

This theory accommodates the innate learning structures used in norm acquisition (Hamlin et al. 2011), while also explaining cross-cultural differences in norms and preferences (Ellingsen et al. 2012; Gächter et al. 2010; Henrich et al. 2001; 2010b; Herrmann et al. 2008). Importantly, the SHH accomplishes this without an appeal to group selection or intergroup conflict. An individual benefits from internalizing successful strategies, and in typical settings where mechanisms for the evolution of cooperation are operating, what is good for the individual winds up also being beneficial for the group. Thus, improving the group's welfare occurs as a side effect of selection maximizing individual payoffs, rather than as the cause of that selection.

What about institutions? By enforcing norms of cooperation, institutions play a critical role in stabilizing payoff structures that simultaneously optimize social and individual welfare. Can the emergence of such institutions be explained by individual-level forces? Indeed, it can. Consider the institution of democratic voting. Under a median voting rule, for instance, individuals engaged in a group cooperation endeavor each vote for a contribution amount, and then all participants are forced to contribute the amount specified by the median voter (Bernard et al. 2013; Deacon & Shapiro 1975; Hauser et al. 2014; Walker et al. 2000). Under such an institution, even self-interested people would vote for contribution to a public good, because individuals earn higher payoffs in a group where everyone contributes. Since the institution forces all participants to behave in the same way, the free-rider problem is eliminated, and individual and collective interests are aligned. Furthermore, similar logic would cause individual-level forces to favor joining or founding such an institution, rather than preferring a scenario where free-riding was possible (and thus cooperation was doomed). Indeed, experiments show that people “vote with their feet” and learn to choose institutions with sanctions over a sanction-free alternative (Güerke et al. 2006; Rockenbach & Milinski 2006). These studies capture the essential components of institutionalized cooperation: When institutions can homogenize individual behavior through norm enforcement, social welfare and individual welfare are maximized by the same strategy.

Thus, cultural evolution and learning need not be linked to group-level selection, and genetic evolution to individual-level selection, as is done in the target article (and in much of the literature on cultural evolution more broadly). Both of these dimensions of the debate regarding human evolution can vary independently (Rand & Nowak 2013). A helpful analogy comes from American politics, where social and fiscal conservatism, two independent dimensions of political attitudes, tend to strongly co-vary because of the United States' two-party system. However, these two variables do not need to covary: An individual can be socially liberal and fiscally conservative (e.g., libertarian) or socially conservative and fiscally liberal. Similarly, scholars can advocate for the importance of cultural evolution without invoking group selection, an intellectual space which is often left unoccupied. It is largely due to historical accident that cultural evolution and group selection have come to be linked (the most successful proponents of the importance of culture are also advocates of group selection). Continuing to develop individual-level accounts of cultural evolution is essential for deepening our understanding of human evolution and prosociality.

The burden of proof for a cultural group selection account

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Abstract: Richerson et al. establish cultural group selection as a plausible force in human social evolution. However, they do not demonstrate its causal precedence for any trait, let alone its “essentialness.” To do so, they must show that a particular group trait was *caused by* cultural transmission, and *directly caused* differences in group fitness.

Richerson et al. have done a tremendous job of establishing the plausibility of cultural group selection (CGS) as a process of social evolution. However, they have not shown that it is “essential” to human cooperation, or even that it has operated on any single trait. Instead, they show that fitness can be partitioned so as to satisfy the conditions for CGS. This is an altogether different – and much weaker – claim.

The total fitness of a population can be carved up in multiple ways and attributed to any number of traits, so long as fitness and trait values covary. This is one of the more pleasing results derived from the Price equation (e.g., Price 1972; see also Hamilton 1975; Marshall 2011; Queller 1992), and it should bury the notion that individual- and multi-level selection accounts are predictively different. An allele that is favored in inclusive fitness or neighbor-modulated models will also be favored in group selection models (and vice versa), because the frequency of that allele is positively correlated with fitness whether we conceive of it as affecting individuals or groups. If CGS favors the same fitness effects as selection on genes (not a given, of course), then the findings in the target article should not be news. The average fitness of individuals is necessarily correlated with the fitness of their groups.

