrasting preferences between group members and, as a consequence, to social tension within the group.

If punishment were as cheap as Guala suggests, one would expect that individuals would readily punish defectors. In contrast, daily-life experience tells us that individuals are reluctant to punish free-riding group members. Denouncing others is often considered a bad habit, even if these others exhibit anti-social behavior. Groups of students assigned to a joint project, for example, are typically not only reluctant to punish free-riders, but even to call in an authoritative person (such as a professor) to resolve the situation. In fact, whistle-blowing is considered more a vice than a virtue, as young children are already being told by their parents or at school. This reluctance to apply seemingly cheap punishment is an indication that the hidden, long-term costs of punishment may be substantial. Economic experiments focusing exclusively on the direct costs of punishment are valuable, but they do not tell much about how cooperation is stabilized in human societies. For a complete understanding, the social costs of punishment should be taken seriously.

When the strong punish: Why net costs of punishment are often negligible

doi:10.1017/S0140525X11001427

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Abstract: In small-scale societies, punishment of adults is infrequent and employed when the anticipated cost-to-benefit ratio is low, such as when punishment is collectively justified and administered. In addition, benefits may exceed costs when punishers have relatively greater physical and social capital and gain more from cooperation. We provide examples from the Tsimane horticulturalists of Bolivia to support our claims.

We agree with Guala that regulation of cooperation by punishment is infrequent and often low-cost, at least in small-scale societies. Analytical models and experimental studies suggest that solutions to cooperative dilemmas do not depend on direct punishment if individuals can opt out of unproductive partnerships (Aktipis 2004; Hauert et al. 2007) or assort with preferred cooperative partners whether kin (Hamilton 1964) or non-kin (Barclay & Willer 2007; Noe & Hammerstein 1994). Guala cites Wiessner (2005), who observes that !Kung who shirk their responsibilities are ignored more often than they are verbally punished. Among traditional Tsimane horticulturalists of Bolivia, most conflicts are between close kin and regular cooperative partners (von Rueden et al. 2009), who generally prefer reconciliation to revenge. Furthermore, defection among parties with few long-term shared interests is more often met with withdrawal and “voting with one’s feet” than with punishment.

Guala does not distinguish second- from third-party punishment, but strong reciprocity theorists argue that both contribute to the maintenance of social norms (Fehr & Fischbacher 2004). There is no consensus over whether third parties often punish or punish “enough.” In experimental games, third-party punishment is least common in small-scale societies (Marlowe et al. 2008), and third parties may be especially wary of becoming involved in serious conflicts. A Tsimane man committed

murder on two occasions, but punishment (public whipping) was administered only after the second murder. The community that sentenced and whipped him was not his resident community but a more acculturated community with more influential men. Non-partisan members of the murderer's own community would not risk the threat of his retaliation.

Punishment occurs when there is minimal risk of (1) losing a valued exchange partner, (2) suffering reputational damage, or (3) provoking retaliation. For example, a low-status Tsimane man was in long-standing disputes with his neighbor over land and with his son-in-law over investment in his daughter. With few allies to support him, the man moved to another village with his family, with plans to return in a few months. The next day, the neighbor harvested the yucca from the man's field, and the son-in-law burned the man's house. The neighbor and son-in-law did not expect reputational damage or retaliation because they had strong kin support within the community, they could not be unambiguously identified as the punishers, and the punished man had few allies.

Guala identifies gossip as a low-cost alternative to direct punishment. Gossip can spread reputation-damaging information while obscuring the source of that information. Individuals may also gossip to gauge and build community support for punishment that is coordinated and more direct. As Guala argues, punishment that is coordinated carries less risk of retaliation and can be more effective at stabilizing collective action than distributed, individual acts of punishment (Boyd et al. 2010; Casari & Luini 2009). Among the !Kung, Wiessner (2005) found that most harsh criticism was delivered by a coalition, and coalition-based punishment was twice as likely to provoke conformity in the accused. Among the Tsimane, most conflicts are confined to the parties directly involved, but on occasion a small, informal gathering of men will act as third-party adjudicators. The most serious conflicts among the Tsimane, such as those involving physical violence, are sometimes discussed in community-wide meetings in more acculturated villages, where influential individuals will try to generate consensus concerning the relative guilt of the parties in conflict. The community may decide to inflict punishment, usually verbal censure, community service, or public whippings on rare occasions. One village has a de facto rule that the whipper not yet be a father; he has no risk then of his children being targets of vengeance.

