Culture does account for variation in game behaviour

By the Roots of Human Sociality team

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Lamba and Mace (L&M) have provided us with a worthwhile empirical effort that they portray as contradicting our prior work. However, this paper actually extends our earlier efforts. Their analyses (1) illustrate large inter-community variation in a small-scale society, (2) show the context-specificity of social behavior, and (3) reveal persistent community-level effects that cannot be traced to purely individual differences across games. These points are all made in our work (1, 2).

L&M's interpretation suffers from a misrepresentation of our empirical work and a misunderstanding of its theoretical basis. Empirically, L&M are incorrect about the supposed "single community sampling" in our cross-cultural project (both Phases I and II). This led to inappropriate comparisons between their between-group variation and ours. Once these inaccuracies are corrected, their data actually show the opposite of what they argue. Theoretically, L&M's critique is premised on the idea that cultural variation must take the form of rigid norms that generate behaviour independent of ecological context or economic constraints, and therefore, observing that behaviour is correlated with environmental variation implies that cultural variation is unimportant. In fact our research is based on the idea that people acquire context-specific expectations (e.g., "men only have one wife") and internalized motivations (e.g., "extramarital sex is wrong") via cultural learning, and that norms may evolve culturally in response to ecological or environmental factors. These expectations and motivations then influence people's decision-making along with other factors, including evolved motivations like self-interest and nepotism. So, as conditions vary across individuals, so too does behaviour even if people share norms. Moreover, norms may vary as a consequence of cultural evolutionary processes responding to different ecological and economic circumstances; when this happens, behavioural differences arising from norms will correlate with ecological or economic variables at the group-level, but not the individual-level. In our theoretical discussion below, we (1) clarify our framework, (2) show how L&M's theoretical preferences slot into our broader framework, and (3) highlight how—on its own—their approach provides little illumination on the origins of large-scale human cooperation.

					Table 1. Roots of Human Sociality Project: Phase I and Phase II							
#	Sites	Games Phase I	# of Phase I Communities (UG)	# of Phase II Communities (DG-UG)	Games Phase II							
1	Hadza	DG, UG	5	4	DG, UG, TPG							
2	Aché	UG, PGG	2	NA	NA							
3	Tsimane	UG, PGG	5	2	DG, UG, TPG							
4	Au	UG	1	3	DG, UG, TPG							
5	Gnau	UG	1	NA	NA							
6	Mapuche	UG, PGG	3	NA	NA							
7	Torguuds	UG	1	NA	NA							
8	Kazakhs	UG	1	NA	NA							
9	Sangu	TG, UG	2	NA	NA							
10	Orma	DG, UG, PGG	5	4	DG, TG							
11	Lamalera	UG	1	NA	NA							
12	Shona	TG, UG	28	NA	NA							
13	Machiguenga	UG, PGG	1	NA	NA							
14	Quichua/Achuar	UG	1	NA	NA							
15	UCLA	UG	1	NA	NA							
16	Accra City	NA	NA	3	DG, UG, TPG, TG							
17	Dolgan/Nganasan	NA	NA	1	DG, UG							
18	Gusii	NA	NA	2	DG, UG, TPG							
19	Isanga	NA	NA	1	DG, UG, TPG							
20	Maragoli	NA	NA	2	DG, UG, TPG							
21	Samburu	NA	NA	1	DG, UG, TPG, TG							
22	Shuar	NA	NA	2	DG, UG, TPG							
23	Sursurunga	NA	NA	3	DG, UG, TPG							
24	U.S. Missouri	NA	NA	1	DG, UG							
25	Yasawa, Fiji	NA	NA	2	DG, UG, TPG							
26	Sanquianga	NA	NA	2	DG, UG, TPG							
27	Emory	NA	NA	1	DG, UG, TPG							
T	Totals		58	34								

DG = Dictator Game, UG = Ultimatum Game, TPG= Third Party Punishment Game, TG=Trust Game, PGG=Public Goods Game

