

# **Cooperation, Culture and Conflict**

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## I Introduction

Cooperation often delivers impressive profits to cooperative agents. A wolf pack can threaten a far larger target than a lone wolf, and can more successfully defend kills against opportunistic pirating by larger predators. When agents have identical (or largely overlapping) fitness interests, these potential profits are often realised. 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 freerider problem, and the notorious challenge cooperation poses to evolutionary biology. Unless that problem can be solved — unless freeriding is impossible, or excluded, or minimised — freeriding destabilises 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 freerider problem, and if it does, we need to ask how the freerider 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 units with overlapping fitness interests, so it is one in which freeriding has been contained (Kaplan, Hooper et al. 2009).

Without alignment of evolutionary interest, there are only four ways cooperation can be stable. (i) Cooperation is profitable, and freeriding is not possible, because those profits depend on all agents paying the full costs of cooperation. (ii) Freeriding is possible, but it can be controlled at zero or trivial cost (perhaps through partner choice, excluding freeriders from benefits from which they would otherwise benefit). (iii) Freeriders can be forced to cooperate or leave by the threat of punishment. Punishment has a cost, but in the right circumstances, those costs can be worth paying; for example, it might allow co-operators to unambiguously identify each other, thus setting up profitable partnerships. (iv) Controlling freeriders has a net cost to the individuals. But groups in which agents cooperate, and in which freeriding is controlled, do better than less cooperative groups. Cooperative dispositions evolve through positive selection on groups, despite the individual costs co-operators pay in their local environment.

Darwin almost always took the individual organism to be the unit of selection, but he made a famous exception in this case, expressing the idea with his customary clarity:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and in increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection. (Darwin, *Descent of Man*, 1871, p166).

In general, evolutionary biologists have been cautious about group selective mechanisms<sup>1</sup>. But human social life has a second feature, one that makes it more likely that group selection has played an important role in hominin evolution. Our attitudes, our motives, our skills and our informational capital depend heavily on social learning. Great apes have some capacity for social learning (Laland and Galef 2009). But most of what great apes learn socially they could learn individually, by trial and error (Tennie, Call et al. 2009). That is obviously not true of the most central life skills of humans in contemporary mass societies. Few of us could invent writing by ourselves, by trial and error. This dependence on social learning for critical skills and information go deep into the hominin past. It is unlikely (though perhaps possible) that the skills required to make good quality Acheulian handaxes could be learned individually, by trial and error. It is even less likely that the succeeding Middle Stone Age Levallois technology could be mastered without massive social input, and specific cognitive adaptations for learning and teaching.

Our extreme dependence on cultural learning is itself an example of cooperation, but it might itself help explain the more general expansion of cooperation in our lineage. The idea is that cultural learning makes group selection more powerful, by increasing the variation between groups, and by reducing the cost to co-operators within groups. To the extent that children learn from their parental generation, not just from their parents in that generation, differences within the group in behaviour will tend to be damped down. That is true of technical skill: 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 punishment, 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, the children of selfish freeriders are less apt to be themselves freeriders too. Oblique transmission can partially mask the greater local success of freeriders. At the same time, the intergenerational transmission of information, customs and values makes the profile of a group sensitive to its generational history; to the quirks of the long-departed, not just to its current environment. Enculturation can result in groups with quite different suites of behaviour living in the same landscape. 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, then, might up-regulate the power of group selection to select for cooperative traits. This idea has been under development for some time (see (Boyd and Richerson 1992; Sober and Wilson 1998; Richerson, Boyd et al. 2003; Boyd, Gintis et al. 2005), but it has been given its most powerful and sustained formulation by Sam Bowles and Herb Gintis, culminating in their (Bowles and Gintis 2011). I have no principled objection to multi-level selection models, but I am sceptical about

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<sup>1</sup> Indeed, these have been extraordinarily controversial within evolutionary biology: see (Okasha 2006; West, Griffin et al. 2007; Godfrey-Smith 2009; West, Mouden et al. 2011).

the Bowles-Gintis picture. The aim of this paper is to explain that scepticism, and to advance an alternative big picture of human social evolution. The picture I present will be different from the Bowles-Gintis version in five ways: (i) I argue that hominin history presents two major transitions in cooperation, and hence poses two deep puzzles about the stability of cooperation, (ii) cooperation pays off for individuals, and not (just) groups; intergroup conflict plays an important role only in the second of these transitions; (iii) I present a different view of the freeriding threat, and the capacities needed for its control; (iv) I defend a different view of the motivational and cognitive preconditions for cooperation; (v) My methodological approach is different: there are serious limits to the model-building strategy of Bowles, Gintis, Boyd and Richerson. It needs to be combined with the construction of detailed historical scenarios that explicitly represent the incremental and coordinated changes that took hominins from the social world of great apes to the social world of complex human society. In the next section, I sketch the Bowles-Gintis view, and introduce a methodological challenge to the model-based explanatory strategy. In section III, I distinguish two cooperation transitions in the hominin lineage. Section IV takes up war and peace, and their supposed role in selecting for cooperation. Section V is devoted to punishment and freeriding, leading to a different diagnosis of the cognitive foundations of human cooperation. Section VI turns to the first cooperation transition, from great ape society to that of the Middle and Late Pleistocene foragers. I defend the view that forager cooperation evolved through individual selection. I then turn to the second transition, at the Pleistocene-Holocene boundary, to farming and to mass society. Bowles and Gintis get their due here: competition between groups really does stabilise cooperation at this transition. I then briefly recap.

