

# Cooperation, Culture, and Conflict

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## ABSTRACT

In this article I develop a big picture of the evolution of human cooperation, and contrast it to an alternative based on group selection. The crucial claim is that hominin history has seen two major transitions in cooperation, and hence poses two deep puzzles about the origins and stability of cooperation. The first is the transition from great ape social lives to the lives of Pleistocene cooperative foragers; the second is the stability of the social contract through the early Holocene transition to complex hierarchical societies. The first of these transitions is driven, at least initially, by individual advantage: cooperation paid off for individual foragers, initially through mutualist interaction, then through reciprocation. This argument leads to a reanalysis of the role of violence and the nature of the freeriding threat to cooperation. But the conditions that select for cooperative individuals in the Pleistocene were eroded in the Pleistocene–Holocene transition. So we need an alternative account of the survival, and indeed the expansion, of cooperation in the Holocene. Group selection driven by intercommunal conflict really may well be central to this second transition.

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## 1 Introduction

Cooperation often delivers impressive profits to cooperative agents through collective action, teamwork, and the division of labour. When agents have identical (or largely overlapping) fitness interests, these potential profits are often realized. But often the profits of cooperation do not depend on every agent fully contributing towards its costs, and in many cases there is no mechanism that automatically shares out profits in proportion to investment. This fact creates the famous free-rider problem, and the notorious challenge cooperation poses to evolutionary biology. Unless that problem

can be solved—unless freeriding is impossible, or excluded, or minimized—freeriding destabilizes cooperation. Thus when we find cooperation in nature, especially between agents who are not closely related, we need to ask whether this form of cooperation generates a free-rider problem, and if it does, we need to ask how the free-rider threat is contained. Those interested in human evolutionary history face these questions, for our lineage has long been remarkably cooperative, and not just within family groups (Kaplan *et al.* [2009]).

One possibility is that cooperative dispositions evolve through positive selection on groups, despite the fact that individual cooperators pay a net cost in mixed groups of cooperators and defectors. In general, evolutionary biologists have been cautious about invoking group selection, perhaps to an unreasonable degree.<sup>1</sup> However, even were a general scepticism about group selection models warranted (which I doubt), there are persuasive reasons for thinking that a new form of group selection is likely to have been important in human evolution. For our social life and individual cognitive character are shaped by cultural learning, and that is true not just of contemporary humans but of ancient ones too.<sup>2</sup> Cultural learning is important to debates about the role of group selection in hominin evolution because it has the potential to make group selection more powerful. Cultural learning can increase the variation between groups, and reduce the cost to cooperators within groups. In particular, if children learn from their parental generation, and not just from their parents in that generation, then cultural learning damps down differences within the group. That is true of technical skill, for example, how to carve a fish hook. But it will also be true of customs of interpersonal behaviour too: greetings and other social rituals; conventions of dress and of social interaction; food preferences; organization of household work and childcare.

If patterns of interaction within a group are typically cooperative—if meat, for example, is typically shared—and if agents tend to acquire the social habits to which they are exposed, cooperative behaviour will be more common, and uncooperative behaviour will tend to be less extreme. This reduces the cost of maintaining cooperation by punishing free riders, both because there are more to punish (more sharing the costs), and fewer targets. Further, to the extent that children learn from the preceding generation, not just their parents,

<sup>1</sup> This caution had its origins in G. C. William's ([1966]) famous critique. That critique was clearly overdrawn, and a second generation of group selection models were developed, initially by D. S. Wilson ([1980]). But reasonable or not, controversy has continued about both the interpretation and applicability of the models. See for example (Okasha [2006]; West *et al.* [2007], [2011]; Godfrey-Smith [2009]).

<sup>2</sup> It is unlikely (though perhaps possible) that the skills required to make good quality Acheulian handaxes (a skill hominins have had for about 1.6 million years) could be learned individually, by trial and error. It is even less likely that the succeeding Middle Stone Age Levallois technology (perhaps 300,000 years old) could be mastered without massive social input, and specific cognitive adaptations for learning and teaching.

the children of selfish free riders are less apt to be themselves free riders too. Oblique transmission can partially mask the greater local success of free riders. At the same time, the intergenerational transmission of information, customs, and values makes the profile of a group sensitive to its generational history, and so differences between groups accumulate (Tomasello [1999]). Oblique and diffuse cultural learning, then, decreases phenotypic variation within groups and increases it between groups. To the extent that it limits migration between groups, it also tends to increase intergroup genetic variation.

Cultural learning creates the conditions under which a new form of group selection could build cooperative traits. This idea has been under development for some time (Boyd and Richerson [1990], [1992]; Sober and Wilson [1998]; Henrich [2004]; Bowles and Gintis [2006], [2011]; Bowles 2008; Chudek *et al.* 2013). However, in the analysis that follows, I shall primarily use the Bowles–Gintis version as my stalking horse. They combine their systematic modelling programme with a clear and explicit hypothesis about the nature of intergroup competition, a hypothesis that they take to have independent support from the archaeological record. Other theorists have developed models of cooperation, but without similarly explicit grounding these models in the material history of hominin evolution (Martin Nowak [2006], for example). Even Robert Boyd and Peter Richerson, who have framed their modelling work in a richly empirical view of human social evolution, are less explicit about the nature of intergroup competition. I return to their views at the end of Section 3, where I will also briefly discuss the idea that group selection plays a critical role in ‘equilibrium selection’, explaining why we often find socially efficient sets of norms and customs, even though many collectively maladaptive sets are stable once they are established. For now, though, my focus is the powerful and sustained formulation of Sam Bowles and Herb Gintis, culminating in their ([2011]).<sup>3</sup> Their picture of cooperation is built on three supports: the experimental literature of behavioural economics; the ethnography and the archaeology of the late Pleistocene and early Holocene; and a set of models.

**Behavioural economics:** In behavioural economics, there is a rich experimental tradition of games of cooperation and defection, often involving experiments with enough real money riding on the outcome to focus an experimental subject’s mind. In these games of cooperation and defection, one typically finds that many agents begin with some tendency to cooperate. If the games involve continued interaction with the same group of players, and if they include the option of punishing freeriding, cooperation is often stabilized

<sup>3</sup> They also differ from some other approaches in developing combined cultural and genetic models, models in which genetic differences between groups play an important role.

at high levels. In those games in which punishment is not possible, it tends to decay. These results are often taken to show that most humans are ‘strong reciprocators’ with a non-instrumental interest in the welfare of others. Often, that interest is benevolent. Strong reciprocators enter interactions willing to cooperate if they expect others to cooperate, even if they would be modestly better off freeriding. But strong reciprocators are also vengeful: they respond to freeriding with punishment, even at some cost and (sometimes) even when they will not interact again with the target of the punishment, so that punishment serves no instrumental purpose (Boyd *et al.* [2005]; Henrich *et al.* [2005]; Bowles and Gintis [2011]).