L&M premise their critique on the claim that our work "mostly" sampled from single communities within sites, and that consequently little consideration has been given to "ecological" and "demographic" variables. In fact, much of our team's work focused on studying the variation among communities within sites. Table 1 shows the number of communities (villages or camps) we studied for each site during both phases of the project. In Phase I (2), 8 out of 15 sites involved 2 or more communities. That means that *less than half* of our ethno-linguistic populations involved only a single community. In total, Phase I obtained data from 58 different communities (30, if you do not count the Shona). In Phase II (3), 11 of our 16 sites involved sampling more than one community. In total, Phase II studied 34 different communities. It is simply not true that prior work involved comparing "mostly" (from L&M's first paragraph) or "predominantly" (L&M's abstract) single communities sampled from larger sites. Terms like "mostly" cannot mean "less than half".

As a team, we conducted analyses very much like those of L&M within each of our sites. In Phase I, for example, Marlowe, Gurven, Ensminger and Barr all obtained samples from five or more different communities within one ethno-linguistic group. Among Hadza foragers, Marlowe (4) shows substantial variation among Hadza camps and a positive relationship between camp size and offers for both the Dictator (DG) and Ultimatum Games (UG), while controlling for the number of siblings and children in the camp—neither of which are significant. Among the Tsimane in Bolivia, Gurven (5) emphasizes community-level variation, and its robustness to explanatory efforts using demographic variables. Building on this, later work examines community size, distance to market and other village-wide variables in nine different Tsimane communities. Even in this larger, more controlled study, they still found that village residence was an important predictor of game behavior (6). Among the Orma in Kenya, Ensminger (7) shows that market integration captures much of the between-community variation in UG offers, while controlling for several demographic variables. Barr (8), working among dozens of Shona communities, takes advantage of a natural experiment that re-shuffled (and reduced) kin ties in some communities. Unlike L&M, Barr also examined actual ecological variables. None of these chapters are cited by L&M (not even in their supplemental), though all are compiled in our Phase I volume.

Because of its obvious importance, we have emphasized this community-level variation in our summary efforts (L&M's Ref 1: Section 7 is devoted to this issue (1)). In a section entitled "Local Group Effects", we highlight that while in *some* of the smallest-scale societies there is *substantial variation among communities in Ultimatum Game offers*, there appears to be much less variation among communities (and across countries) in large-scale societies—in the UG (also see 2, 9).

In Section 7 (L&M's Ref 1) we open with (1: 811):

Our analysis suggests that group-effects may be important, and this opens the question of how to define a group. In the above analyses, ethnolinguistic markers were used to define group membership,

¹ The "ecology" referred to in the title of L&M's paper boils down to their measure of community size. We agree that ecology places constraints on population size, but the idea that it is an ecological variable makes little sense. Consider the population of the Los Angeles basin, which has expanded by several orders of magnitude over the last 200 years. Clearly, population size cannot be equated with ecological constraints, unless "ecology" also includes cooperation, technology, institutions, and markets.

but non-ethnolinguistic regional groupings or smaller local clusters (e.g., villages) may be more appropriate. Our data allow some comparisons. Such small-scale tests permit us to control for a number of variables, including climate, language, regional/national economy, local buying power of the game stakes, and local history...

We then proceed to highlight the above community-level variation. The closing paragraph of this section begins with (1: 811):

In general, the micro level variation we observed contrasts with the UG results from the U.S. and Europe in which university students, who speak different languages and live thousands of miles apart, behave quite similarly. Of course, it is possible that variation exists within contemporary societies, but this variation is not represented in university populations (Ferraro & Cummings 2005).

L&M's paper proceeds as if this entire section of our Phase I summary and our entire edited volume on Phase I (2) do not exist.

One might still fault us for having any "single community" samples. However, even this would be misleading. Of the seven "single communities" from Phase I, five involved efforts to address precisely the issues that L&M highlight. In New Guinea, Tracer (10) compared two villages from different ethnolinguistic groups (the Au and Gnau) that lived only 1.5 km apart. There were no significant differences in ultimatum game offers between the villages. In Mongolia, Gil-White compared two linguistically distinct groups of herders in the same region, the Torguuds and Kazakhs (11). To account for both the similarities and differences he found, Gil-White hypothesized that local norms had responded to ecological pressures. In the Ecuadorian Amazon, Patton (12) compared two different ethno-linguistic groups living in the same village, and found substantial differences. Other studies that represent direct offshoots of our project similarly compared ethno-linguistic groups inhabiting the same region, and discovered sharp differences (13).