## II Cooperation Through Group Selection

The Bowles-Gintis picture of cooperation is built on three supports: the experimental literature of behavioural economics; 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 having subjects play games of cooperation and defection, often involving experiments with enough real money riding on the outcome to focus an experimental subject's mind. This tradition now includes subjects from a wide variety of cultures, including small scale subsistence cultures. 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 stabilised at high levels. In those in which punishment is not possible, it tends to decay. Bowles and Gintis read the results of this tradition as showing that most humans have "social preferences"; they are "strong reciprocators". Most have 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 punishment serves no instrumental purpose.

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), so an obvious possibility is that apparently other-regarding preferences are an artefact of the experimental situation (Guala 2012). In these contexts, agents are falling back on default behaviours which are tuned to ongoing interaction amongst mutually known and communicating agents. In such interactions, it would often be imprudent to act as if you were indifferent to the welfare of others<sup>2</sup>. 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. There is as much reason to treat experimental games subjects' decisions as reflecting a stable preference structure as there is with other market behaviour. The strong reciprocator profile is by no means universal, and the imprint of local culture on agent dispositions is very considerable (Henrich, Boyd et al. 2004), perhaps most saliently in typical response to punishment (Herrmann, Thöni et al. 2008; Gächter and Herrmann 2009). But Bowles and Gintis argue that it is widespread; and, moreover, that there is no culture in which the typical agent is a rational maximiser of economic resources.

Suppose they are right: agents have non-instrumental concerns for the welfare of others, and those concerns motivate (at least in part) prosocial, cooperative behaviour. As Elliott Sober and David Sloan Wilson point out, it does not follow that an agent who acts from prosocial motives thereby suffers a fitness cost (Sober and Wilson 1998). 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). The suggestion is that strong reciprocation is indeed a widespread psychological profile, and that the cooperative practices of human social worlds depend on this profile. But it evolved because it typically paid individuals to be good co-operators. Bowles and Gintis resist this reciprocation and reputation based account of the selective benefit of cooperation. Instead, they defend a group selective mechanism. 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 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 twentieth century Europe, despite its massive wars. On their view, this signature of conflict is no accident: the Pleistocene record reveals rapid, high amplitude climatic change, so 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

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<sup>2</sup> Ken Binmore interprets the experimental results this way; see his (Binmore 2006; Binmore 2010).

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. While these models do not directly confirm the historical hypothesis that cooperation evolved by group selection, Bowles and Gintis take the models to show that the 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:

- (a) The size of Pleistocene forager bands.
- (b) The cost of failure and the value of victory in intergroup competition.
- (c) The price of altruism within a group (especially punishment's price).
- (d) The effect of punishment on the cooperative behaviour of others.
- (e) The value of altruists to a group, when it is in conflict with another.
- (f) The effects of cultural transmission of sharing norms in reducing the within-group costs of altruism.
- (g) The balance between individual selection and individual learning on the one hand, and the effects of the collective transmission of norms, values and customs on the other.
- (h). The relative costs and benefits of having a psychology that absorbs and responds to local norms and values.

The complexity of the phenomenon means that there is no master model, in which all these ingredients are represented, and a set of plausible trajectories generated. Instead, the emergence and stability of each ingredient (helping, punishment, responsiveness to norms, intergroup aggression) is modelled separately, but each tending to tell a similar story. As they see it, the complexity of this list is no accident, for 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 (i) socially transmitted fitness levelling practices within groups (food sharing, monogamy) reduce the local cost of altruism, and (ii) agents' psychology enables them to recognise, internalise, and respond to norms (otherwise punishment is seen as mere aggression, and is met with aggression).

I shall argue in V that this lack of a master model is a serious problem, one that exposes the limits of the strategy of explanation-via-modelling. Models are important: they show whether a mechanism (say, coordinated punishment) can work in a wide variety of environmental contexts, or whether it depends on a very specific set of features of agents, situations, payoffs. But when the explanatory target has evolved incrementally, as the result of interactions between many changing traits, we do need a unified representation of the evolutionary trajectory, and hence we need to combine

modelling with a detailed, explicit historical scenario: one that identifies the increments of change, the interactions between the coevolving traits, and the changing environmental context of the evolutionary trajectory.

Scenario-building has a poor reputation in evolutionary biology, derided as mere story-telling: see especially (Gould and Lewontin 1978). If a scenario meets three conditions, this easy contempt is unwarranted. A credible scenario should (a) rely only on well-understood, uncontroversial evolutionary mechanisms (and here models play an important role), and (b) it should be detailed. Jointly, these two conditions set a high bar for internal coherence. The scenario will not depend on exotic mechanisms or near-miraculous coincidences. Third: the scenario should have many points of articulation with the known historical facts. These articulation points are not tests as standardly understood. For our knowledge of the facts will often play a role in constructing the scenario rather than being discovered by using the scenario as a guide to empirical investigation. But they do provide an external and empirical constraint on the scenario; the more, the better. To the extent that we can construct a detailed, internally coherent scenario of the incremental evolution of human cooperation, and one that articulates with the palaeoanthropological record of hominin behaviour, we have gone beyond mere story telling to a candidate explanation (I have attempted to construct such a scenario, satisfying these conditions, in (Sterelny 2012).

No defender of the group selection picture has developed a scenario, a detailed specification of the incremental steps that take us from the very limited forms of cooperation found in great apes to human forms of cooperation. Instead, the group selection model rests on the idea that we have strong, cross-cultural evidence that humans are typically psychologically altruistic, but are also given to vengeful moralising. 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 as well. Strong reciprocators paid a fitness tax. The trait evolved anyway. Archaeology and ethnography tell us that hominins became humans in an environment of intense intergroup competition, and modelling tells us that norm-sensitive, parochial altruism can evolve by group selection in such environments.

