The Evolutionary Origins of Cooperation in the Hominin Lineage: A Critique of Boyd and Richerson's Cultural Group Selection Account

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The origin of human cooperation poses an evolutionary puzzle. In order for cooperation to evolve, our Pleistocene ancestors must have overcome the free rider problem, in which noncooperators reap the benefits of cooperation without paying the costs. Cultural group selection accounts offer a potential solution to this problem. In this article, I evaluate Boyd and Richerson's influential account. I argue that it cannot explain the evolutionary origins of human cooperation because it presupposes cooperative behaviors among our Pleistocene ancestors. Although Boyd and Richerson's account may explain the expansion of cooperation in hominin evolution, it cannot explain how cooperative behaviors first emerged.

1. Introduction. The adoption of cooperative behaviors by a group of organisms is often highly profitable to individual agents, increasing individual fitness payoffs compared to those in noncooperative groups. If the collective benefit of cooperation is shared equally among the individuals without regard to individual investment, then those individuals who defect will be at a selective advantage, as they will reap the benefits of cooperation without paying the costs. This free rider problem, if not solved, leads to the erosion of cooperation within a group. Since cooperation within the hominin lineage is common and often involves interactions between unrelated individuals, any plausible explanation for the evolutionary origins of human cooperation must explain how our lineage overcame this problem.

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Two general types of solutions have been put forward to explain how cooperative, group-beneficial behaviors spread among our early hominin ancestors. The first posits group-level selection, whereas the second argues that human cooperation evolved through selection acting on individuals. They differ in how they categorize the cooperative behaviors of our Pleistocene ancestors. Those who advocate a group selection account hypothesize that cooperative behaviors, such as food-sharing or collective hunting, were altruistic behaviors, beneficial to the group yet costly to the individual (Richerson and Boyd 2005; Bowles and Gintis 2011). For cooperative behaviors to evolve under this scenario, selection must have favored those groups with higher frequencies of cooperative individuals and must have occurred at a rate sufficient to offset the selection against cooperative individuals within groups. Proponents of the individual selection account, in contrast, argue that the earliest cooperative, group-beneficial behaviors of our Pleistocene ancestors were mutualistic (Binmore 2006). That is, they claim that these cooperative behaviors maximized individual fitness while also increasing the average fitness of group members.

Sterelny (2016) develops a compelling new account of the evolution of cooperation in the hominin lineage. He claims that the earliest cooperative behaviors, which first emerged during the transition from great ape to Pleistocene forager social lives, were individually advantageous, mutualistic behaviors. To support his individual selection account, Sterelny argues against the plausibility of group selection accounts. He takes Bowles and Gintis's (2011) account as his "stalking horse," since it offers "a clear and explicit hypothesis about the nature of intergroup competition" (Sterelny 2016, 33). Bowles and Gintis claim that high levels of intergroup warfare during the Pleistocene led to intergroup competition and group extinction. Sterelny marshals convincing evidence against this account, arguing that the levels of intergroup warfare required by this model were unlikely to have obtained. His arguments, however, do not undermine the plausibility of group selection accounts, more generally, because he does not adequately address the account of Boyd and Richerson (2009a). Over the past few decades, Boyd and Richerson have developed a highly influential account of cultural group selection to explain the origin of cooperation. Whereas Bowles and Gintis posit intergroup warfare followed by group extinctions as the primary mechanism, Boyd and Richerson develop three different mechanisms of intergroup competition: social extinction, social migration, and between-group transmission of cooperative behavioral variants. Because these mechanisms are less reliant on lethal intergroup conflict, Boyd and Richerson's account does not fall prey to Sterelny's critique.