Building directly on these earlier results, especially those related to community size, our Phase II analyses included the size of individual communities, along with numerous demographic and economic controls. Thus, all of our findings are controlled for community size (not mean community size within sites), and most include multiple communities within each site.

L&M also suggest that we did not address the problem of non-independence in Phase II (3). We addressed it in multiple ways, both by including continental controls to deal with the relatedness among ethno-linguistic populations and by using clustered robust standard errors, clustering on either community or ethno-linguistic group (different analyses). Clustering at the site-level is a more conservative test than what L&M did. We considered the HLM approach used by L&M, but after extensive consultation with statisticians and econometricians, we determined it was not appropriate for our dataset. Moreover, since we had clear theoretically-driven hypotheses to test, L&M's analytical approach, was not attractive.

In Phase II, we also performed analyses within each ethno-linguistic group or site, examining community effects and demographics among the Hadza (14), Yasawans (15),

Tsimane (16), Au (17), Orma, Dolgan/Nganasan (18), Gusii (19), Maragoli, Shuar (20), Sursurunga (21), Sanquianga (22) and in Accra City (23).² The Missouri UG data is not distinguishable from UGs done in places as diverse as Detroit, UCLA, Kansas City, and Switzerland (9).

Their initial claim leads them into a second error. L&M want to argue that they find a degree of inter-community variation—in the Public Goods Game—roughly comparable to what we found in the UG. They found that 4% of the variation in monetary contributions occurs between communities and they say that this is roughly the same as the 12% we found in the UG. Beyond the obvious point that 12% (UG, Phase I) is three times greater than their 4%, there are three reasons why this equation is misleading.

To begin, L&M's comparison of variances misleads because it assumes we have only one community per ethno-linguistic group, and then compares the variation *among their* communities to our variation among sites. This claim leads to an inappropriate comparison. as more than half of our sites involve multiple communities. Let's examine their claim that the variation they observe across communities is equivalent to the variation we observed across sites. Table 2 shows the variance partitions for five different behavioural game measures from Phase II. First, note that the variation across all communities is always *higher* than the variation across sites—for all five experimental measures. This means L&M's comparison minimizes the differences in favour of their preferred claim. Next, look at the right-most column, which shows the variation that exists across communities within our sites. We get relatively small amounts of variance that range from 1.8% to 4.5%. Ergo, most of the between-group variation we observe is NOT due to variation across communities within sites—as L&M charge. Most of the variation is across sites. L&M's estimate of 4% is at the high end of Table 2, but this is consistent with our prior observation that the smallest-scale societies are at the high end of community-level variation (see below). Of course, our theoretical approach in no way requires that betweengroup variation occur among sites, but L&M seem to suggest this is important. Nevertheless, their analyses are inappropriate and Table 2 shows that their central claim is off target.

Table 2: Partitions of variance at difference scales							
Phase II	Across all	Across sites	Across communities				
Pilase II	communities	ACIOSS SILES	within sites				
DG offers	15.0%	10.5%	4.5%				
UG offers	26.5%	23.5%	3.0%				
TPG offers	14.3%	10%	4.3%				
UG MAO	31.3%	29.5%	1.8%				
TPG MAO	40.7%	37.9%	2.8%				
DG=Dictator Game, UG=Ultimatum Game, TPG=Third Party							
Punishment Game, MAO=Minimum Accept Offer							

² These chapters are part of the Phase II volume for our project, which has not been published yet. However, they were all cited in L&M's reference #3 (supplemental), and we would have gladly made these chapters available to L&M, had they asked.

Second, we ask whether L&M's comparison of variances for a Public Goods Game (PGG) and their salt game, to our UG, was appropriate. Table 2 shows that even across three different—but structurally very similar—bargaining games the variation across communities and sites varies dramatically. L&M would have us believe it is sensible to compare structurally different experiments, one involving salt, with our UG.

