cooperative. We thought they probably figured that the cooperators were initially fining the non-cooperators and the non-cooperators then fined the cooperators in revenge.

In the massive case studies we had worked through, we did not find many cases of blind revenge. Hence, we decided to move to the next step in the lab and give participants an opportunity to communicate and decide on their own rules. Those who engaged in self-governance then did not use fines very often. They increased their levels of cooperation to the point that their net benefits were very close to optimal. Thus, the combination of agreement and discussion first and evidence that others were cooperating, led to a much better result than an externally designed sanctioning system without a set of rules that the participants had agreed to.

Although in the Janssen et al. (2010) study we did not give participants an opportunity to design their own rules, we gave them the opportunity to simultaneously engage in communication and use of fines, the use of fines alone, and the use of communication alone. As Guala comments, when communication and punishment opportunities were combined, the subjects did the very best in the lab.

There are several issues being debated by a variety of very distinguished scholars. There is no question that humans have the capability of engaging in serious punishment of each other; but that should not lead us to conclude that the way of achieving long-term sustainability is by enabling participants to punish each other without enabling them to engage in serious discourse about the rules they want to adopt and how they should be observed and sanctioned. When participants in a dilemma setting are able to engage in serious discussion, debate about their joint future, and agree on rules that limit strategies, they have much less need to use punishment against defectors. Monitoring each other and initially shaming those who do not comply with their rules is, however, an essential component for sustaining that cooperation over time. Stronger sanctions are not often needed, but their authorization backs up the use of mild sanctions when rule-breaking behavior is initially observed. Our recent research related to forestry institutions around the world demonstrates that when the users monitor each other's behavior in a forest, forest conditions are substantially enhanced (Coleman 2009; Coleman & Steed 2009; Chhatre & Agrawal 2009).

I am glad to see these issues being raised in a way that makes it possible to move forward to a better understanding of the role of punishment in overcoming social dilemmas of various kinds.

Importing social preferences across contexts and the pitfall of over-generalization across theories

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Abstract: Claims regarding negative strong reciprocity do indeed rest on experiments lacking established external validity, often without even a small "menu of options." Guala's review should prompt strong reciprocity proponents to extend the real-world validity of their work, exploring the preferences participants bring to experiments. That said, Guala's approach fails to differentiate among group selection approaches and glosses over cross-cultural variability.

We agree with Guala that it can be difficult to draw conclusions about human evolution from highly controlled experimental games. Controlling any and all third variables facilitates replication and repetition, enabling comparison of behavior across experiments (Guala 2005). However, striving for internal validity introduces a double-edged sword: Economic games provide insight, but they present only a rough approximation of the real world. Strong reciprocity arguments often strive to connect game play to real life by citing anecdotal evidence. Nevertheless, though we endorse caution in interpreting experiments, Guala himself overlooks the incorporation of real-world aspects into recent field-based economic games. This research allows greater insight into the societies under investigation. Moreover, we take issue with both Guala's homogenizing account of group selection theories and his failure to acknowledge variability across subsistence groups. That said, we believe the present article should spur strong reciprocity theorists to further explore the variable social preferences exhibited by participants.

A narrow interpretation of experimental economic games – an uncontroversial reading of the evidence, as Guala notes – suggests that "punishment mechanisms are useful *methodological devices to observe social preferences*" (sect. 5, para. 2, italics in original). We agree. These social preferences have been sometimes termed "informal norms," including norms of fairness and reciprocity (Guala 2008). For example, Western participants are annoyed and often angry if another participant has a larger net gain than they do (Dawes et al. 2007; Fehr & Gächter 2002). If internal validity is rigorously sought within experiments and maintained across experiments via replication, we can expect any differences in game play to correspond to differences in social preferences applied by participants to the experimental context. The issue with external validity arises because game play, by virtue of experimental control, is far-removed from the real-life situations strong reciprocity theorists seek to explain.

We agree that the simple design of many games necessitates caution in interpretation. We do not mean that all economic games are overly simplistic, but that it is difficult to make inferences without control groups of sorts. Many experiments cited by strong reciprocity theorists do not allow for coalition formation, reputation building, or less expensive punishment options. Rockenbach and Milinski (2006) found that reputation formation matters: Public goods contributions were greater when costly punishment and indirect reciprocity (i.e., withholding cooperation) were united with reputation building, and participants preferred to join these groups. Similarly, Jacquet et al. (2011) have demonstrated that both negative and positive reputational consequences external to the game context enhance cooperation within the game context. Egas and Riedl (2008) found that low-cost and high-impact punishment best promotes cooperation. These results support the idea that costly punishment is probably not as common when "the full menu of strategies" (target article, sect. 6, para. 3) is available.

Guala's primary concern is the extent to which economic games reflect punishment mechanisms "in the wild." Though in the past Guala (2008) applauded the MacArthur Foundation–sponsored Economic Man studies, in the present article he emphasizes that the incidental introduction of cultural practice by some researchers (Henrich et al. 2005, Table 4) and participants (Henrich et al. 2005, sect. 8) is not equivalent to an experiment designed to reflect on the particular population of study. Guala is not the only observer to raise concerns about the external validity of field-based games such as Economic Man (e.g., Gurven & Winking 2008); however, he overlooks more recent efforts to bring external validity to economic games in the field context. Notable recent field studies have endeavored to match games to context, and to derive clear insights about costly monitoring and punishment within a particular cultural group (see Jack 2009; Lamba & Mace 2010; Rustagi et al. 2010).

Despite the strengths of the present review, Guala risks the same pitfall for which he criticizes others: over-generalization.