In this article, I aim to further support individual selection accounts of the origin of cooperation by taking aim at Boyd and Richerson's group selection account. I argue that it cannot explain the evolutionary *origin* of cooperation

within the hominin lineage because all three mechanisms of intergroup competition that they develop presuppose cooperation among Pleistocene foragers. I will show that each of these mechanisms depends on social practices, population structures, or between-group information channels that are only likely to obtain if groups have already evolved certain cooperative behaviors. Thus, although these accounts might be able to explain the expansion of cooperation during the Holocene, they cannot explain how cooperative behaviors originated and spread within the hominin lineage in the Pleistocene. Because of the implausibility of these group selection accounts, I conclude that cooperation first emerged in our Pleistocene ancestors from individual-level selection acting on mutualistic cooperative behaviors.

2. Cultural Group Selection and Social Learning. For group selection to occur, there must be stable between-group variation that both is heritable and has a differential effect on group fitness. Fitter groups will then outcompete groups that are less fit, leading to the spread of traits that enhance group fitness. These conditions often fail to obtain in the case of genetic group selection because genetic adaptation typically occurs so slowly that between-group migration will swamp any group-level variation. Richerson and Boyd (2005) and other proponents of cultural group selection argue that group selection on cultural variants is not similarly affected by between-group migration. Within the hominin lineage, the early evolution of the capacity for social learning, or the process whereby individuals learn from others through imitation or teaching, provides mechanisms for maintaining the stable, group-level cultural variation necessary for group selection to occur.

Social learning has the potential to make cultural group selection a more powerful evolutionary force for two reasons. First, it enables cumulative cultural adaptation. Because humans have evolved the capacity for social learning, when one lucky individual discovers a beneficial cultural innovation via trial-and-error learning, it can be acquired by other members of the group through imitation or teaching, preserved in the population, and passed on to future generations. Second, because much social learning is biased, it tends to decrease within-group behavioral variation while stabilizing between-group variation. For example, a conformist learning bias leads individuals to prefer more over less common behavioral variants. Biased social learning potentiates group selection in the hominin lineage by stabilizing between-group variation and tamping down within-group variation, despite plausible levels of migration between Pleistocene forager bands. Whereas migration of individuals between groups leads to genetic mixing, the conformist bias would encourage new migrants to adopt common and successful local behavioral variants, thereby maintaining the between-group behavioral differences that are necessary for cultural group selection. For these reasons, proponents of cultural group selection argue it is likely to have been a powerful force in the evolution of cooperation within the

hominin lineage (Henrich 2004; Richerson and Boyd 2005; Bowles and Gintis 2011).

3. Implausibility of Boyd and Richerson's Account of Intergroup Competition. Boyd and Richerson (2009a) have developed a pluralistic account of group selection with three different mechanisms that aims to explain the evolution of cooperative behaviors in the Pleistocene. Here, I discuss each of these mechanisms in turn to show why they cannot adequately account for the evolutionary origins of human cooperation.

3.1. Social Extinction Cannot Explain the Evolutionary Origins of Cooperation. Of the three mechanisms proposed by Boyd and Richerson, the mechanism of social extinction bears the closest resemblance to the Bowles-Gintis account of lethal intergroup conflict and extinction. It also requires competition followed by selective group extinction, but it differs in two key respects. First, the causal features that lead one group to thrive while a neighboring group goes extinct need not be lethal intergroup conflict. For instance, one group could be weakened because of population decline from environmental or resource stress or social discord. Second, this mechanism of group selection does not require that individuals of a group die during an extinction event. Instead, all that is required is that the group as a social unit disbands, and the individuals disperse throughout the population, "tak[ing] shelter with friends and relatives in other groups" (Boyd and Richerson 2009a, 3285). Because of biased social learning, these disbursing individuals will likely adopt the cultural or behavioral variants of the successful groups they join. If cooperative behavioral variants tend to make groups more successful, for instance, in collective defense against hostile neighbors or during times of environmental hardship, then these behaviors will spread throughout the population as less cooperative groups suffer social extinction at higher rates. In this way, group selection via social extinction aims to explain the evolution of cooperative behaviors without necessitating high rates of intergroup warfare.