In these experimental games, agents typically interact anonymously, simultaneously, and without communication. Such interaction is not typical of human social experience (especially pre-modern human experience). An obvious possibility is that in these unnatural contexts, agents are falling back on default behaviours that are tuned to ongoing interaction amongst mutually known and communicating agents (Binmore [2006], [2010]; Guala [2012]). Bowles and Gintis resist this suggestion, arguing that in experimental games, agents respond to changes in the incentive structure in rational ways. If (for example) punishment costs more, or is less effective, rates of punishment decline. The strong reciprocator profile is by no means universal, and the imprint of local culture on agent dispositions is very considerable (Henrich *et al.* [2004]; Herrmann *et al.* [2008]; Gächter and Herrmann [2009]). But Bowles and Gintis argue that it is widespread.

The presence of prosocial motivation shows the impact on human psychology of life in a cooperative world. Joan Silk, Felix Warneken, and others have shown important differences between human and great ape prosocial psychology (Silk *et al.* [2005]; Warneken and Tomasello [2009]). But the presence of prosocial emotion does not by itself show the impact of group selection. If there is a reliable link between others’ welfare and your own fitness, individual-level selection can build prosocial motivation into us. There is a rich tradition arguing that in human social environments a good reputation is an asset of enormous value, and that the most reliable way of seeming to be a good social partner is to be a good social partner (Alexander [1987]; Frank [1988]; Boehm [2012]; Baumard *et al.* [2013]). Perhaps strong reciprocity is indeed a widespread psychological profile, and one on which the cooperative practices of human social worlds depend. But it evolved because it paid individuals to be good cooperators. As always, these are average rather than invariable outcomes. The disposition to invest in reputation by actually committing to prosocial norms can be an individual adaptation, even if it occasionally propels an unlucky individual, over-investing fatally, to martyrdom. Bowles and Gintis resist this reciprocity-and-reputation-based account of the selective benefit of cooperation, arguing that in the typical

environments of human prehistory, agents with social preferences were not just psychologically altruistic; their prosocial dispositions imposed a fitness cost on them compared to the less prosocial members of their group. This psychological profile is common in the population only because groups rich in prosocial agents tend to eliminate groups poor in them.

**Archaeology and ethnography:** In developing the view that human cooperation evolved through group selection, Bowles and Gintis rely heavily on ethnology and (especially) archaeology. In their view, there is compelling evidence of intense intergroup conflict in the late Pleistocene and early Holocene, resulting in rates of violent death much higher than war-torn twentieth-century Europe. As they see it, this signature of conflict is no accident: the Pleistocene record reveals rapid, high-amplitude climatic change, so that human groups would have frequently been faced with crises threatening their very survival. Many did not survive. Given the intrinsic forager capacity for population growth, most of the middle and late Pleistocene shows remarkably little sign of an expanding population. So the second leg of their tripod is the archaeology of human violence, a physical record of serious, literal struggle for existence amongst human groups.

**Models:** Bowles and Gintis ([2011]) present a set of interrelated models aimed at showing that their historical hypothesis is credible. The psychology of strong reciprocation can spread through group selection, if we model the interactions within and between groups making plausible assumptions about the size of bands, the costs and benefits of conflict to groups and individuals, and the interactions of cultural learning with conflict. The evolution of human cooperation is complex and multifaceted, and so it is represented by a set of models. This complexity is not noise; these interactions matter. As Bowles and Gintis see it, the origins and stability of human cooperation depend on the simultaneous (and coevolving) construction of individual and social traits. For example, punishment is effective in inducing cooperation only because socially transmitted fitness-levelling practices within groups (food sharing, monogamy) reduce the local cost of altruistic punishment of free riders, and because agents' psychology enables them to recognize, internalize, and respond to norms (otherwise punishment is seen as mere aggression and is met with aggression).

To summarize: This view of human cooperation rests on the idea that we have strong, cross-cultural evidence that humans are typically psychologically altruistic, but are also given to vengeful moralizing. This psychology sustains cooperation both directly, by prompting helpful action, and indirectly, by prompting sanctions on those that try to exploit helpfulness. This profile is not just psychologically altruistic; in a wide range of environments relevant to its evolution and stability, it was evolutionarily altruistic too. Strong reciprocators paid a fitness tax, but the trait evolved anyway because groups

with high proportions of strong reciprocators flourished at the expense of other groups. Archaeology and ethnography tell us that hominin life evolved in an environment of intense intergroup competition, and modelling tells us that norm-sensitive, parochial altruism can evolve by culturally mediated group selection in such environments.

In this article, I shall argue that there is something importantly right about this view of human cooperation, but there is something important missing from it, too. Most crucially, I argue that hominin history experienced two major transitions in cooperation, and hence poses two deep puzzles about the stability of cooperation. The first is the transition from great ape social lives to the lives of mid- to late-Pleistocene cooperative foraging; the second is the stability and expansion of the social contract through the early Holocene transition to complex hierarchical societies. In the first of these transitions, cooperation pays off for individuals. Intergroup conflict plays an important role only in the second of these transitions. One message, then, is that no single species of models cleanly captures the expansion of hominin cooperation; the ecological and social bases of its costs and benefits changed through the course of the evolution of our lineage.

## **2 Two Social Revolutions**

There have been two revolutions in human social life, not one. The first is the transition from great ape social lives to those of the egalitarian foraging bands of the mid- to late-Pleistocene. Hominins probably evolved from ancestors who lived in social worlds somewhat similar to those of living chimps: they lived in intimate, but multi-family, groups; these groups had a quite marked social hierarchy; they were probably territorial; there were limited forms of cooperation; there was social learning and communication, but no active teaching; and their foraging was probably assisted with some rudimentary technology. By 75 kya, their descendants—our species—still lived by foraging and in intimate social worlds. But much else had changed. In particular, hominins had become obligate cooperators. As a core part of their subsistence strategy, humans hunted large game (a strategy dating back at least 400 kya—to 1.7 mya, if recent reports are correct (Bunn [2007]; Bunn and Pickering [2010])). Until perhaps 75 kya, they did so with short-range weapons without single-shot lethality. Such hunting demanded cooperation (Stiner [2002]; Jones [2007]; Boehm [2012]).