His failure to differentiate among theories of (what he terms) "group selection" does a disservice to the understanding of this area of study. There is a significant difference between biological group selection and gene-culture coevolution (for discussion, see West et al. 2011). By describing propensities to internalize norms as an aspect of our innate psychology and explaining the cooperation-enhancement of some norms as the product of cultural group selection, gene-culture coevolution theory affords greater variability across groups than does biological group selection theory. While important, these distinctions are admittedly sometimes obscured in the literature, even though connections can be separately drawn between biological group selection and strong reciprocity, and between gene-culture coevolution and strong reciprocity (e.g., Fehr et al. 2002).

The above distinctions are important because, at the empirical level, Guala provides a simplified view of small-scale societies that minimizes variation among them. Guala distills the variety of punishment behaviors outlined in Boehm's (1999) research, drawing generalizations about homicide in hunter-gatherers, among other things. Boehm (1999) himself reports that a dearth of punishment data required him to use unsystematic methods of sampling. Today, better archived ethnographic materials afford more systematic gleaning of examples of punishment (though the cases themselves remain anecdotal). Additionally, by dwelling on fission-fusion as a conflict management strategy, Guala overlooks ecological variation that influences the availability of this strategy. For example, 25% of hunter-gatherers in a sample of 340 societies are actually sedentary (Marlowe 2005), making fission a less ready solution for conflict.

Guala's review of negative strong reciprocity provides a useful platform for subsequent work. We would like to see more even-handed treatment of both the relevant theories and the available ethnographic data. That said, we agree that, regardless of their cultural group, participants face a contrived social situation in economic game experiments. Investigators need to focus on the preferences participants bring to experimental games, including (1) explaining the origins of these preferences, (2) understanding how they manifest in real-world situations, and (3) accounting for individual- and group-level differences in preferences.

Culture: The missing piece in theories of weak and strong reciprocity

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Abstract: Guala does not go far enough in his critique of the assumption that human decisions about sharing made in the context of experimental game conditions accurately reflect decision-making under real conditions. Sharing of hunted animals is constrained by cultural rules and is not "spontaneous cooperation" as assumed in models of weak and strong reciprocity. Missing in these models is the cultural basis of sharing that makes it a group property rather than an individual one.

Guala rightly draws attention to the fact that human decision-making under experimental game conditions cannot be extrapolated directly to decisions made under the real conditions. For example, the Ju/'hoansi (!Kung san) make decisions in real life that contradict their behavior in experimental game conditions (Wiessner 2009). The disconnect relates to decisions being predicated on both a biological and cultural heritage (Read 2010a); hence, the behaviors observed in a game context are a complex mixture of background predispositions and the conditions specified in the game context, and need not mirror decisions made during daily life.

Guala does not go far enough, though, in his discussion of the disjunction between experimental and real conditions. In an endnote he observes that current theories of reciprocity based on game theory have not drawn upon the concept of reciprocity previously developed in anthropology (e.g., Sahlins 1972/1974) to account for the informal exchange of goods and services that is part of social life in human societies (see Note 2 in the target article). However, he does not follow up on his observation and instead limits his argument to a discourse on weak versus strong reciprocity, as if the only matter at issue is whether we account for cooperative behavior in human societies by one or the other of these two competing theories.

Running deeper than the surface issue of whether experimental evidence for strong reciprocity can be extrapolated to behaviors in natural conditions, is whether our perception of cooperative behavior in human societies has been framed correctly in the first place. Guala, like most researchers in this area, accepts uncritically the notion that small-scale human societies such as hunter-gatherers can be characterized as "acephalous social orders based on *spontaneous cooperation*" (sect. 8, para. 2, emphasis added). From the assumption of "spontaneous cooperation," it follows that relevant evolutionary questions are: How and under what conditions will there be selection at the individual level for cooperation as a trait? And, how and under what conditions will a population composed of individuals with a cooperation trait be stable against invasion by a "free-rider" trait?

The problem with formulating cooperation in this manner, along with its attendant questions, lies in the lack of evidence that individuals in small-scale societies are spontaneous cooperators. Consider how food resources are shared. In a hunter-gatherer society such as the Ju/'hoansi, food resources "in the wild" are collectively owned, in the sense of collective rights of access, by a residence group of families closely related through culturally constituted kinship relations (see Read 2001; 2007, for the difference between biological and cultural kinship). Rights to those food resources depend on membership (temporary or permanent) in a residence group. Collective ownership of resources changes into individual ownership by the mode of procurement and characteristics of the resources. Resources that come in small units are accessible to any able-bodied adult on a regular basis, and have low risk of failure on each procurement episode (such as, but not limited to, vegetal foods); these are transformed from collective into individual ownership through foraging. Resources that come in relatively large units are differentially accessible by adults according to individual skills, and have high risk of failure on a given procurement episode (such as game animals); these resources are considered to be collectively owned through hunting. For the latter, ownership changes from collective to individual according to culturally specified rules of sharing that remove decisions about sharing from the individual hunter to the group as a collectivity. Among the Ju/'hoansi, for example, the cultural rule is that the owner of the arrow that killed the animal (who need not have been present during the hunt) distributes the meat from the animal (Marshall 1976). Among the Netsilik Inuit, seals killed in winter hunting through their breathing holes in the pack ice were distributed in accordance with a culturally constituted system of "sealing partners" (Balikci 1970). Cultural rules like this make meat-sharing a group-level, not an individual-level, trait (Read 2012).

In general, resources that are individually owned are not subject to cultural rules of sharing. Individually owned resources are shared within a family (with a culture specific definition of what constitutes a family) and without cultural rules. Sharing within a family corresponds to "spontaneous cooperation." However, we need neither weak nor strong reciprocity to account for sharing and cooperation within a family.

Individually owned resources allow for individual decisions about whether they should be kept or given to others, but the