But just because we could view selection as taking place at the group level does not mean we should. Although individual-level and multi-level fitness partitions are *predictively* equivalent, they are not *causally* so (Birch & Okasha 2015; Okasha 2015; see also Okasha & Paternotte 2012). Sometimes, group traits directly cause group fitness, but at other times the relationship between the two is merely correlational. Using the wrong fitness partition will lead one to infer causality where none exists and, consequently, mischaracterize the adaptation. If there is individual-level variation that *directly causes* variation in individual fitness (Fig. 1A), then an individual-level partition is best. Of course, individual variation in traits will also directly affect trait variation at the group level; this is what Williams (1966) meant in saying that “a herd of fleet deer” will simultaneously appear as a “fleet herd.” In this instance, the target of selection is the fleetness of individuals, rather than that of the groups they make up. Conversely, trait variance at the group

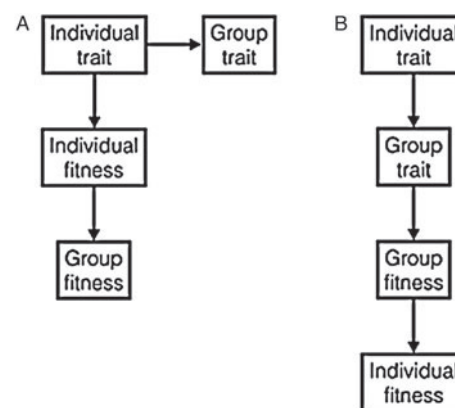


Figure 1 (Barclay & Krupp). Causality in individual and group selection. Arrows show the direction of direct causal effects. (A) An individual-level partition is justified when the individual trait directly affects individual fitness and there is no direct relationship between the group trait and group fitness. This results in an individual adaptation. (B) A group-level partition is justified when only the group trait directly affects group fitness and there is no direct relationship between the individual trait and individual fitness. This results in a group adaptation. Adapted from Okasha (2015).

level that *directly causes* variance in group fitness (Fig. 1B) is best handled by a group- or multi-level partition.

Consider warfare as an illustration. In typical battles where some live and die on each side, individual fitnesses cause group fitness through simple summation. In fights where the loser is annihilated (e.g., the losing battleship is sunk), however, individual fitness is directly caused by group fitness – individuals succeed or fail *because* their group succeeds or fails. A multi-level partition, such as CGS, is only warranted in the latter sort of case.

The burden of proof for a CGS account, then, is considerably heavier than what the target article presents. First, CGS needs to be tested on a case-by-case basis; it cannot be accepted wholesale because it cannot be distinguished from alternative fitness partitions in this way. A hypothesis for a *particular* group trait must be set up against alternative hypotheses. Second, the evidence must demonstrate the direct causality of the link between the group trait and group fitness (Fig. 1B), beyond mere correlation. Third, the evidence must show that the group trait has evolved and is maintained specifically by cultural transmission. While Richerson et al. do not ignore these issues, their “sketch of the evidence” falls short of making their case compelling.

Many alleged examples of group selection likely reflect individual-level adaptations. The requirements for group, as opposed to individual, adaptation are rather imposing: It is rare for individual human fates to be so intertwined with their group’s fate that group success directly causes (rather than merely correlates with) individual success, such as all group members succeeding or failing together as a unit because of their group’s composition. Generally, we can expect group traits to directly cause group adaptation only when partners are clonal or when there is extreme repression of competition (Gardner & Grafen 2009; Okasha & Paternotte 2012), neither of which describes the human condition well. The examples given by Richerson et al. do not come close to meeting this criterion. Conflicts that lead to the success or failure of entire groups would, but such circumstances are rare.

Moreover, many cases of ostensible cultural transmission are explainable as strategic, individual responses to existing socio-ecological circumstances. Violent defense of one’s honor – a key aspect of the “Culture of Honor” – in the Southern United States is often given as a shining example of cultural transmission (e.g., Nisbett & Cohen 1996; Richerson & Boyd 2005). However, current variation in income inequality fully accounts for any cultural difference in homicide rates between the northern and southern states (Daly & Wilson 2010). Similarly, behavioral differences between collectivist and individualist cultures are supposedly maintained by internalized social norms and beliefs (e.g., Markus & Kitayama 1991), yet these differences can disappear when the expectations of the different cultural groups are matched (Yamagishi et al. 2008).