Ecological cooperation was powered by socially transmitted craft and natural history skills. By the later Pleistocene, humans cooperatively extracted high-value resources with great efficiency. By this time, they were masters of a regionally varied and elaborate technology, which they used in combination with a detailed knowledge of their local environment

(Foley and Gamble [2009]). There are significant uncertainties about Pleistocene social life, but there is good reason to believe that local communities cooperated ecologically, reproductively and informationally; indeed, there is good reason to believe that these aspects of cooperation coevolved, in mutually supporting ways (Sterelny [2007], [2011]).

This view of Pleistocene foragers depends on both archaeological and ethnographic data. Simple foraging cultures known from the historical and ethnographic record are remarkably egalitarian, without institutions of political leadership, and without marked heritable differences in wealth (Boehm [1999]; Smith *et al.* [2010]; Flannery and Marcus [2012]). This pattern is robust: many forager societies from different environments and with different cultural origins are known from ethnography. Consider the contrast between the Australian deserts, Central American rainforests, and the arctic tundra. The most brutal environments were not exploited by Pleistocene foragers of 75 kya, but those foragers were subject to the extreme and often rapid climate oscillations of the Pleistocene. They too needed mobility, flexibility, and risk-reduction strategies (Shultziner *et al.* [2010]). We should be cautious, given the ecological differences between the Pleistocene and the late Holocene, and given that physical symbols of individual and group identity seem to have developed only in the last hundred thousand years (Henshilwood and d'Errico [2011b]). Even so, the reoccurring features of ethnographically-mapped foraging life probably fit Pleistocene foragers. If so, Pleistocene foraging groups were mobile, coping with variation in foraging success by sharing rather than storing food. That is true in part because much foraging was meat-focused, and animal protein typically is difficult to store and preserve. Their foraging successes depended on profound knowledge of their local environment, and on diverse and sophisticated technology. Foraging was a highly skilled activity, and so the foraging lifeway relied on rich, high fidelity, social learning and teaching. Foraging bands were small, perhaps typically groups of twenty to thirty. They were egalitarian: no adult had formal, mutually recognized authority over others, and differences in wealth were not marked. Bands were typically divided into families, but those families were not usually closely related, so bands were not usually just a single extended family. These bands did not exist in a social vacuum; they would often be linked to others through alliances, reciprocity, and kinship ties, thus forming a 'metaband' that would come together in favourable moments of seasonal plenty (Boehm [2012]).

The transition from great ape to forager social life took millions of years, and the reciprocity-based economies of later Pleistocene foragers probably evolved via mutualist foraging (Tomasello *et al.* [2012]; Sterelny [2014]). Around 10 kya, at the Pleistocene–Holocene transition, a second social revolution began, with the transition to farming and to a sedentary society,

perhaps initially mediated by increased use of storage and increased management of wild resources (Testart *et al.* [1982]). Human groups grew in size and in social complexity. They became markedly inequalitarian, with the emergence both of great differences in wealth and formal political power. They became much more anonymous and interactions with strangers became routine (Seabright [2010]; Flannery and Marcus [2012]; Sterelny [2013]). To explain the evolution and elaboration of human cooperation, then, we need to explain, first, the slow formation of cooperative foraging lifeways and, second, the elaboration of cooperation in the Holocene transition to complex societies—societies characterized by massive projects of collective action, and by routinely cooperative interactions with strangers. Group selection provides a partial explanation of cooperation in the Holocene world of hierarchy and anonymity, but it does not explain the cooperative framework of the first transition.

### 3 War and Peace in the Pleistocene

Foragers did not live in a utopian paradise. The lack of central authority imposes real costs as no one can safely prevent minor quarrels escalating into violent ones. Murder rates are high, perhaps very high (Seabright [2010]; Boehm [2012]).<sup>4</sup> Even so, foragers live in egalitarian, communitarian environments, safely relying on one another for support. Bowles and Gintis propose to explain the civic virtues of generosity, modesty, and mutual aid in an egalitarian society by appeal to selection for military virtues. It is true that human psychology is sensitive to the in-group/out-group distinction, and it may well be true that the mechanisms that make agents suspicious of outsiders also promote cooperation towards insiders (Haidt [2012]); we are primed to see the world in tribal terms (Richerson and Henrich [2012]). Even so, it is most unlikely that the psychological and behavioural profile that makes a forager a prosocial team player is the same as the profile delivering victory in violent conflict. For a raiding melee, one wants hyper-aggressive, violent risk takers. Before the development of professional military groups that deliver success through discipline, coordination, and the division of military labour, victory goes to the group with more berserker ragers (all else equal; see (Keegan [1988])).<sup>5</sup> But those most valuable in warrior encounters make

<sup>4</sup> Hill *et al.* ([2007]) estimated the Hiwi death rate from violence at an astounding 37% of all adult deaths, of which about half are within-group conflicts. The figures from African forager cultures suggest a rate almost two orders of magnitude lower. Hill and his colleagues suggest that the African figures are the result of effective colonial policing, and hence the Hiwi figures may be more relevant to Pleistocene social lives, but this is very controversial. Brian Fergusson suggests that the Hiwi figures are the results of colonial invasion of Hiwi lands (Ferguson [2013a]), and Hill and colleagues' own figures show the colonial impact to be severe. That said, they claim that on the Hiwi's own recollections, the pre-colonial world was even more violent.

<sup>5</sup> While Pleistocene animals were probably much more dangerous than contemporary ones given the effects of extinction and improved weapons, Hill *et al.* ([2007]) suggest that predation and



uncomfortable neighbours in more peaceful times, where their risk taking and ready use of violence is likely to find expression within the group.<sup>6</sup> Given the dangers such individuals pose, it is no surprise that forager groups see them as a threat rather than an asset. Forager societies sometimes deal lethally with such threats. Data on capital punishment in forager society is patchy at best, but Chris Boehm has attempted to collect what we have and present it systematically.<sup>7</sup> The best guess seems to be that those collectively killed in forager society are most often hyper-aggressive individuals. Often, they are repeat offenders, unable to control their impulses to violence; they would make good raiders but poor neighbours.