### **III Two Social Revolutions**

In my view, there have been two revolutions in human social life; not one; there are two cooperation problems to solve, 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; their foraging was probably assisted with some rudimentary technology. By 75kya, their descendants, our species, still lived by foraging, and in intimate social worlds. But much else had changed. In particular, hominins had become obligate co-operators, and not just in narrow circles of close kin. As a core part of their subsistence strategy, humans hunted large game for hundreds of thousands of years (probably dating back at least 400 kya). Until perhaps 75kya, 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 had become co-operative foragers, extracting with great efficiency a wide array of high value plant and animal resources from their local environment. 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 co-operated ecologically, reproductively and informationally; indeed, there is good reason to believe that these aspects of co-operation coevolved, in mutually supporting ways (Sterelny 2007; Sterelny 2011).

This view of Pleistocene foragers depends in part on direct archaeological data. But it is also guided by ethnography. Simple foraging cultures known from the historical and ethnographic record are remarkable egalitarian, without institutions of political leadership, and without marked, heritable differences in wealth (Boehm 1999; Smith, Hill et al. 2010). There are a large number of forager societies known from ethnography, and since these have different historical origins, and face very different physical and biological challenges, it is reasonably safe to take the re-occurring features of foraging life as guides to these Pleistocene foragers<sup>3</sup>. If so, Pleistocene foraging groups were: (i) mobile; (ii) hence they coped with variation in foraging success by sharing rather than storing food (iii) Their technology was diverse and sophisticated, with its manufacture and use relying on rich, high fidelity, social learning and teaching. (iv) bands were small, but not typically tiny one-family units: more often, they might be groups of 20/30, divided into families, not typically closely related; (v) meat-focussed; (vi) egalitarian: no adult had formal, mutually recognised authority over others, and differences in wealth were not marked. (vii) These bands would often be linked to others through alliances, reciprocation 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 lives took millions of years. Around 10 kya, at the Pleistocene/Holocene transition, a second social revolution began, with the transition to farming and to a sedentary society. 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: interactions with, and even dependence upon, strangers became routine (Seabright 2010; Sterelny forthcoming). Bowles and Gintis provide a partial explanation of the survival of cooperation in this Holocene world of hierarchy and anonymity, but they do not explain the cooperative framework of the first transition. They do not explain the incremental evolution of the individual capacities and social

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<sup>3</sup> The physical environments of ethnographically known foragers are very varied: consider the contrast between the Australian deserts; Central American rainforests; the arctic tundra. Some of these might not have been exploited by Pleistocene foragers of 75 kya, and it is true that were not pushed to the less productive fringes of the biological world by farming pressures. But it is also true that they were subject to the extreme and often rapid climate oscillations of the Pleistocene, so they too needed mobility, flexibility, and risk-reduction strategies. So its very likely that Pleistocene foragers were egalitarian (Shultziner, Stevens et al. 2010).

organization that allowed egalitarian forager bands to emerge from a great-ape-like social world. I begin with an analysis of the likely impact of intergroup conflict, and then turn to punishment and the freerider problem.

#### **IV War and Peace in the Pleistocene**

Foragers did not live in a Utopian paradise. They bicker (Boehm 2012). More seriously, 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). 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. But 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 rage (all else equal, of course). But those most valuable in warrior encounters make uncomfortable neighbours in more peaceful times, where their risk taking and lack of inhibition in the use of violence are likely to find expression within the group<sup>4</sup>.

I very much doubt that there are genes whose only effect is up-regulate patriotic violence. Nothing we know about the emotions suggests the existence of mechanisms so fine-tuned; fine-tuned enough to enable us to up-regulate the propensity for psychotic rage against foreigners, while leaving the other hormonal knobs as they were. Given the danger 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>5</sup>. The best guess seems to be that those collectively killed in forager society are most often hyper-aggressive individuals. Often, they are a repeat-offenders, unable to control their impulses to violence; they would make good raiders. In sum, then, the genes which amplify tendencies for aggressive risk-taking in intergroup conflict, and the genes which amplify tendencies to empathise with one's associates and (or) 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. Bowles and Gintis model the evolution of sensitivity to the insider-outsider distinction, but their analysis of altruism lumps the civic and the military virtues. 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

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<sup>4</sup> The Norse sagas expression this tension particularly vividly. The Norse were small scale farming cultures, so military virtue was prized. But those who had in spades were difficult and dangerous allies, peeing almost as much inside the tent, as out of it.

<sup>5</sup> See especially (Boehm 2012) pp 83-85, and his commentary on (Guala 2012).

evolution. In developing this idea, they depend heavily on the archaeology of the Pleistocene-Holocene transition. The archaeological evidence they cite does indeed seem to show that this was a period of serious intercommunal violence. 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 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. Hence 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. So while it is indeed likely that the dawn of the Holocene was a period of intense between-group competition, that may not be true of the Pleistocene.

As noted above, the forager template was established much earlier: the current consensus is coalescing around the idea that by around 75kya Pleistocene foragers fall within the range of variation known from the ethnographic record: they were egalitarian, mobile cooperative bands, with sophisticated and increasingly diverse artefacts, skilled natural historians, and beginning to use projectile weapons (see for example (Henshilwood and d'Errico 2011; Henshilwood and Dubreuil 2011; Lombard and Haidle 2012). I doubt that this social organization was formed in the crucible of intergroup violence. Conflict between forager bands would impose higher risks and fewer benefits than conflict between farming groups. (i) 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. (ii) They have little wealth in material form; they have few goods worth seizing. (iii) Farmers work alone on family plots; hunters often travel together, so they are in a position to offer one another mutual support, and their fieldcraft makes them dangerous targets (Kelly 2005). (iv) 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>6</sup>. (v) Moreover, 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.

