LETTER

Culture does account for variation in game behavior

Lamba and Mace's critique (1) of our research (2–4) is based on incorrect claims about our experiments and several misunderstandings of the theory underpinning our efforts. Their findings are consistent with our previous work and lead to no unique conclusions.

Lambda and Mace (1) incorrectly claimed that we "mostly" sampled from single communities within sites, and that we ignored "ecological" and "demographic" variables. In fact, much of our work focused on studying the variation among communities within sites. In phase I (2), 8 of 15 sites involved multiple communities, and in phase II (3, 4), 11 of our 16 sites sampled from multiple communities. Several sites included 5 communities*, and 1 site included 9 communities (5).

During both phases, we conducted analyses like Lamba and Mace's (1) within each of our sites (2–4). Except for community size, which emerged as a focal predictor (4), we studied versions of all the key variables (age, network centrality, and siblings) of Lamba and Mace (1) in some populations. Occasionally, these were significant, but none had consistent effects across populations, games, or in retests years later. Lamba and Mace (1) also failed to find any predictors that were consistent across their experiments, despite trying dozens of variables. Moreover, their predictors are neither theoretically well-grounded nor particularly ecological. Nonetheless, Lamba and Mace (1) concluded that "ecology drives variation in cooperation."

Our analyses show that the key claim of Lamba and Mace (1), that the fraction of variation they observed for monetary games (4%) among communities is comparable to the fraction we observe among our sites (12% for ultimatum game offers in phase I) is not correct, even allowing for their assumption that $12 \approx 4$. Table 1 partitions the variation for five game measures from phase II (3). The variation among communities within sites [what Lamba and Mace (1) calculated] is always smaller than the variation among sites. Lamba and Mace's estimate of 4% within their site (1) is consistent with our data, but their data tell us nothing about the variation across sites (contrary to their claim).

Our theoretical framework is also not made clear, because Lamba and Mace (1) claimed that our approach holds that only norms matter, and that norms cannot evolve in response to ecological variation. They further imply that if demographic or ecological variation is important, norms cannot be. Our research is based on the idea that people can acquire context-specific expectations (e.g., "one wife per man") and internalized motivations (e.g., "extramarital sex is wrong") as a consequence of cultural learning. These expectations and motivations then influence their decision making along with other factors, including evolved motivations linked to self-interest and genetic relatedness (2). Thus, as conditions vary, so too does behavior, even if people share such norms.*

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1. Lamba S, Mace R (2011) Demography and ecology drive variation in cooperation across human populations. *Proc Natl Acad Sci USA* 108:14426–14430.

 Henrich J, et al., eds (2004) Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies (Oxford Univy Press, Oxford).

3. Henrich J, et al. (2006) Costly punishment across human societies. Science 312: 1767–1770.

 Henrich J, et al. (2010) Markets, religion, community size, and the evolution of fairness and punishment. Science 327:1480–1484.

 Gurven M, Zanolini A, Schniter E (2008) Culture sometimes matters: Intra-cultural variation in pro-social behavior among Tsimane Amerindians. J Econ Behav Organ 67:587–607.

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^{*}See http://ssrn.com/abstract=1971990 for additional details.

Table 1. Partitions of variance for phase II data

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| Game measures | Across sites, % | Across communities within sites, % |
|---------------|-----------------|------------------------------------|
| DG Offers | 10.5 | 4.5 |
| UG Offers | 23.5 | 3.0 |
| TPG Offers | 10 | 4.3 |
| UG MAO | 29.5 | 1.8 |
| TPG MAO | 37.9 | 2.8 |

DG, dictator game; MAO, minimum accept offer; TPG, third party punishment game; UG, ultimatum game.