In sum, then, the genes that amplify tendencies for aggressive risk-taking in intergroup conflict, and the genes that amplify tendencies to empathize with one's associates and to enhance one's respect for local customs might both be altruistic. Such genes may make it more likely that agents will act in ways that accept personal fitness costs while enhancing the fitness of their associates. But they are most unlikely to be the same genes. I very much doubt that there are genes whose only effect is to up-regulate patriotic violence. Nothing we know about the emotions suggests the existence of mechanisms fine-tuned enough to up-regulate the propensity for psychotic rage against foreigners, while leaving the other hormonal knobs as they were. Thus Bowles and Gintis lump the civic and the military virtues.<sup>8</sup> All models must make simplifying assumptions, but this is a simplification too far, even if Bowles and Gintis are right about the importance of war. This I doubt, and to this I now turn.

The Bowles and Gintis view of the evolution of cooperation depends on the idea that the struggle for resources between groups has played a pervasive role in human evolution. In developing this idea, they depend heavily on the archaeology of the Pleistocene–Holocene transition. The archaeological evidence they cite does indeed show that this was a period of serious inter-communal violence, though even here there is some suspicion that intergroup violence in the early Holocene was patchy and occasional rather than endemic (Bar-Yosef [2010]; Ferguson [2013a], [2013b]). But this was not the high noon of Pleistocene forager life; rather, it coincides with the origin of farming, and farming changes the costs and benefits of conflict. As farmers clear and

other encounters with animals cause far fewer deaths than encounters with humans and, for this reason if for no other, the stresses and dangers of hunting are not equivalent to those of human to human violence.

<sup>6</sup> The Norse sagas express this tension particularly vividly. The Norse were small-scale farming cultures so military virtue was prized. But those who had it in spades were difficult and dangerous allies, almost as dangerous to their allies as their enemies.

<sup>7</sup> See especially (Boehm [2012], pp. 83–5), and his commentary on (Guala [2012]).

<sup>8</sup> They treat tolerance and patriotism separately. As they analyse it, tolerance is self-regarding conflict avoidance; it is not an altruistic form of civic virtue.

improve land, and as they store crops, they create a valuable target. The more farmers add value to their land, the more their land and its products are worth seizing. Crops need to be tended and guarded against theft, and hence farmers are immobile and often isolated, with each family tending their own land. Their location in space and time can be predicted, and this makes them vulnerable to raids. These facts are common knowledge, giving even the peaceably inclined a temptation to strike first.

The peak of forager egalitarianism was certainly much earlier than the Pleistocene–Holocene transition. Current opinion is coalescing around the idea that Pleistocene foragers began to fall within the range of variation known from the ethnographic record to be between about 120 kya and 75 kya, though Richard Klein continues to favour a later and more abrupt change around 50 kya (see, for example, (Henshilwood and d’Errico [2011a], [2011b]; Henshilwood and Dubreuil [2011]; Lombard and Haidle [2012]; Klein [2013]; Klein and Steele [2013])). There is no direct archaeological evidence of epidemic intergroup conflict in this period. Such evidence might well not survive, even if the late-middle Pleistocene were a theatre of raiding and strife. But there is no compelling theoretical reason to think that the record is misleading, and that forager egalitarianism was formed in the crucible of intergroup violence. To the contrary: I think there are persuasive reasons for thinking that conflict between forager bands would impose higher risks and fewer benefits than conflict between farming groups.

First, foragers are more difficult targets. In contrast to farmers fixed to their fields, the precise location of forager camps will often not be known to neighbouring groups, especially those with whom relations are strained. Moreover, while farmers often work alone on family plots, hunters often travel together, so they are in a position to offer one another mutual support, and their fieldcraft and access to weapons makes them dangerous targets (Kelly [2005]). In sum, foragers are more difficult and dangerous as targets. Second, they are less tempting. They have little wealth in material form and have few goods worth seizing. Unless an annihilating raid is an option, taking either sex as slaves (or sexual resources) would be a very risky business. Intensive (hence expensive) supervision would be necessary to prevent captives absconding back to their own territories (having slit a few convenient throats on departure).<sup>9</sup> Finally, mutual hostility would impose a heavy tax on foraging efficiency. Foraging even as a group in border areas would be risky, lone women foragers (the menopausal grandmother with her digging stick) would be especially vulnerable to ambush.

<sup>9</sup> It is no accident that industrial slaving in Africa involved driving captives long distances from their original homes. Unless they escaped immediately, they had very little prospect of finding their way home.

In short, war between foragers does not look like a paying proposition. Of course, wars might still have been quite common. Despite having many costs and few benefits, no doubt from time to time foragers sank into mutually hostile relations. Intergroup conflict is, and surely was, part of the foraging spectrum (Otterbein [1997]). But the group selection model goes beyond the claim that tension and violence was endemic; it claims that the road to forager success in the Pleistocene was through the successful prosecution of violence. It claims we are the descendants of those that fought and won, rather than being the descendants of those that avoided fighting. But it is one thing to show that forager inter-communal violence was quite common, another to show that engaging in violence was a successful strategy.

Bowles and Gintis disagree. They suggest that that the unstable Pleistocene climate, with its sharp and rapid fluctuations, would have imposed frequent crises, threatening groups with extinction, intensifying the struggle for shrinking resources, and forcing groups into conflict. Life was too tough for peace. Those fluctuations, they suggest, explain the very modest growth in overall population over the middle to late Pleistocene (see also Richerson and Boyd [2013]). I remain sceptical. The very instability of the Pleistocene makes it likely that mortality was disturbance-dominated rather than the result of accumulating resource stresses.<sup>10</sup> Pleistocene population expansion may have been limited by brutal blizzards, terrible floods, and wildfires sweeping through landscapes: events that do not make murdering the neighbours especially tempting. Moreover, to the extent that we have an ethnography of famine (see Boehm [2012], pp. 274–8), it suggests that foragers respond to famine with social atomization. Bands split into family units as the population spreads itself more thinly over landscapes in response to its lowered carrying capacity. Fission–fusion becomes fission–more–fusion. That response was probably particularly adaptive in the Pleistocene, with its lower population densities. But if the initial response to famine is to disaggregate, to fragment into even smaller daily units of association, the option of attempting to expropriate the neighbour's territory is taken off the table.<sup>11</sup> Organized inter-communal violence depends on agreement and coordination; and coordination in turn relies on aggregation, on the fusion cycle of fission-fusion living. No doubt when splinters of one metaband met splinters from another, in periods of famine and atomization, there were often tensions, and these sometimes erupted into violence. But the cost of violence was probably high: to the direct risks of combat we need to add the indirect risks of fracturing friendly and cooperative relations with one's own allies, by dragging them into

<sup>10</sup> Pleistocene forager skeletons show no evidence of such resource stress; they look to be much healthier than early farmers (Cohen [2009]).