Compared to the Bowles-Gintis account, the mechanism of social extinction expands the range of possible conditions under which group selection can account for the spread of group-beneficial yet individually costly behaviors. Nevertheless, I contend, it is highly unlikely to account for the evolutionary origin of cooperation in our Pleistocene ancestors. I first argue that the mechanism of social extinction is most plausible if a population exhibits certain structural features (i.e., metaband formation) that are only likely to obtain in populations where cooperative behaviors are already common. Then, I show how Boyd and Richerson's example of social extinction drawn from the ethnographic literature, which does not involve metaband formation, cannot explain the evolution of cooperation, since the assimilating groups already engage in highly cooperative behaviors.

According to Boyd and Richerson, social extinction is most likely to oc-cur if individuals from one group have relatives or friends in another group. The likelihood that this mechanism was a driving force in the evolutionary origins of human cooperation therefore depends on the existence of genetic and friendship ties between Pleistocene forager bands. Although our knowl-edge of the social organization of early hominins is incomplete, there is an emerging consensus that small egalitarian forager bands of the middle to late Pleistocene would aggregate to form metabands during seasonal windfalls or around water sources in arid lands (Barnard 2011; Boehm 2012). Forager eth-nography suggests these periods of aggregation are also times of mate forma-tion. If this account accurately describes the lifeways of our forager ancestors, then metaband formation offers the most plausible mechanism for individuals from one forager band to develop friendship and kinship ties with members of other bands. It is precisely these intergroup ties that drive the Boyd-Richerson account of social extinction: you are much more likely to abandon your group during hard times if you know you will be welcomed by family and friends in a neighboring group. However, this mechanism cannot account for the evolu-tionary origins of cooperation, I argue, because the practice of metaband for-mation—which is precisely what enables an individual to make friends and forge familial ties with members outside one's own band—involves a host of cooperative behaviors.

Consider Barnard's (2011) account of seasonal metaband formation in the Ju/'hoansi foragers in the Kalahari.[1] The Ju/'hoansi, who live in an arid region with few year-round water holes, follow yearly patterns of dispersal and ag-gregation. During the wet season, small forager bands of 25–30 individuals live dispersed throughout their territory hunting small game and foraging for edible plants around seasonal water holes. These small bands then aggregate around permanent water holes during the dry season, forming metabands, in which up to five or six small bands live together. Seasonal patterns of aggrega-tion and dispersal allow Kalahari foragers to optimize the use of limited water resources. In addition, the dry season aggregation of foraging bands provides opportunities for interbreeding between members of different bands. These kin-ship relations forged through interbreeding then serve as the foundation for coinsurance and trading partnerships as well as defensive networks between bands.

For this practice of seasonal aggregation to become established in the hom-inin lineage, however, individuals and small forager bands would first need

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1. There is an epistemic risk in using ethnographic data from extant forager bands to reason about our Pleistocene ancestors. However, because of the paucity of other empir-ical data, nearly all those engaged in debates about the evolution of cooperation accept this risk while acknowledging that evolutionary accounts based in part on this evidence are, at best, how-plausibly explanations.

to solve certain cooperation problems. Because the permanent water hole is a predictable and necessary resource, there is the possibility that a single forager band could monopolize it (Sterelny 2012). To prevent a minority from seizing control, the bands must have mechanisms in place that encourage resource sharing and contain overassertive groups who attempt to exploit or control these resources. Within-group mechanisms of bully control—for example, when group members cooperate to ostracize, rebuke, or even expel a would-be chief who attempts to dominate the group—are cooperative behaviors thought to be necessary to maintain the stability of egalitarian forager bands (Boehm 2012). These within-group leveling mechanisms and the cooperative behaviors they encourage and reinforce would likely facilitate peaceful and cooperative metaband formation as well. Additional forms of cooperation are also probable preconditions for peaceful metaband formation. For instance, evidence from the ethnographic record suggests that individual bands demonstrate goodwill to other bands within the metaband by sharing food from successful hunting and foraging excursions. These cooperative displays then facilitate mating among members of different groups, which in turn heightens the bonds between foraging bands. Thus, it seems likely that cooperative behaviors must already be common within small forager bands before they can peaceably aggregate into seasonal metabands. Insofar as the mechanism of group selection via social extinction relies on metaband formation to establish between-group family and friendship ties, it is unable to explain the evolutionary origins of cooperation.