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, foragers might still have sunk into mutually hostile relations. Almost certainly, they were not unknown. Intergroup conflict is, and surely was, part of the foraging spectrum. 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 the successful prosecution of violence. We are the descendants of those that fought and won, rather than being the descendants (say) of those that typically avoided fighting. It is one thing to show that forager intercommunal violence was

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<sup>6</sup> It is no accident that industrial slaving in Africa involved driving captives long distance from their original homes; unless they escaped immediately, they had very little prospect of finding their way home.

quite common; another to show that engaging in violence was a successful strategy. There is no evidence that hostility was so close to universal that war was inescapable: that groups not adapted to prosecute war were doomed. Unless conflict was inescapable, hostility was not a winning strategy, enhancing forager fitness. Our ancestors are more likely to be drawn from those foragers that enjoyed the peace dividend.

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, 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 forthcoming)). There are two problems with this suggestion. First: the very instability of the Pleistocene makes it likely that morality was disturbance-dominated rather than the result of accumulating resource stresses<sup>7</sup>. Pleistocene population expansion may have been limited by brutal blizzards; terrible floods; wildfires sweeping through landscapes; events that do not make murdering the neighbours especially tempting. Second, to the extent that we have an ethnography of famine ((see (Boehm 2012) pp 274-278)), it suggests that foragers respond to famine with social atomisation. 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 fission. 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>8</sup>. Organised intercommunal 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 atomisation, there was 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 conflicts and feuds not of their own making, as news of violence slowly leaks back to the kin and to the allies of the opposing splinter.

There is no doubt that intercommunal violence is part of the forager spectrum of social life; the Yanomami are enough to show that. But while intercommunal violence undoubtedly was part of the human evolutionary experience, ethnography does not suggest that intercommunal 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. Moreover, 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 organised 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

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<sup>7</sup> Pleistocene forager skeletons show no evidence of such resource stress; they look to be much healthier than early farmers (Cohen 2009).

<sup>8</sup> That is especially true if, as Boehm suggests, famine imposes serious stresses on within group norms of cooperation (see (Boehm 2012) pp 274-278).

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) valorise 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 a 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. I know turn to the complex set of issues around punishment and freeriding.

### **V Punishment, Shirkers and Bullies**

It is plausible that the control of freeriding depends on the threat of punishment. It is also plausible that punishment is costly. Perhaps the experimental games of cooperation and defection show that modern humans are willing to punish despite its costs, but how did that disposition originate, and why does it persist, despite its costs? The standard view is that it is easy to explain the stability of collective punishment as a mechanism that deters freeriding, but difficult to explain its origins. When the willingness to punish is common, its cost is low, both because punishment is rarely necessary, and because the costs are divided amongst all those engaged in punishment. Conversely, when its rare (and all traits are initially rare), it is very expensive, for freeriders have not yet learned to desist through fear of punishment, and because the cost is spread across the few rather than the many.

This standard view is somewhat problematic: for many agents, enmity and resentment is not a limited resource: they have plenty to go around. Given this human capacity to bear a grudge against the many, analyses of punishment tend to understate costs, especially risk costs. The fact that an agent does not rebel at the time against public criticism and shaming does not mean that there will be no trouble later on. One of the poster examples from ethnography of successful collective punishment is the shaming of Cephu, a hunter that attempted to steal meat by stealth (Turnbull 2012). Cephu was shamed by collective disapproval; humbled, apologised, allowed food to be taken from his family. But even in this case, punishment caused ill-feeling within a group: Cephu's family ultimately moved away, and migrating out can be important cost to forager groups relying on multiple independent sampling of local resources as a risk reduction strategy. Obviously, long-lasting enmities within a group can be still more expensive, given the known propensity of forager societies for violence. Even when the willingness to punish is widespread across a community, coordinated punishment is not risk-free, and hence it is costly.

So as I see it, then, the standard line on punishment understates the puzzle of the supposedly easy case: the stability of punishment once it is common. Bowles and Gintis have the opposite opinion. Punishment is not a reflex: an agent's willingness to punish is sensitive to his assessment of its cost and effectiveness. Punishment is a conditional strategy: it invades as a conditional, threshold-dependent strategy. Punishers punish only when (perhaps initially through chance) they reach a threshold in the local environment. This strategy allows their frequency to grow, since coordinated punishment is not too expensive, and the threat of punishment, allied to the knowledge of past punishment, induces non-punishers to cooperate. So punishers

are compensated for the costs of punishment by the rewards of cooperation. It is true that some non-punishers gain these rewards without paying any punishment (or signal) costs: they piggy-back on punishers in their local social environment. But since punishers enforce cooperation through punishment only when those willing to punish are locally common, most of the rewards of cooperation go to those who signal their willingness to punish. Punishment invades as a conditional strategy, as a signal and response system that enables players with that strategy to benefit from cooperation. Of course, it does not invade independently of costs of punishment, and benefits of cooperation. But Bowles and Gintis claim that under reasonable estimates of these costs and benefits, punishment can invade. But there is a deep tension in this picture.

On the one hand, Bowles and Gintis, in company with many others, take the control of freeriding to be critical in establishing a cooperative social environment, and they take it that freeriding must be controlled by punishment. If so, coordinated punishment must evolve early in the transition from great ape to sapiens-like social worlds<sup>9</sup>. The tension in the picture arises because these models also tacitly assume capacities to signal, to interpret signals and to coordinate in inflicting punishment; capacities that would only evolve late, because they evolve only in a social environment that is already much more cooperative than those revealed by great ape ethnography. First: the models assume that punishers reliably and effectively signal their willingness to punish, and others receive and understand those signals. These models assume both a transparent informational environment (information is reliably available) and that signals are understood without serious error. These signal pickup assumptions are quite rich. For the signals themselves are guarantees of future courses of action, rather than natural signs of past cooperation or defection. Tracking a punishment threshold depends on active signalling and interpretation, not information leakage via cues.