<sup>11</sup> That is especially true if, as Boehm suggests, famine imposes serious stresses on within group norms of cooperation (see Boehm [2012], pp. 274–8).

conflicts and feuds not of their own making and without their consent, as news of violence slowly leaks back to the kin and to the allies of the opposing splinter.

So while inter-communal violence was undoubtedly part of the human evolutionary experience, ethnography does not suggest that inter-communal tension poised on the edge of violence was the default state of forager life. Some foragers do live in a state of permanent tension with their neighbours, but many do not. It is striking that while Pleistocene cave art reflects the importance of hunting and sex, there is very little sign of preoccupation with inter-human violence (Guthrie [2005]). Furthermore, Boehm's ethnography of collective punishment tells against the idea that forager values are organized around the importance of war. His analysis suggests that the disruptive threat posed by alpha warriors within the group was more important than their military value in conflicts between groups. If that is right, these values should be reflected elsewhere, in the mythological and narrative life of the group. Cultures of honour built around ownership of herds (and other easily stolen resources) valorize the warrior, as did the early farming proto-states of the Homeric Greek world. Are warriors the heroes of forager moral tales? Boehm's analysis suggests that many forager cultures would have regarded Achilles as an egotistical thug and a threat to public safety rather than a hero. I predict that ethnography will reveal a systematic difference between foragers on the one hand, and herding and early farming cultures on the other: groups with stored and heritable wealth will celebrate military heroes, mobile forager bands will not.

To summarize the argument so far: The evolution and stabilization of cooperation involved a double pulse, with a slow establishment of social foraging in small egalitarian bands in the early to mid Pleistocene, followed much later by the elaboration of the social contract in the more complex and less equal societies of the Holocene. The direct archaeological evidence of inter-communal competition is relevant only to the second pulse. Likewise, cost-benefit considerations do not suggest an epidemic of inter-communal violence in the middle Pleistocene.

It is, of course, possible to defend cultural group selection models of the evolution of cooperation that do not depend on literal conflict between groups. As Richerson and Boyd have pointed out, the climatic fluctuations of the Pleistocene often imposed difficult and challenging conditions on early humans, and all else being equal, cooperative groups would obviously respond to such challenges more effectively than less cooperative groups (Richerson and Boyd [2013]). It is indeed possible that harsh and unpredictable conditions imposed selection for cooperation on groups; but, if so, group-level selection for cooperation merely supplemented selection on individuals for the capacity to form and sustain cooperative relations with others, or so I shall argue in the

next section. But before I turn to mutualism and reciprocity in the Pleistocene, there is a final version of cultural group selection to consider. Game-theoretic analyses of social environments often show that there is no single equilibrium strategy or set of strategies. Punishment in particular can stabilize prosocial norms, but it can also stabilize maladaptive norms too (Boyd and Richerson [1992]). Likewise, less cooperative equilibria are often as stable as more cooperative ones. Often, more cooperative strategies do poorly in uncooperative environments. Cultural learning magnifies the apparent problem of multiple equilibria. For in social, interactive environments, it often pays to conform to others' expectations, even when the local customs are collectively inefficient.<sup>12</sup>

It has been suggested that group selection (partially) solves the 'equilibrium selection problem': those groups with more efficient norms displace those with less efficient ones (Boyd and Richerson [1990], [1992]; Bergstrom [2002]; Henrich [2006]; Chudek *et al.* 2013). I am sceptical. First, while it is true that human social worlds are remarkably cooperative, it would be a mistake to overstate the extent to which human social systems find their way to efficient solutions to the various cooperation and coordination problems they face; ethnography reveals many strikingly maladaptive packages of customs (Edgerton [1992]; Diamond [2005]). More importantly, game-theoretical models of actual populations are massively idealized and, in this context, this idealization matters. For example, while food sharing in forager societies is organized around risk reduction and reciprocity, individual sharing decisions are influenced by many factors, and these will vary from case to case and individual to individual. Individual temperament, social signalling, family politics, and influences of the local social network all weigh variably on individual decisions. Foragers are contingent cooperators, but no specific game-theoretic version of contingent cooperation will precisely capture the food-sharing customs of even small groups. Human populations have significant standing variation in their behavioural phenotypes; they are not homogenized at a local optimum by stabilizing selection, and hence not trapped at such equilibria. The 'equilibrium selection problem' is overstated.

I turn now to the idea that Pleistocene forager cooperation paid off for individuals.

#### 4 Foraging, Mutualism, and the Folk Theorem

There is a long tradition of evolutionary thought suggesting that harsh conditions select for cooperation (Kropotkin [1902]). Thus, for example,

<sup>12</sup> For example, in markets with no fixed prices, every agent has an incentive to bargain and haggle, even though the system as a whole imposes heavy transaction costs on the whole market.

cooperative breeding is much more common amongst Australian birds (facing an environment both fluctuating and arid) than it is in the world as a whole (Cockburn [2013]). This general picture of cooperation as a response to environmental stress might well fit Pleistocene hominins. They lived in tough times. More importantly, given the limits of their technology large carcasses—a large resource—could be secured only through collective action. In important cases, the benefits of cooperation were delivered immediately, and to all, for example, when the size and cohesion of a group enabled it to detect, avoid, or repel a serious predator. The same was true when the group as a whole hunted collectively or collectively drove another predator from its kill. In these cases, collective action was a mutualism generating a profit shared on the spot, rather than depending on reciprocity (in Trivers' sense). Immediate-return mutualism is not completely free of free-rider problems, as in any risky or stressful activity agents can be tempted to hold back. But this form of cooperation does not pose problems about discount rates, the certainly of future interaction, or tracking individuals and their generosity over time. In my view then, cooperation began amongst Pleistocene foragers in forms that did not depend on reciprocity, and hence on mechanisms for tracking and policing (see also Tomasello *et al.* [2012]).

