



Reply to Zefferman et al.: Cultural institutions can provide adaptive benefits for costly cooperation

We appreciate the close reading Zefferman et al. (1) give our paper (2). Using a sample of men from a small-scale pastoralist society, we analyzed the relationship between participation in low-risk stealth raids and leadership in high-risk battle raids with reproductive success (2). We found that greater participation in low-risk stealth raids was associated with an increased number of wives and children, whereas leadership in high-risk battle raids was not. Despite the fact that leadership in battle raids imposed serious mortality risks, battle leaders were not reproductively disadvantaged compared with other men. We conclude our report by stating that our results support the “general proposition that warriors participating in small-scale warfare tend to receive fitness-enhancing benefits” (2). Zefferman et al. (1) argue that the data we present do “not warrant such a general claim” because of the lack of an association between battle raids and reproductive success.

We disagree with Zefferman et al.’s (1) assessment for two reasons. First, battle raids are of limited utility for making inferences about warfare in small-scale societies generally. Battle raids by 21st century East African pastoralists present a high risk of death for participants who attempt to capture livestock while armed with automatic weapons. This

type of high-risk conflict is exceedingly rare among nonpastoralist small-scale societies (3). Although “battles” do occur among such groups, the mortality rate for aggressors is usually low because warriors seek to minimize their risk. Stealth raids, in which a small group of warriors engages in low-risk attacks, are the most common pattern of small-scale warfare. Thus, the fact that we do not find a result for battle leaders tells us little about small-scale warfare generally.

Second, adaptive models of small-scale warfare predict that warriors will individually benefit from their participation and that these benefits will confer reproductive advantages (3). We found that elders who were reported to have participated in a greater number of low-risk stealth raids had more wives and children than other men. The positive relationship between raiding and reproductive success is consistent with predictions from adaptive hypotheses for participation in warfare, providing support for the “general proposition that warriors participating in small-scale warfare tend to receive fitness-enhancing benefits” (2).

Zefferman et al. argue that cultural institutions are necessary to account for high-risk cooperation on battle raids (1, 4). We agree and do not intend our analyses to imply that cultural institutions are not important.

Previously, we have argued that cultures can create incentive systems to promote risk-taking in warfare and that these commonly provide individual benefits for warriors, some of which may be adaptive (5).

A full understanding of human warfare will consider the role of cultural institutions, including the possibility that they may provide adaptive benefits for participants.

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- 1** Zefferman MR, Baldini R, Mathew S (2015) Solving the puzzle of human warfare requires an explanation of battle raids and cultural institutions. *Proc Natl Acad Sci USA*, 10.1073/pnas.1504458112.
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 - 4** Zefferman MR, Mathew S (2015) A theory of human warfare: Group-structured cultural selection. *Evol Anthropol*, 10.1002/evan.21439.
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The authors declare no conflict of interest.

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