There are cases of social extinction, however, that do not require preexisting familial or friendship ties between groups. Although it might be easier to decide to abandon your group for another if you have friends or relatives already there, if times are hard enough and your group is in serious decline, you might still decide to take your chances and attempt to assimilate into another more successful group. Boyd and Richerson, in fact, consider ethnographic reports that suggest social extinction occurred without prior metaband formation or kinship ties. They offer the case of the Mae Enga of Papua New Guinea, who are often considered to be one of the best models of Pleistocene and early Holocene forager lifeways (Soltis, Boyd, and Richerson 1995). Ethnographic reports of Mae Enga intergroup conflict suggest that social extinctions did occur and defeated clans were assimilated into the victorious clans. Moreover, these reports provide no indication that individuals from defeated groups had any close kinship or friendship ties to the victorious groups in which they settled. The Mae Enga would thus seem to offer evidence that group selection via social extinctions could plausibly have occurred without prior metaband formation and without preexisting cooperative intergroup ties.

A closer look at anthropologist Meggitt's (1977) account of social extinctions, however, shows that Mae Enga foraging clans exhibited reasonably

complex social and political institutions and conventions that would require preexisting cooperation. For instance, he argues that militarily successful Mae Enga clans were able to rapidly assimilate defeated clans (typically within a generation) because they had political and social conventions that rewarded assimilation, allowing individuals from defeated clans to achieve true clan member status. Once assimilated, these individuals would benefit from the land rights and economic and military aid granted to true clan members. Political and social conventions, such as land and resource sharing, impose individually costly yet group-beneficial behaviors on group members and require cooperative behaviors, such as punishment, to enforce them. They are therefore only likely to evolve in groups in which cooperative behaviors are already common.

From these considerations, we can conclude that group selection via social extinction is unlikely to have been an important driving force in the evolutionary origins of cooperation in the hominin lineage, since it is unlikely that noncooperative Pleistocene forager bands would have friends or family in neighboring groups.

3.2. Selective Migration Cannot Account for the Evolutionary Origins of Cooperation.   The selective migration of individuals from less successful to more successful groups is a similar mechanism of group selection, but it does not require that groups become socially extinct. Cooperative behavioral variants can spread within a population without any intergroup conflict or group extinctions, if individuals "vote with their feet" and differentially migrate from certain groups to others (Boyd and Richerson 2009b). On this view, individuals will preferentially migrate from groups with lower average fitness to groups with higher fitness. If cooperation increases overall group profits and these profits are shared among all members, then individuals in less cooperative groups will have an incentive to migrate into more cooperative groups where individual payoffs are likely to be higher. According to the formal model presented in Boyd and Richerson (2009b), this net migration into cooperative groups will result in an increase in the frequency of cooperative behavioral variants within the total population. This occurs because more cooperative groups will tend to stabilize at a larger size than less cooperative groups.

Although this model captures features of modern migration, it is implausible as an account of the behavior of our Pleistocene ancestors. The mechanism implicitly requires certain population structures and informational channels that would likely only obtain after cooperative behaviors had evolved in the hominin lineage. Consider the informational requirements that must be met for this process to occur. First, migrants must know the average individual payoff both in their group and in a neighboring group in order to decide whether migration is in their best interest. In addition, they must be able to

estimate the discounted payoffs that they are likely to receive as new immigrants to the group. (Joining even a much more successful group as a slave, for instance, is highly unlikely to improve one's welfare.) Although these informational requirements are likely to be met in modern and even some ancient societies, I suspect that the informational environment of Pleistocene foragers was not nearly so transparent.[2]

