Reply to: Broad definitions of enforcement are unhelpful for understanding evolutionary mechanisms of cooperation.

J. Arvid Ågren[1,*], Nicholas G. Davies[2,*], and Kevin R. Foster[3,Ψ]

[1] Department of Organismic and Evolutionary Biology, Harvard University

arvid_agren@fas.harvard.edu

[2] Department of Infectious Disease Epidemiology, London School of Hygiene and Tropical Medicine

nicholas.davies@lshtm.ac.uk

[3] Department of Zoology and Department of Biochemistry, University of Oxford

kevin.foster@zoo.ox.ac.uk

* These authors contributed equally

Ψ To whom correspondence should be addressed

While Engelhardt and Taborsky[1] agree with the core argument of our recent article[2]—that enforcement is central to the evolution of cooperation—they go on to suggest i) that our use of the word "enforcement" is semantically problematic and ii) that we neglect to distinguish between behavioural manipulations that occur via helping or harming. We find no merit in these points.

First, semantics. Englehardt and Taborsky object that our use of 'enforcement' does not correspond exactly with their everyday use of the word. The fit between common parlance and the terminology of evolutionary biology is an old concern[3], but one that can be mitigated by clearly defining terms[4]. Our definition of enforcement—an action that evolves, at least in part, to reduce selfish behaviour within a cooperative alliance—reflects the established usage for describing mechanisms like partner choice, punishment, and reward in cooperative systems across all scales of life (e.g. see Figure 2 in West et al. 2006[5]). Moreover, it was precisely because of the subjectivity of language that we also provided an extensive theory supplement that defines enforcement mathematically (see also Box 1 in our original piece[2]). Instead, Englehardt and Taborsky provided an "everyday-language" definition of enforcement—"an action involving manipulation by force to the benefit of an actor at the expense of a receiver"—that is so vague that it would draw in examples of both predation and parasitism. This illustrates why everyday-language definitions are often insufficient for evolutionary biology.

The second key point of Engelhardt and Taborsky is that we do not sufficiently distinguish between the promotion of cooperation through harm and through the provision of incentives or help. Again, we disagree. Our review explicitly distinguished between harming and helping mechanisms of enforcement (Table 1 in our original piece[2]) and gave numerous examples of each. We also reject their point that manipulation by harming versus helping are so different that distinguishing them is "essential". Consider, for example, a host controlling its microbial symbionts either by differential harming or differential feeding, as is thought to occur in the mammalian microbiome via various antimicrobial peptides and glycosylated mucins respectively[6]. To increase the relative abundance of a beneficial symbiont, the host can preferentially feed cooperative symbionts, preferentially intoxicate non-cooperative symbionts, or both. But, importantly, the different mechanisms can have exactly the same evolutionary

effects on cooperation. Therefore, while we appreciate that harming and helping mechanisms of enforcement can have their differences[2], they have a lot more in common to the extent that they will be sometimes indistinguishable in their effects on cooperative evolution.

The utility of our framework[2] becomes clear when one looks beyond Englehardt and Taborsky's focus on the animal behaviour literature. One of the major advances in evolutionary biology of recent decades is the recognition that the principles of social evolution apply equally to selfish genetic elements, microbes, mutualisms, and societies[7]. Restricting focus to animal behaviour[1] prevents one from recognizing the shared principles and establishing the common vocabulary needed to understand the evolution of cooperation across all biological systems.

References

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