Moreover, coordinated punishment requires not just a genuine willingness to punish, but actual coordination in punishment, against uncooperative, often dangerous targets. If this mechanism is seen as explaining the initial foundations of a cooperative world, the informational load on this model is implausibly high. We expect signal-comprehension-coordination capacities to evolve incrementally in a cooperative world; they cannot be assumed for free as an explanation of the origins of such a world. Second: the models assume that nonpunishers cooperate in response to punishment, rather than counter-punish<sup>10</sup>. This assumption is far from trivial, for in experimental games, punishment quite often attracts counter-punishment rather than cooperation. The best guess is that punishment only induces cooperation when it is seen as legitimate. Agents respond to punishment with cooperation only, or typically, when they see that they have previously violated some legitimate expectation. Otherwise (of course) punishment is seen just as aggression. Thus punishment is most effective in controlling freeriding only in late-evolving social environments;

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<sup>9</sup> The social world of great apes is not typically one of interactions only amongst close kin, so cooperation evolved in a world of overlapping, only partially coordinated evolutionary interest: kin selection might be some of the story, but it is not most of the story.

<sup>10</sup> "Nonpunishers are a plausible ancestral state for the evolution of punishment. They do not cooperate or punish, nor do they respond to unverified threats of punishment. However, once they have been punished, they cooperate in subsequent periods in order to avoid more punishment" (p151)

environments in which something like norms, or at least legitimate expectations, of cooperation are established and salient to all<sup>11</sup>.

I noted in section II that Bowles and Gintis offer no master model of the evolution of cooperation: no model that represents all the critical individual and social traits, with their changing, interacting trajectory over time. They have no choice: no master model would be tractable. But human cooperation is a complex phenomenon that has evolved gradually, incrementally, with coordinated changes in individual traits and the social environment. Their modelling strategy does not provide an explicit representation of the incremental sequences of changes that took the hominin lineage from a great ape social world to the social world of behaviourally modern foragers. Instead, the natural modelling strategy is decompositional: to take each aspect of the cooperation complex (punishment, norm-sensitivity, reputation effects, insider-outsider discrimination, moral emotions) and to model its emergence and stability separately. This strategy makes it easy to tacitly assume, in modelling the evolution of one ingredient of the cooperation stew, backgrounded but important factors that have yet to be cooked. That is one reason why we need a detailed and explicit scenario specifying the changing lineage as a whole.

So the lack of a master model masks an ambiguity about the emergence of punishment. To explain the stability of cooperation, it seems as if it must emerge early, but early hominins probably did not have the cognitive capacities need to make it effective. The modelling tradition also tends to mischaracterize the freeriding threat. For theories of the evolution of cooperation have typically backgrounded the capacities that make cooperation profitable, and foregrounded the problem of dividing the profit in ways that ensure the stability of cooperation (Calcott 2008). But cooperation is typically profitable only through coordinated action, and coordination is far from trivial. Indeed, when we take seriously forager ethnography, the problem of coordination is especially pressing when capturing coordinated punishment. It is common ground that unchecked freeriding would destabilize cooperation. 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 their fare share on social goods, and they obviously threaten the stability of forms of cooperation that depend on reciprocation. But there is a second form of freeriding: bullying exploiters, who use their power to take what they want. Forager ethnography identifies the threat posed by exploitative alpha males. They 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, of its sexual resources). But even if they do not achieve local dominance, their behaviour and personality is a flashpoint of conflict, disputing the local social network of coordinated action and mutual obligation; the local network that enables foragers to manage risk.

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<sup>11</sup> Incentives (and the denial of incentives) might be game-theoretically equivalent to punishment, but they are probably not motivationally equivalent. Instead of public shaming and social distance, control of freeriding through partner choice and positive incentives not to freeride might have been especially important early in the growth of cooperation (Noë 2001).

The evolution of cooperation literature tends to model freeriding as shirking. For example, in experimental games, freeriders simply do not contribute to common pool resources; they make stingy proposals as first player in ultimatum games; they do not punish unfair offers as spectators of ultimatum and dictator games. These games capture shirking, but they do not capture the aggressive use of power for egocentric ends. But, arguably, in explaining the origins of human cooperation, bullying poses the most critical freerider problem. First: great ape social life is typically bully-dominated. Until alpha bullying was controlled, the distinctive features of human social life could not establish. Great apes live and act in an immediate-return economy. That is adaptive in a world dominated by bullies. There is no incentive to invest in food processing, adding value by (say) cooking food in a safe central place, if it is likely to be taken by anyone above you in the power hierarchy. Similarly, there is no incentive to spend hours or days making and curating artefacts, if these too are likely to be lost to anyone stronger. 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. Second, ethnography shows that the foragers themselves regard bullying as the most serious threat to their social lives. Bullies— would-be alphas — attract most serious and hence most expensive punishment. Third, bully control is more difficult than shirker control. Bullies are (typically) much more 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>12</sup>. Fourth, while bullies are controlled reasonably well in ethnographically visible forager worlds, the mechanisms of control depend on late-evolving features of the human cooperation suite. Despite their potential for trouble, efficient, well planned and decisive action by a coalition can eliminate alpha trouble makers. However, coordinated, relatively safe assassination of a violent trouble maker depends on much of the full suite of behaviourally modernity: language, planning, explicit norms, kinship systems, technology.

In the forms we know from ethnography, then, bully control is both risky and 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*, 1.7 mya. So we need an explicit, incremental account of bully control, as part of an explicit scenario identifying the sequence of changes that took hominins from great ape to human sociality.

In explaining the transition in hominin sociality, we need to explain the decline of hierarchy. Pleistocene egalitarian bands did not evolve from a world of *pan economicus*; from associations between equal, egoistic economic maximisers. Very likely, the earliest hominins lived in social groups dominated by alpha males.