For the mechanism of selective migration to drive the evolution of cooperative behaviors, individuals from one group must possess information about the welfare of members in another group. Learning about the average welfare of individuals in another group is relatively easy in modern societies. Free and transparent information flow connects many modern nations. In small-scale Pleistocene forager worlds, the only informational channels connecting neighboring bands likely relied on repeated, close intergroup contact. Our best evidence suggests that Pleistocene forager bands did have such intergroup contacts during seasonal metaband formation (Barnard 2011; Boehm 2012). Members from different bands would be able to assess the welfare of individuals from neighboring bands, for instance, when they settled together around a permanent water hole during the dry season. Although families likely had separate hearths, nothing would prevent others from observing things such as average family size or the patterns of consumption, which offer evidence of hunting and foraging success. This knowledge by itself, however, is not sufficient to drive selective migration. In addition, individuals must know the way a group treats new migrants, since they are unlikely to achieve the average individual payoff of the new group until they are fully assimilated. Knowledge of this sort also likely requires repeated, close interaction between groups. Recent forager ethnographies suggest that metaband formation provides individuals extensive knowledge of the practices of members of neighboring groups (Hill et al. 2014). This evidence suggests that even small-scale forager societies could form sufficiently transparent between-group informational channels to obtain knowledge of the average individual payoffs of members in neighboring groups. Even so, selective migration cannot explain the evolutionary origins of cooperation because metaband formation itself relies on preexisting cooperation, as I have argued previously. Thus, in order to establish the transparent between-group informational channels necessary for group selection via selective migration to be a driving force in the evolution of cooperation, individuals must have already engaged in cooperative behaviors.

3.3. Between-Group Transmission Cannot Explain the Evolutionary Origins of Cooperation.   The third group selection mechanism Boyd and Richerson

2. Sterelny (2003) discusses informational transparency in an evolutionary context. An environment is informationally transparent if it allows agents to respond adaptively to specific, reliable cues and honest signals.

(2002) develop is strikingly different from the others. The mechanism of between-group transmission of cooperative behavioral variants aims to show how cooperative behaviors and the norms that underwrite them can spread between groups. Unlike the other mechanisms, this one does not posit intergroup competition and selection favoring more cooperative groups. Instead, cooperative behavioral variants spread in a population through biased social learning. Specifically, the prestige bias leads individuals in one group to imitate the successful cooperative behaviors of members of another group. Since it can account for rapid evolutionary change without group extinctions, this mechanism plays a central role in Boyd and Richerson's pluralistic account of the evolution of human cooperation.

For cooperative behaviors to spread via this mechanism, certain conditions must be met. As with the other cultural group selection accounts, different behaviors and norms must become common and persist in different groups, and these group-level differences must yield different average individual payoffs. However, for group selection to occur via between-group transmission of cooperative variants, two additional conditions must be satisfied. First, individuals must exhibit a prestige bias that leads them to discriminate between two behaviors in favor of the one that yields the higher individual payoff. Second, individuals in one group must have knowledge of the norms and common behaviors of individuals in a neighboring group and must consider cultural models from both groups when determining which behavioral variants to adopt.

This biased transmission mechanism, I argue, is unlikely to explain the evolutionary origins of cooperation. Although Boyd and Richerson (2002) argue that different groups often have knowledge of the behaviors and norms of nearby groups, I doubt sufficient cultural contact would exist between Pleistocene forager bands unless the two bands had already developed cooperative ties, likely founded on kinship. In the previous section, I argued that until the practice of metaband formation is well established within the hominin lineage, it is unlikely that sufficiently transparent informational channels would connect groups to enable selective migration. The informational requirements for the biased transmission mechanism are even more stringent. For selective migration, an individual only needs to know that members of the neighboring group are better off—that they receive higher average payoffs over there than we do over here. For the biased transmission mechanism, just knowing that members of another group have higher average payoffs is insufficient; in addition, an individual needs to know why members in the other group tend to be more successful. This additional informational requirement makes this mechanism even less likely to have been an important evolutionary force early in the hominin lineage.