However, reciprocity eventually became important.<sup>13</sup> With the invention of high-velocity projectile technology, and with the shift to smaller game in the 'broad-spectrum revolution' (Stiner [2001])—probably triggered by declining numbers in the favoured large game species—hunting parties became smaller, and a foraging division of labour probably began to emerge. Once it did, the breadth of resources—large game, small game, birds, fish, and a great variety of plant food—rewarded specialization and a division of labour (Stiner [2001], [2002]). These resources are concentrated in different places and they are best harvested with specialized equipment. Often, efficient foraging depended on specialized expertise too. Plant-based resources are very important to most foraging peoples and, as a consequence, many of them have developed extraordinarily rich and sophisticated ethnobotanies (Berlin [1992]). But these were late changes: specialized toolkits and projectile weapons appear perhaps 75 kya. The shift to smaller game depended on local conditions, but probably began about 30 kya (Stiner [2001]). So forager economies based on reciprocity, rather than on immediate-return mutualism, may be relatively recent, established only in the last 100k years or so. Reciprocity also makes illness and injury survivable. This is especially important for a mobile biped.

<sup>13</sup> Human life history changed at the same time that ecological and informational cooperation expanded, and these life history changes—the increased expense of children through their size, their long immaturity, their metabolic demands, and the physiological stress of childbirth—selected for reproductive cooperation, though this is more kin-based than other forms of recent human cooperation (O'Connell *et al.* [1999]; Hawkes [2003]; Hrdy [2009]).

A four-legged carnivore that injures a leg can still be quite mobile; not so a hominin. A life of foraging, and especially a life of hunting large game in close confrontation, imposes serious and repeated risks of injury; Neanderthal skeletons often show signs of trauma (Klein [2009]). Simple nursing and support makes these survivable. Without them, a broken arm or leg would probably be fatal.

So at some stage in the Pleistocene, there was a gradual shift from cooperation dependent on mutualism and immediate return to cooperation dependent on reciprocity. That form of cooperation faces more threatening free-rider problems, but it can still be stabilized by selection in favour of cooperative individuals. There are a cluster of game theory results collectively known as ‘the folk theorem’, which identify the environments that select for cooperation based on reciprocity (Binmore [1994]). Reciprocity-based cooperation evolves when there are profits to be had from cooperation and when the cooperating parties share in those profits. Cooperation is favoured if interactions are frequent; if the outcome of interactions are identified and remembered, so cheats are exposed; and if cheats are sanctioned or excluded at costs that are low compared to the profit of cooperation. Bowles and Gintis reject these folk theorem models of the stability of reciprocity-based cooperation, because the models assume that social worlds are transparent. But I think they were. Pleistocene humans foraged and lived together, with long and intimate histories of interaction. Families had individual hearths, but these were not physically screened off from prying eyes. It would not be difficult to track the general pattern of production and consumption of your neighbours. Recent work by Kim Hill reinforces this perspective. He reports that foragers have extensive and direct knowledge not just of those in their immediate band, but of those in their local cluster of groups (Hill [2012]).

The size of forager bands, and of local band clusters, is critical to this issue of transparency. The larger the group, the less likely it is that members have rich mutual knowledge. My argument supposes that the unit of daily association is in the region of 20 to 30, and that local clusters do not swamp individuals’ capacities to recognize one another. Robin Dunbar has suggested that we can remember and slot into a social map around 800 to 1000 individuals (Dunbar [2003]). There is very little direct evidence of total population size, and its division into groups, in the middle to later Pleistocene (that is, before about 100 kya). But these numbers are broadly consistent with ethnography and the historical record.<sup>14</sup> There is, for example, no sign of human groups exhausting their most favoured resources before about 100 kya.

<sup>14</sup> With exceptions: Pete Richerson has pointed out to me that some foragers associate regularly with strangers (Murphy and Murphy [1986]).

From that time, the resource base expands, but expansion does not become pervasive until the broad-spectrum revolution (Stiner [2001]), and that does not begin before the last 50 kya; later, in most places. Bowles and Gintis think Pleistocene social worlds were larger—and hence not sufficiently transparent—arguing, first, that genetic data indicate larger focal populations than my 20 to 30 guestimate and, second, that the average band size is not the crucial measure. Even if most bands were in the 20 to 30 range, it is quite possible that most agents lived in much larger units. These considerations are unpersuasive. Forager ethnography indicates that forager bands often have customs of fusing into metabands (around permanent water, if they are arid lands foragers; in seasonal or windfall booms, in other cases). These are often periods of mate formation (Barnard [2011]; Boehm [2012]). The genetic signal is a measure of the local mate market, not the unit of daily economic interaction. If anything, it speaks to the size of the metaband. Second, it is true that some so-called ‘complex forager societies’ support large local groups. But these are based on dense, predictable food resources and on storage. The salmon-fishing cultures of the Pacific North West are classic examples. There is no archaeological signal of complex forager cultures in the middle and later Pleistocene, and while that may change, it would be very surprising indeed to discover that the dominant demographic experience of such foragers was life in complex forager cultures. Little about Pleistocene demography is certain, but it is reasonably safe to assume that Pleistocene demography is compatible with the folk theorem.

In brief then: Foragers lived in such intimate social worlds that detecting freeriding was fairly simple. Of course, deterring freeriding was another matter. Nonetheless, the intimacy and long mutual history of forager communities would make it possible to coordinate joint action, and reputation in such communities is an important asset. Life prospects often depended on social capital: on an agent’s network of allies and friends (Smith [2010]). Thus the costs of deterrence would often have been worth paying, both to protect material and social resources, and as an investment in reputation. To this I now turn, showing how the capacities and incentives to control freeriding evolved.

## **5 Punishment, Shirkers, and Bullies**

It is common ground that unchecked freeriding destabilizes cooperation. As a consequence, the evolution of cooperation literature is preoccupied with freeriding; with identifying the costs of its control through punishment; and with explaining why these costs are sometimes paid. But freeriding comes in two forms: shirking and bullying. Shirkers accept others’ generosity but are not themselves sources of generosity: they are idle, not producing much



themselves, or they are stingy, unwilling to share their produce. Either way, shirkers do not pay for their fair share of social goods, and they obviously threaten the stability of forms of cooperation that depend on reciprocity. The evolution of cooperation literature tends to model freeriding as shirking (though not without exception; see Gavrillets [2012]). For example, in experimental games, free riders simply do not contribute to common pool resources, they make stingy proposals as first player in ultimatum games, and they do not punish unfair offers as spectators of ultimatum and dictator games. While these games capture shirking, they do not capture bullying, the aggressive use of power for egocentric ends and the second form of freeriding.