Fortunately, we do not have to guess (and neither did L&M) about whether it is sensible to compare the UG to the PGG. Consider our prior work, which deployed both the PGG and UG in the same ethno-linguistic group. Among the Tsimane, the inter-community variation in the PGG represents 27% of the total variation, while in the UG it represents only 13% (5). The intercommunity variation in the PGG used by L&M is twice that for the UG in the same ethno-linguistic group. This means that the best estimate for our ethno-linguistic variation in the monetary games is *six times* the size of L&M's.

Finally, we were pursuing hypotheses regarding the emergence of large-scale societies, and specifically interested in market exchange and fairness with anonymous others. In Phase I, several studies made it clear that the PGG often taps other social norms, unrelated to the monetary exchange context we were interested in (7), and that PGG contributions were uncorrelated with UG offers (24). Even in the West, the PGG does not tap strong norms in the one shot game, as contributions split between zero and 100% (25). Given these 2004 findings, and our repeated emphasis on how daily life and the medium of exchange might influence game play through social norms (see section 8 of L&M's Ref #1), it seems odd to critique our studies, which focus on monetary bargaining games, using cooperation games (PGG), especially involving food/spice. Yet, L&M do not address this, even in their large supplemental materials.

On the theoretical side, L&M do not accurately portray the culture-gene coevolutionary theory they criticize; in its place they provide weak and inconsistent demographic correlations, with debatable theoretical relevance. Their lack of understanding of the cultural evolutionary theory they critique is illustrated by their claim that models of the emergence of group norms rely on conformism. Conformism is but one kind of learning in a much larger class of models that show how various mechanisms create norms, including reputation (26), signalling (27), and other transmission biases (28). There is no conformism in any of these models. This point is summarized in L&M's references #2 (29) and #3 (3). Moreover, even those models that use conformist biases assume it is only one weak factor in decision-making, alongside mechanisms that use payoffs (30, 31). Moreover, modeling work shows that conformist transmission will frequently evolve to a non-trivial degree in a structured population in which the only interactions are public goods games (31).

The most significant misunderstanding of our theoretical approach is the notion that *only* local norms matter, that individuals do not evaluate costs, benefits, kinship, or reciprocity. In L&M's reference #1 (1) our team lays out the Beliefs, Preferences and Constraints (BPC) model (p. 812-814). This approach argues that, as a consequence of living and learning in a certain place with particular ways of doing things, individuals acquire *context-specific* sets of expectations and internalized motivations that then influence their decision-making

along with many other factors, including other evolved motivations like self-interest and genetic relatedness (9, 32). We have emphasized the importance of modeling and measuring these preferences using decision-theoretic tools, which allow trade-offs to be formalized and preferences to be estimated (e.g., 33).

The first sentence of our discussion section in L&M's reference #1 (1) is:

Understanding the patterns in our results calls for incorporating proximate-level decision-making models from behavioural economics, which have increasingly drawn insights on human motivation and reasoning from psychology and neuroscience (Camerer 2003; de Quervain et al. 2004; Sanfey et al. 2003), under the ultimate-level evolutionary umbrella created by culture-gene coevolutionary theory (Baldwin 1896; Boyd & Richerson 1985; Campbell 1965; Cavalli-Sforza & Feldman 1981; Durham 1991; Pulliam & Dunford 1980).

Now, imagine one takes an experimental tool to a population (say, the Parhari Korwa) where that particular tool does not strongly cue any local norms, or cues them only weakly and to varying degrees in different communities. What would the BPC approach predict? Since internalized normative motivations would play little role, we would expect many other factors to increase their relative impact on decision-making. To the degree that these other factors vary by community, we would expect communities to vary. By contrast, in places where the game-context strongly cues local norms, we would expect more uniformity at the individual and community level, and less relative influence of other factors. However, there still could be important variation if there were significant economic or ecological variation among communities. Once properly understood, the kinds of evolutionary/environmental forces that L&M emphasize are merely subcomponents of the integrated culture-gene coevolutionary approach we used, most likely to emerge when strong norms are absent *or when* people are paired with relatives or with frequent partners.