To imitate successful behaviors, an individual needs to know which of the many behaviors of the observed cultural model are responsible for that model's success. Sometimes the likely cause of success will be reasonably

transparent. For instance, if I observe the males in a hunting party camouflaging themselves with ochre before a hunt and then see them return with a successful kill, I might reasonably infer that using ochre was partially responsible for their success. Likewise, if I observe the use of a particular tool to butcher an animal or witness an innovative food preparation technique, I might reasonably infer that the tool use or the cooking technique was responsible for the increased food yield. Other times, however, identifying the behaviors responsible for a member's higher payoff might be opaque. Consider reproductive cooperation in the form of alloparenting (Hrdy 2009). This practice involves older women, such as older sisters or grandmothers, assisting a mother in provisioning and caring for her offspring after they have been weaned. Reproductive cooperation of this sort is a group-beneficial behavior: it increases average payoffs for all individuals in the group, since it allows for an increase in average family size. Because postmenopausal women attend to older children, women of childbearing age can reduce their interbirth intervals (Hawkes et al. 1998). To the casual observer, this relatively complex causal story is unlikely to be clear. An individual might recognize that the observed group was more successful but might not be able to identify the specific cooperative behaviors that cause this success.

This informational problem can be overcome if an observer can mimic all the behaviors of members of the successful group. In this case, the observer need not distinguish the actual cause of success from other behaviors. For example, the application of ochre before hunting might be part of a ritual to animal spirits, but the observer need not distinguish this causally inert ritual from the causally relevant ochre use if he mimics both behaviors before hunting.[3] However, copying all the behaviors of a cultural model might be challenging for cooperative behaviors, such as alloparenting. Cooperative behaviors typically have frequency-dependent fitness values and are only advantageous in groups where they are common. Thus, even if an observer can identify or merely mimic the successful behaviors of a cultural model from a more cooperative group, those same behaviors would likely be disadvantageous in a group where they are uncommon. Consider the case of food sharing. If I observe that members in another group are more successful and also see that they share food after hunting or foraging, I may correctly infer that food sharing is partially responsible for their higher individual payoffs, or I may simply choose to mimic all the behaviors of these successful cultural models. Either way, if I then copy this behavior and begin sharing food with members of my own group, they would likely take me for a sucker, gladly accepting my offerings of food but not sharing theirs in return. Since the cooperative behavior

3. I thank Colin Allen for this example and helpful discussion about my reply to this objection.

leads to a decrease in individual fitness in my group, it is unlikely to be copied and spread within the group.

I suspect that most cooperative behaviors that are group beneficial yet individually costly (i.e., precisely the behaviors whose evolution Boyd and Richerson aim to explain) are likely to have relatively opaque causal structures as well as frequency-dependent fitness values. Identifying the right behavior to imitate from the myriad of behaviors—some of which might be maladaptive—most likely requires close, repeated interactions, which in turn requires preexisting cooperation. Moreover, mimicking the successful cooperative behaviors from one group in another uncooperative group are unlikely to be similarly successful when transplanted into the new group. For these reasons, it is unlikely that the mechanism of biased transmission of behavioral variants can explain the evolutionary origins of cooperation.

4. Conclusion. In this article, I have completed the critique of group selection accounts of the evolution of cooperation begun by Sterelny (2016). While he successfully argued against the Bowles-Gintis account of intergroup warfare and extinction, I have shown the implausibility of Boyd and Richerson's three alternative mechanisms. Although these group selection mechanisms may offer plausible explanations for the expansion of cooperative behaviors and institutions in the Holocene, none of them can explain the evolutionary origins of cooperation in the Pleistocene. Instead, I have shown that each mechanism depends on social practices, structural features of the population, or informational channels that are highly unlikely to obtain unless certain cooperative behaviors are already common within the population. This failure of the best group selection accounts to explain the origin of cooperation among our Pleistocene ancestors suggests that the first cooperative behaviors in the hominin lineage likely evolved via individual selection for cooperative behaviors that were beneficial to both the individual and the group.

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