Bullying exploiters use their power to take what they want. Arguably, in explaining the origins of human cooperation, bullying poses the most critical free-rider problem. First, bullying is the initial problem: it was the primitive condition of hominin life. Great ape social life is typically bully-dominated, and as a consequence great apes live and act in an immediate-return economy. The transition to a delayed-return economy was a fundamental aspect of the transition from great ape to hominin social worlds. Late hominin social worlds rewarded investment and delayed consumption (Woodburn [1982]). This transition depended on bully control, but it did not depend on shirker control. For until alpha bullying was controlled, there was no incentive to invest in food processing or elaborate technology. There is no incentive to add value by cooking food in a safe central place or by developing forms of storage if food is liable to be taken by the stronger. Similarly, there is no incentive to invest time in making artefacts, if these too are likely to be seized.

Second, ethnography shows that the foragers themselves regard bullying as the most serious threat to their social lives. Bullies threaten the fabric of cooperation through violence and the threat of violence. If they succeed in establishing local dominance, they will of course take a disproportionate share of the band's resources (probably, especially, access to reproductive females). But even if they do not achieve local dominance, their behaviour and personality is a flashpoint of conflict, disrupting the local social network of coordinated action and mutual obligation; the local network that enables foragers to manage risk. As a consequence, bullies—would-be alphas—attract the most serious and hence most expensive punishment.

Third, bully control is more difficult than shirker control. Bullies are dangerous, so effective control is much riskier. Alphas and potential alphas pose a threat because of their combination of physical prowess and social support. They are typically large, dangerous males. They typically have the support of allies either through kin or through recruitment. They are dangerous, but often that makes their support worth having. Both factors ramp up the risks of confrontation. Despite the power of a well-bonded coalition, the risk costs

remain very serious.<sup>15</sup> Nonetheless, despite the risks, forager societies do keep the bullying problem under reasonable control. However, the coordinated, relatively safe assassination of a violent troublemaker depends on the full suit of modern behaviour: language, planning, explicit norms, kinship systems, and technology. In the forms we know from ethnography, then, bully control is dependent on sophisticated, late-evolved features of human social life. Yet at least the partial control of bullies must have evolved by the middle Stone Age: for central-place foraging and other forms of delayed-return behaviour date back at least to *erectus*, at about 1.7 mya. So we need to explain how anti-bully coalitions can form and exert pressure prior to the evolution of language, norms, explicit kinship systems, or stand-off technology.

Some of the cognitive tools needed were probably available at the great ape/hominin split. In the intimate world of proto-hominin society, alphas were both known and resented. Chimps sometimes mob alphas in moments of high arousal, as anger or frustration spreads through some contagion-like mechanism (de Waal [1982]). So the basic motivation for alpha control was probably primitively present. But the impact of mobbing on alphas is ephemeral, with extended control depending on more systematic and sustained pressure. The hard problem is to explain the emergence of the trust and coordination needed to stabilize a coalition so it sustains pressure.

I suggest that trust is secured by an interaction between the social emotions and a history of successful cooperative interactions in foraging and collective defence. The road to bully control begins with an initial expansion of ecological collaboration, perhaps first as collective defence against predators and then as power scavenging, driving predators from kills. Collective defence was probably first, both because changes in early human habit (from forest to open woodlands and grasslands) made them more vulnerable to predation, increasing the selective benefit of cooperation, and because collective defence does not pose a division of the profits problem. If defence is successful, everyone in the group automatically benefits.<sup>16</sup> But power scavenging—driving small to medium size predators (at first) from their kills as a mob armed with sticks and throwing stones—probably evolved early, too. Even in the face of an unequal

<sup>15</sup> For an example of collective punishment that resulted in death and injury in the enforcement of a coalition, see (Boehm [2012], pp. 261–2). Informational transparency—the intimacy of early band society—works both ways. In early hominin society, still with a power hierarchy, alphas probably identified potential foci of danger and resistance, and were likely to have threatened these individuals and their associates. Great apes do this; Frans de Waal's gripping descriptions of chimp politics show that alpha males have the social intelligence to recognize the threat posed by internal coalitions, and the vigilance and determination to disrupt those coalitions by punishment (de Waal [1982]).

<sup>16</sup> These are not quite stag hunts, in the sense modelled by Skyrms ([2003]), for one still might prefer others to bear more of the costs. Even so, the problems of monitoring and controlling defection are much eased.

distribution of the food at the kill site, all or most would benefit—just as groups of male chimps benefit from monkey hunts even though kills are not divided evenly. As collective activity expands (even though the profit at first is not divided equally), early hominins are evolving cognitive skills for coordination, partner choice, signalling, and investing in reputation. They also build affective bonds: successful action in concert (especially in situations of high arousal) builds friendship and trust. Agents with a history of successful collective action will bond. Those bonds can be very deep and powerful indeed if the collective action is both prolonged and stressful. This is very vividly expressed in soldiers' war memoirs (see, for example, Fraser [2001]).

On this view, the foundations of coalitional control of alphas were formed deep in hominin history. Hominins probably became markedly more cooperative than other great apes from about three million years or more ago, as they lived in seasonal, open environments, and used tools to shift their diet towards meat and other challenging but high-value foods (McPherron *et al.* [2010]). The physical, biological, and social environment of the late australopithecines and early habilines selected for increased capacities to cooperate. In the early stages of the transition to cooperation, adult bonds were probably made habitual through association, as adults began associating for instrumental reasons. Acting together, they were safer or more successful than when foraging alone. As climate changed and hominins found themselves in open woodland and grassland, it was safer to forage with one or two others, each eating what they found, but each contributing to vigilance. If specific associations become habitual, and these turn into a successful and persistent partnerships, each will begin to associate the others' presence and acting with the other with success and with reward. They learn to like being with one another because being with one another leads to good things. They learn to trust one another to be vigilant.

The ecological trigger that shifted early hominins towards cooperation remains a matter of conjecture. The crucial point is that early and simple forms of ecological cooperation built the cognitive and social preconditions for anti-dominance coalitions: tolerance, trust, and habitual patterns of association. Pleistocene cooperation—both the domestic policing of potential alphas and ecological cooperation in hunting and foraging parties—depended on trust, and trust is built through a history of successful interaction. These early enforcement coalitions would not have the coordination and communication skills needed to carry out the planned assassinations Boehm describes. But nor would their targets have contemporary skills of detection and evasion.