This approach also makes sense of the fact that L&M get different results for money and salt. Social norms are context-specific, and it would be surprising if people did not feel different about food vs. money. For over a decade, our project team has been studying how contextual differences in games might differently cue local norms (2, 3). We have compared alternative treatments using different mediums, correlated DG, UG and PGG results from the same people, examined the linkage between game findings and actual cooperation, and conducted extensive and systematic post-game interviews (15, 21, 34-37). In this vein, L&M's comments about the lack of "personality" effects echo our own discussion of "dispositional" effects (L&M's ref #1, p. 814 (1)). Of course, viewed from this perspective, both PGG and the salt game are incomparable with our efforts because they in no way tap the "market exchange" context that was our focus (3).

While L&M's theoretical concerns actually fit nicely within the broader theory we have laid out, we do not think their demographic measures are particularly well connected to theory, and the references they cite do not facilitate this connection. After trying dozens of variables, L&M find that age and festival invitees are associated with monetary PGG contributions. They do not offer any strong theoretical justification, and given the large number of variables they studied, it is possible that theirs is an unreliable correlation.

Consistent with this, we have studied dozens of small-scale societies and several different games. Occasionally we have found age effects, though they are not robust across games or through time. Regarding festival invitees, L&M see this as "network size". We too suspected that networks might be important for game play—though we used 2-person games.³ Our approach was to actually measure people's location in social networks, and use this to predict game play. Centrality has a positive relationship in our trust games, but no relation to DG, UG, and TPG game measures (15, 38).

For the salt game, L&M again examined dozens of variables and this time found that two different variables predicted cooperation, the number of adult sisters and the community size. Now, the context-specificity of norms provides a ready hypothesis for why salt and money might be treated differently, but L&M do not provide any theoretical reasons why having sisters, for example, should matter when it is salt but not when it is money. L&M suggest that the differences in which variables are significant predictors for salt vs. money might have to do with the structure of the game, or procedural differences, but how their theories predict this is not clear. Why should one use his number of adult sisters as a kinship cue when it is about salt but not when it is money? Our own work shows that each players' mean genealogical relatedness is not predictive of offers in the DG, UG, and TPG (15). In summarizing our findings, we have sought to emphasize only those variables that are both theoretically-derived and produce robust results across multiple games (3).

Except for community size (1, 3, 4, 39), we have previously found ephemeral effects for all of L&M's key variables (or versions of them: age, network centrality, siblings) in one group or other, or in one game or another. However, none of their preferred variables have proved robust across groups, games, or in re-tests years later. None are even robust across L&M's two experiments. Our experience indicates that if they did the UG in their communities, they would find different predictors yet again.

Regarding community size⁴: we agree that potent genetic evolutionary forces in a species like humans will often lead to less cooperation in larger populations. This is one of the points of departure for our theoretical and empirical enterprise. We expect that this was the situation for much of our evolutionary history. Community sizes would expand and cooperation would decline. Oversized communities would fragment—a fact that much ethnography supports (3, 40, 41). The issue, then, is to understand how some human societies managed to overcome this evolutionary dynamic—the situation L&M document—and expand. Thus, L&M's empirical demonstration of this relationship (at least with salt) further sharpens the puzzle, but does not illuminate a path to the solution.

In conclusion, we had previously offered and tested one set of hypotheses regarding the evolution of complex human societies with large-scale cooperation and anonymous exchange (42, 43). We welcome alternative accounts, especially targeted at explaining the patterns of variation we found, such as the positive association with markets. We

³ Their "network measure" is the number of people a person says he or she invited to their big party. This does not strike us as a particularly good way to operationalize and measure network data.

⁴ L&M claim we conflate community size and socio-political complexity. In fact, we correlate our measures of community size with a measure of socio-political complexity (2)—a strange thing to do if one conflates them.

hypothesized, tested, and replicated such associations across two phases of our project. L&M, however, provide no such account, and instead substitute demographic correlations that are not robust across their own experiments. The intercommunity variation both echoes our prior findings and theoretical expectations, effectively sharpening the puzzle we're aiming to solve.

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