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<sup>12</sup> For an example of collective punishment that resulted in death and injury in the enforcement coalition, see (Boehm 2012) pp 261-262.

Hierarchy can only have declined by the evolution of coalitions that constrained dominant's power, but how could such coalitions establish. Frans de Waal's gripping descriptions of chimp politics show that alpha males have the social intelligence to recognise the threat posed by internal coalitions, and vigilance and determination to disrupt those coalitions by punishment (de Waal 1982). 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. If the target of the coalition can identify and act against key figures before they have rallied full support, then being part of an incipient anti-dominance coalitions would be very dangerous indeed; their targets are targets precisely because they are so dangerous.

The members of a potential anti-dominance coalition must agree on the need for action, and on its target; they trust one another to act despite the risks of action, and they must be able to time and coordinate their actions. How could these capacities be available early in the evolution of a cooperative hominin world; before the emergence of language, norms, explicit kinship systems, or stand-off technology? Some 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. So the hard problems is to explain the emergence of the trust and coordination needed to sustain pressure.

I suggest that trust is secured by an interaction between the social emotions and a history of successful co-operative interactions in foraging and collective defence. Robert Frank has argued that the moral emotions secure trust precisely because they are emotions and hence not under topdown control: they function both as difficult-to-fake signals of stable behavioural dispositions, and as relatively resilient stabilisers of those dispositions (Frank 1988). Dan Fessler and I have argued that these internal motivational levers stabilise, and are stabilised by, external economic ones. Partial solutions to trust problems secure a pattern of association that is valuable in itself, which acts as a further signal of agent quality to third parties, and which strengthens the subjective bonds of mutual affiliation (Sterelny 2012; Fessler and Quintelier forthcoming). Agents with a history of successful collective action 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)).

Thus the road to co-operation begins with an initial expansion of ecological collaboration; perhaps first as collective defence against predators, and then perhaps as bully scavenging, driving predators from kills. I think 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 co-operation, and because collective defence does not pose a division of the profits problem. If defence is successful, everyone in the group automatically benefits. But bully scavenging — driving small to medium size

predators (at first) from their kills as a mob armed with sticks and throwing stones could evolve early, too. Even in the face of an unequal 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 of co-ordination, 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.

It is not known when hominins became markedly more cooperative than other great apes. But the working assumption of this paper is that it began three million years or more ago, with hominins living in seasonal, open environments, and using tools to shift their diet towards meat and other high value foods, but challenging resources (McPherron, Alemseged et al. 2010). So cooperation was increasing in our lineage by then, if not before. The physical, biological, and social environment of the late australopithecines and early habilines selected for increased capacities to cooperate, and such capacities can evolve gradually, perhaps initially through general learning mechanisms. In particular, the motivation to act with others may well have begun as a learned association between collective action and reward, which then becomes genetically assimilated. In the early stages of the transition to co-operation, 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 turn into a successful and persistent partnership, each will begin to associate the others' presence, and acting with the other, with success, with reward. They learn to like being with one another, because being with one another lead to good things. They will learn to trust one another to be vigilant. To the extent that the environmental change that makes foraging in company safer persisted, selection that favoured those that are more tolerant and accepting of others' presence, those that find it easier to establish such partnerships. Social bonds that were initially mediated by quite general learning mechanisms come to have a more specific genetic component. So relatively early forms of ecological cooperation build the cognitive and social preconditions for anti-dominance coalitions. Pleistocene co-operation — both the domestic policing of potential alphas and ecological cooperation in hunting and foraging parties — depends on trust, and trust depends on the coupling of a history of successful collaboration with prosocial emotion.

If the cooperation expansion began with the early habilines or late australopithecines, it began amongst hominins that did not have the social, linguistic, or technical sophistication of our species and its near-contemporaries. But acting in concert, with a common purpose, has lead to a psychology very different from the last common ancestor of the hominins and chimps. Bowles and Gintis focus on strong reciprocity. In doing so, they follow the long tradition of work on the evolution of cooperation that focuses on dividing the profit of cooperation rather than explaining how those profits are generated. However, profitable cooperation also depends on coordination and the division of labour, so Michael Tomasello is right to argue that the most important single cognitive difference between humans and chimps is that humans form joint intentions, which result in joint action (Tomasello, Carpenter et al. 2005;

Tomasello and Carpenter 2007). As team sports show, humans find collective activities intrinsically rewarding. Chimps will collaborate for instrumental ends, but in contrast to young children, they abandon collaborative activity as soon as those instrumental purposes are served (Warneken forthcoming). Our evolutionary history of cooperation has led to motivational changes; both the other-regarding preferences of strong reciprocators, and to finding intrinsic reward in joint action. But there was also an important cognitive change. Joint intention presupposes mutual awareness of others' intentions; of the theatre of action; and of the collective activity in question. As Tomasello puts it, agents engaging in genuine joint action can form a "bird's eye" representation of the collective activity, and this enables them to coordinate, to divide labour, to switch roles flexibly. The capacity for collective intentionality evolved as cooperation became pervasive and entrenched in our lineage, and as it evolved, it made cooperation more profitable, by turbocharging hominin capacities to coordinate in collective action.

I have harped on about the importance of explaining the profit of cooperation, not just presuming it, but the main line of theorising is of course right in treating the division of those profits as critical to the stability of cooperation. I shall argue that Pleistocene foragers benefited from cooperation as individuals. But many Holocene farmers may not have, and so I think Bowles and Gintis are right in focusing on group benefit at the Pleistocene-Holocene transition and the transition to sedentary society.