Richerson et al. wave away alternative explanations by toppling a straw-man of “evoked culture” that they readily admit no one holds

and by relegating as “narrow” the interpretation of experimental research. They also ignore the fact that CGS explains genetically detrimental helping by invoking the “mistakes” of an adaptive learning mechanism (Barclay & Van Vugt 2015). More generally, the study of cooperation has long been hindered by confusion between proximate and ultimate causation (Barclay 2012; West et al. 2011), and we can now add to the list a persistent confusion over the utility of the group selection concept itself. We look forward to future work on CGS that convincingly demonstrates *both* the causal relationship between group traits and group fitness and the transmission of these traits by cultural means.

The cooperative breeding perspective helps in pinning down when uniquely human evolutionary processes are necessary

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Abstract: The cultural group selection (CGS) approach provides a compelling explanation for recent changes in human societies, but has trouble explaining why our ancestors, rather than any other great ape, evolved into a hyper-cooperative niche. The cooperative breeding hypothesis can plug this gap and thus complement CGS, because recent comparative evidence suggests that it promoted proactive prosociality, social transmission, and communication in Pleistocene hominins.

Richerson et al. address two key changes in human evolution, the first being how cooperation could evolve in the small-scale Pleistocene societies of prehistoric times, and the second being how these small-scale societies successfully evolved into much larger and more complex societies during the Holocene. The authors’ case for a role of cultural group selection (CGS) in the second transition is strong. However, we will argue that the adoption of cooperative breeding suffices to explain the origin of human hyper-cooperation in early forager societies, as it resulted in increased prosociality and social transmission and favored the emergence of language.

Richerson et al. mention cooperative breeding as a possible trigger of the process involving CGS, but argue that this alternative hypothesis is difficult to test independently. However, recent comparative work exploring the psychological and cognitive consequences of cooperative breeding in nonhuman primates now increasingly allows us to identify general patterns that reliably emerge whenever a primate species adopts cooperative breeding. It is thus most parsimonious to assume that such psychological and

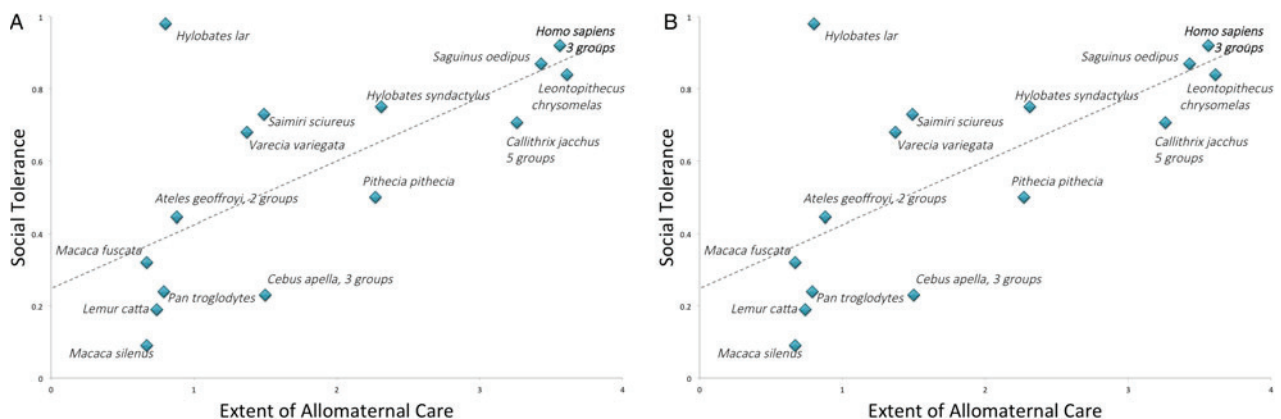


Figure 1 (Burkart & van Schaik). The relationship between allomaternal care and (A) proactive prosociality and (B) social tolerance. Humans fit the general primate trend and do not represent an outlier.