Coordinated sanctioning, however, may not be necessary to explain why individuals punish free-riders and non-punishers. Another explanation, which Guala does not discuss, relies on inter-individual differences in formidability, endowments, or in the expected gains from successful cooperation. Individuals with greater physical or social capital can punish with less risk of retaliation and with greater efficacy, and those who anticipate greater relative gains from cooperation are more willing to absorb costs of punishment to achieve those gains. In general, inter-individual differences can be powerful catalysts of cooperation, transforming prisoner's dilemmas into mutualisms and resolving second-order dilemmas of who punishes (Olson 1965; Ruttan 2008). Among the Tsimane, 66% of adjudicated conflicts were arbitrated by men in the top 10% of coalitional support within their community (von Rueden et al. 2009). These individuals can steer conflict outcomes in their favor and their actions are less likely to be challenged.

Inter-individual differences in the costs to punishing contribute to the establishment of leaders and followers. Collective action, particularly in large groups, often depends on leaders bearing the costs of coordination and punishment in return for a greater share of the spoils (Hooper et al. 2010). Tsimane men do not gain more direct material benefits from organizing collective fishing events or acting as leaders in face-to-face collective action games (von Rueden et al. 2010), but long-term reputational benefits may be non-trivial. Positive reputations can serve as insurance against times of need (Boone & Kessler 1999; Gurven et al. 2000) or as signals to mates and allies of

quality or cooperative intent (Bliege Bird & Smith 2005). Where joint production is subject to greater economies of scale, such as in agricultural societies, coordination and punishment by leaders may pay even greater dividends.

We encourage more study of the role of inter-individual differences in the generation of punishment and cooperation. In the lab, players often feel equally entitled and motivated, while subject endowments are too often windfalls; these conditions rarely hold in natural settings. As Guala recognizes, context matters in shaping how social preferences impact behavior (Gurven & Winking 2008; List 2006; Wiessner 2009), so caution is required when making inferences from particular experimental games. Some experimental games, however, have introduced asymmetries into the effectiveness with which players punish (Nikiforakis et al. 2011), into decision-making authority over the distribution of public good shares (van der Heijden et al. 2009), or into initial player endowments, as a function of individual inputs to joint production (Konigstein 2000). With greater understanding of the pervasiveness of inter-individual differences and other cost-reducing conditions, punishment may not appear so altruistic after all.

Perspectives from ethnography on weak and strong reciprocity

doi:10.1017/S0140525X11000860

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Abstract: To add ethnographic perspective to Guala's arguments, I suggest reasons why experimental and ethnographic evidence do not concur and highlight some difficulties in measuring whether positive and negative reciprocity are indeed costly. I suggest that institutions to reduce the costs of maintaining cooperation are not limited to complex societies.

Guala's target article makes a most welcome contribution to the discussion of strong reciprocity, crossing disciplines to compare the findings of economic experiments and ethnographic evidence from small-scale egalitarian societies, "in the wild." It comes as no surprise to anthropologists that the two do not concur; cooperation in the wild is tamed by emotions accompanying kinship, a factor lost in experiments that hinge on anonymity (Wiessner 2009). Moreover, the one-shot material consequence of punishment in experiments in no way parallels the multi-shot social consequences of the same in real life. Grudges from punishment, particularly by third parties, are infinitely retrievable and accrue; punishment begs retribution, petty or pernicious, that so disrupts cooperation.

Significant also is Guala's point that positive and negative strong reciprocity are not the flip side of the coin. Cooperation in small-scale societies is driven largely by benefits, not by blows, whether social or physical. Strong punishers are not rewarded for their sacrifices while strong positive reciprocators are revered. Among the Kalahari Bushmen, pushing back to regulate weak reciprocity provides the spice of daily life, but frequent harsh punishers, particularly the few third party punishers, are despised and called *tshi n'ai* or "biting thing." In 62% of Bushman conversations that involved some social sanctioning where the camp leader was present, the leader refrained from sanctioning in order to save his clout for subsequent mediation (Wiessner 2005).

Whether positive and negative reciprocity are costly and thus truly "strong" is difficult to measure in the field. For the six out of 124 cases of sanctioning among the !Kung Bushmen that I