## **VI Foraging and the Folk Theorem.**

There are a cluster of games theory results collectively known as "the folk theorem" (Binmore 1994). These results identify the environments which select for co-operation based on reciprocation. Co-operation evolves when there are profits to be had from co-operation, and when the co-operating parties share in those profits. Sharing is reliable 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 co-operation. Pleistocene foragers satisfied these conditions. First: they lived in environments in which co-operation was profitable. Given the limits on their technology, a crucial resource, large game, could be secured only through collective action. In important cases, the benefits of co-operation are delivered immediately, and to all: for example, when the size and cohesion of a group enables it to detect, avoid, or repel a serious predator. The same is true when the group as a whole hunts collectively, or collectively drives another predator from its kill. In these cases, collective action is a mutualism generating a profit that is shared on the spot, rather than depending on reciprocation (in Trivers' sense). Immediate return mutualism does not pose problems about discount rates, the certainty of future interaction, or tracking individuals and their generosity over time.

Reciprocation 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

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<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 co-operation, though this is more kin-based than other forms of recent human co-operation (O'Connell, Hawkes et al. 1999; Hawkes 2003; Hrdy 2009).

revolution (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, a great variety of plant food — rewarded specialisation and a division of labour (Stiner 2001; Stiner 2002). These resources are concentrated in different places; they are best harvested with specialised equipment (some, like fish, absolutely require specialised equipment). Often, efficient foraging often depended on specialised expertise too. For example, plant-based resources are now 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: specialised 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 cooperative economies based on reciprocity, rather than on immediate return mutualism, may be relatively recent, establishing only in the last 100 k years or so.

When co-operation is beneficial through reciprocal altruism, as an agent returns a favour with a favour, so that co-operating agents are advantaged by delayed but increased returns, it is of critical importance that groups are small, with repeated interaction, and these were just the groups Pleistocene foragers lived in<sup>14</sup>. It is also critical that agents have rich, accurate information about each others history of cooperation and cooperation failure. Bowles and Gintis doubt that this condition is satisfied, but since foragers lived in such intimate social worlds, detecting freeriding was fairly simple. They foraged and lived together. 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. Of course, deterring freeriding was another matter. Nonetheless, the intimacy and long mutual history of forager communities would make it possible to co-ordinate 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, Hill et al. 2010). Thus the costs of control would often have been worth paying, both to protect material and social resources, and as an investment in reputation.

## **VII The Holocene: Farms, Wars, Priests, Chiefs.**

I have just argued that 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. The Pleistocene-Holocene transition to farming, to a sedentary life, and eventually to life in larger scale societies eroded the basis of the Pleistocene social contract. The mutualistic 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

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<sup>14</sup> Bowles and Gintis think there is genetic data suggesting that many foragers lived in groups larger than the 20-30 bands I have been envisaging, and for which the folk theorem suggests stable reciprocity-based cooperation. But the size of the local mate market is likely to be very considerably larger than the unit of daily ecological interaction. 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 data, if anything, is telling us about the size of the metaband.

Pleistocene as a world queerer than we have imagined, rightly emphasising the sharp contrast between Pleistocene and Holocene social worlds (Richerson forthcoming). 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 stabilised Pleistocene co-operation.

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 also suppress grain-bearing plants' competitors, so a larger fraction of total productivity is made available to human consumption. Farming supported denser and larger populations. In turn, size and density allows increased specialisation. So Holocene worlds were more differentiated. They are less intimate, less informationally transparent, and the expectation of repeated interaction is 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. To a much greater extent than for foragers, their wealth is stored in an externalised, alienable form: years of their labour, indeed, generations of their labour, can be seized from them. For they invest their time and labour improving their land: clearing debris and weeds; early forms of fertilisation 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. Forager's wealth mostly consists of his 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 were 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 much 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, Borgerhoff Mulder 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 hierarchy. In contrast, forager economies have not been based on slavery, because foragers are skilled, mobile, and must often be armed (Kaplan, Hooper et al. 2009).

Collectively, these changes undermined the stability conditions of forager cooperation. Groups are larger, much less transparent, and elites are in effect alpha freeriders who have escaped collective control, and so the profits of cooperation are largely lost to many who help earn them. In particular, grain farming societies ultimately became extraordinarily unequal (Kaplan, Hooper et al. 2009). Yet co-

operation 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, as farming became established. So we have a puzzle: collective action survived despite the fact that as social and political hierarchy develops, an ever smaller share of the profits of co-operation flow 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 topdown, command and control decision making norms. Selection on groups was strong, and the threat of intergroup violence eroded low ranked individual's temptation 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 co-ordination. Decisions are urgent; the stakes are high, as are the costs of free-riding. But once they exist, military elites will be tempted to self-aggrandising 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) through increased vulnerability to external enemies. Being poor amongst your own was likely to be better than being a slave of the neighbouring tribe. If the cost of social disruption was military vulnerability, that cost was probably evident to potential malcontents. In forager societies, elite control depends on trust and familiarity amongst coalitions of control; it depends on face to face interactions. That familiarity and trust is eroded in farming worlds. They are larger; moreover, farmers work in family units rather than in teams of equals. So in the Holocene, the mechanisms that controlled incipient elites in the Pleistocene failed, while group-group rivalry and the threat from outside gave those that were 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.

Let me finish by briefly restating the main claims of this paper. Hominin history is a history of two major transitions in cooperation, not just one, and while group selection fuelled by intercommunity conflict very likely played a key role in stabilising cooperation and collective action in the transition to farming, it was much less important in the emergence of cooperation amongst the egalitarian Pleistocene foragers. Forager cooperation did face a freerider problem, but its character and consequences are not well captured through the standard approach of models and experimental games. More generally, a genuine explanation of the growth of hominin cooperation requires a combination of a model-based strategy (of the kind so impressively exemplified by Bowles and Gintis) with historical scenario building. We need a narrative explanation to go with formal theory and models.