## 6 The Holocene: Farms, Wars, Priests, Chiefs

Pleistocene foragers cooperated because it was mutually beneficial. There were great advantages to cooperation, and in an intimate, simple, egalitarian, and

socially transparent world, most individuals had a fair share of those profits and a stake in enforcing cooperation on the recalcitrant. Once cooperation became an established feature of hominin life, cooperation based on individual benefit would indeed build the conditions that make cultural group selection effective. For as noted earlier, high-volume, high-fidelity social learning (itself a form of cooperation) tends to suppress phenotypic variation within groups and enhance phenotypic variation across groups. Given this, it would be surprising indeed if there was no group-level selection in favour of more cooperative groups. One reason for resisting cultural group selection models of the origins of cooperation is that they depend on social practices that are themselves special cases of cooperation (as Dubreuil [2012]) notes in his commentary on these ideas). So these models are more naturally seen as helping to explain cooperation's expansion and transformation.

A particularly important case is the Pleistocene–Holocene transition. For the Pleistocene–Holocene transition to storage and resource management, thence to farming, to a sedentary life, and eventually to life in larger-scale societies eroded the basis of the Pleistocene social contract. The mutualist explanation of stable cooperation in the Pleistocene cannot explain the stability of cooperation and collective action in the Holocene. In a splendid and evocative recent paper, Peter Richerson and Robert Boyd describe the Pleistocene as 'a world queerer than we have imagined', rightly emphasizing the sharp contrast between Pleistocene and Holocene social worlds ([2013], p. 263). But contrast is symmetrical. To Pleistocene agents, the Holocene would have seemed very alien: the new worlds of the Holocene undermined both the objective cost-benefit profile and the conditions of mutual information that stabilized Pleistocene cooperation.

The most fundamental change was that for an increasing proportion of the human population, the transition from the Pleistocene to the Holocene involved an economic revolution: the shift from a life as a mobile forager to life as a sedentary farmer (Bogucki [1999]; Bellwood [2004]; Cohen [2009]). This economic change had pervasive effects on just about every feature of human life. Farmers tap into resources lower in the food web and they suppress grain-bearing plants' competitors, so a larger fraction of total productivity is made available to human consumption. Hence farming supported denser and larger populations. As Bourke ([2011]) has shown, there is positive feedback between group size and social complexity: larger, denser populations support increased specialization. So Holocene worlds were more differentiated. They were less intimate, less informationally transparent, and the expectation of repeated interaction was less secure. Moreover, early farmers were endemically insecure. In contrast to foragers, a farmer waits months between planting and harvesting, and is exposed to risk (storm, drought, pests, theft) for all that period. They are also dependent on storage,

and early forms of storage were inefficient and risky. Their wealth is stored in an externalized, alienable form: years of their labour—indeed, generations of their labour—can be seized from them. They invest their time and labour improving their land, in clearing debris and weeds, and in early forms of fertilization and irrigation. As they do, the costs of moving become ever higher, and their land and its produce becomes an ever greater temptation to others. Foragers' wealth mostly consists of their embodied capital (skills, strength, health) and social capital (their network of kin and allies). Neither are alienable in the same way.

Perhaps most importantly of all, Holocene social worlds became more hierarchical. The early Holocene saw the emergence of formal political elites, with the widespread emergence of chiefdoms and other pre-state political formations (Bogucki [1999]). Political inequality emerged in conjunction with greatly increased economic inequality. Economic success in a farming world depends most on material resources—most especially fertile land—and land can be accumulated and inherited, often resulting in increasing differentiation in wealth as generations turn over (Shenk *et al.* [2010]). This potential for economic inequality is aggravated by the fact that much farming work requires little skill, and the costs of supervision and control are low compared to the profits generated by forced labour. So farming societies are often slave-owning societies, further increasing social inequality. In contrast, forager economies have not been based on slavery, because foragers are skilled, mobile, and must often be armed (Kaplan *et al.* 2009).

Collectively, these changes undermined the stability conditions of forager cooperation. Groups were larger, much less transparent, and elites were in effect free riders who had escaped collective control. The profits of cooperation were largely lost to many who help earn them. In particular, many grain farming societies became extraordinarily unequal (Kaplan *et al.* [2009]). Yet cooperation and respect for the social contract continued through the Holocene. For example, Peter Bogucki's survey of the origins of human society documents impressive public works (for defense, irrigation, ceremony) through a range of early farming societies. So we have a puzzle: collective action survived despite the fact that as social and political hierarchy developed, an ever smaller share of the profits of cooperation flowed to those lower in the hierarchy.

Here the group selection model comes into its own. Bowles and Gintis are right in pointing out that the early Holocene was a world of intergroup conflict, and that this selects for cohesive groups and for top-down, command-and-control, decision-making norms. Selection on groups was strong, and the threat of intergroup violence eroded low ranked individuals' temptations to resist elite control, if the cost was local social disruption. Forager collective decision-making is rarely urgent: if the choice is when and where to move (for

example), the time frame of discussion and consensus formation suffices. An environment of intergroup tension and raiding selects for command-and-control coordination. Decisions are urgent and the stakes are high, as are the costs of freeriding. But once military elites exist, they will be tempted to self-aggrandizing strategies. Those strategies will be difficult to resist, both because of the threat of retaliation by newly powerful elites (influential because of their coordinating role), and through increased vulnerability to external enemies. Being poor amongst your own was likely to be better than being a slave or a trophy of the neighbouring tribe. If the cost of social disruption was military vulnerability, that cost was probably evident to potential malcontents. In forager societies, the control of potential elites depends on trust and familiarity amongst coalitions of control; it depends on face-to-face interactions. That familiarity and trust is eroded in the larger worlds of farming. Moreover, farmers work in family units rather than in teams of equals. So in the Holocene, the Pleistocene mechanisms that controlled incipient elites failed, while group-group rivalry and the threat from outside gave the relatively poor an incentive to continue cooperating. Very likely, the farming societies that survived were the ones in which the poor were risk averse, and where elites managed to maintain practices of collective action.

In this article I have argued that hominin history has seen two major transitions in cooperation, and hence poses two deep puzzles about the origins and stability of cooperation. The first is the transition from great ape social life to the life of Pleistocene cooperative foragers; the second is the stability of the social contract through the early Holocene transition to complex hierarchical societies. I have argued that the first of these transitions was driven, at least initially, by individual advantage: cooperation paid off for individual foragers. That argument led to a reanalysis of the role of violence and the nature of the freeriding threat to cooperation. But the conditions that made cooperation stable in the Pleistocene were eroded in the Pleistocene–Holocene transition, and so we need an alternative account of the survival, and indeed the expansion, of cooperation in the Holocene. Group selection driven by inter-communal conflict really does seem central to this second transition.

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