## References

- Alexander, R. (1987). The Biology of Moral Systems. New York, de Gruyter.
- Barnard, A. (2011). Social Anthropology and Human Origins. Cambridge, Cambridge University Press.
- Bellwood, P. (2004). The first farmers: the origins of agricultural societies Oxford, Wiley-Blackwell.
- Berlin, B. (1992). Ethnobiological Classification: Principles of Categorization of Plants and Animals in Traditional Societies. Princeton, Princeton University Press.
- Binmore, K. (1994). Game Theory and the Social Contract: Volume 1: Playing Fair. Cambridge, MIT Press.
- Binmore, K. (2006). "Why Do People Cooperate?" Politics Philosophy And Economics **5**: 81-96.
- Binmore, K. (2010). "Social Norms or Social Preferences?" Mind and Society **9**: 139-157.
- Boehm, C. (1999). Hierarchy in the Forest. Cambridge, Mass, Harvard University Press.
- Boehm, C. (2012). Moral Origins: The Evolution of Virtue, Altruism and Shame. New York, Basic Books.
- Bogucki, P. (1999). The Origins of Human Society. Oxford, Blackwell.
- Bowles, S. and H. Gintis (2011). A Cooperative Species: Human Reciprocity and Its Evolution Princeton, Princeton University Press.
- Boyd, R., H. Gintis, et al. (2005). The Evolution of Altruistic Punishment: Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life. H. Gintis, S. Bowles, R. Boyd and E. Fehr. Cambridge, MIT Press: 215-227.
- Boyd, R. and P. Richerson (1992). "Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups." Ethology and Sociobiology **13**: 171-195.
- Calcott, B. (2008). "The Other Cooperation Problem: Generating Benefit." Biology and Philosophy **23**(2): 179-203.
- Cohen, M. N. (2009). "Introduction: Rethinking the Origins of Agriculture." Current Anthropology **50**(5): 591-595.
- Csibra, G. and G. Gergely (2011). "Natural pedagogy as evolutionary adaptation." Philosophical Transactions of the Royal Society B **366**: 1149-1157.
- Currie, T., S. Greenhill, et al. (2010). "Rise and fall of political complexity in island South-East Asia and the Pacific. ." Nature **467**: 801-804.
- de Waal, F. (1982). Chimpanzee Politics: Power and Sex Amongst the Apes. New York, Harper and Row.
- Fessler, D. and K. Quintelier (forthcoming). Some Noncommittal Musings on Subjective Commitment, Objective Commitment, and Biological and Cultural Evolution. Signaling, Commitment, and Emotion. B. Calcott, B. Fraser, R. Joyce and K. Sterelny.
- Foley, R. and C. Gamble (2009). "The Ecology of Social Transitions in Human Evolution." Philosophical Transactions of the Royal Society B **364**: 3267-3279.

- Frank, R. (1988). Passion Within Reason: The Strategic Role of the Emotions. New York, WW Norton.
- Fraser, G. M. (2001). Quartered Safe Out Here: A Recollection of the War in Burma. London, Akadine Press.
- Gächter, S. and B. Herrmann (2009). "Reciprocity, culture and human cooperation: previous insights and a new cross-cultural experiment." Philosophical Transactions Royal Society London, B **364**(1518): 791-806.
- Godfrey-Smith, P. (2009). Darwinian Populations and Natural Selection. Oxford, Oxford University Press.
- Gould, S. J. and R. Lewontin (1978). "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." Proceedings of the Royal Society, London (Series B) **205**: 581-598.
- Guala, F. (2012). "Reciprocity: Weak or strong? What punishment experiments do (and do not) demonstrate." Behavioral and Brain Science **35**: 1-59.
- Guthrie, R. D. (2005). The Nature of Paleolithic Art. Chicago, University of Chicago Press.
- Hawkes, K. (2003). "Grandmothers and the evolution of human longevity." American Journal of Human Biology **15**(3): 380 - 400.
- Henrich, J., R. Boyd, et al., Eds. (2004). Foundations of Human Sociality. Oxford, Oxford University Press.
- Henshilwood, C. and F. d'Errico (2011). Middle Stone Age Engravings and Their Significance to the Debate on the Emergence of Symbolic Material Culture. Homo Symbolicus: The Dawn of Language, Imagination and Spirituality. C. Henshilwood and F. d'Errico. Amsterdam, John Benjamins: 75-96.
- Henshilwood, C. and B. Dubreuil (2011). "The Still Bay and Howiesons Poort, 77-59 ka: Symbolic Material Culture and the Evolution of the Mind during the African Middle Stone Age." Current Anthropology **52**(3): 361-400.
- Herrmann, B., C. Thöni, et al. (2008). "Antisocial Punishment Across Societies." Science **319**,(7 March): 1362 - 1367.
- Hewlett, B., H. Fouts, et al. (2011). "Social learning among Congo Basin hunter-gatherers." Philosophical Transactions of the Royal Society B **366**: 1168-1178.
- Hrdy, S. B. (2009). Mothers and Others: The Evolutionary Origins of Mutual Understanding Cambridge, Harvard University Press.
- Jones, M. (2007). Feast: Why Humans Share Food. Oxford, Oxford University Press.
- Kaplan, H., P. Hooper, et al. (2009). "The evolutionary and ecological roots of human social organization." Philosophical Transactions of the Royal Society, London, B **364**: 3289-3299.
- Kelly, R. (2005). "The evolution of lethal intergroup violence." Proceedings of the National Academy of Science **102**(43): 15294-15298.
- Laland, K. and B. Galef, Eds. (2009). The Question of Animal Culture. Cambridge, Mass, Harvard University Press.
- Lombard, M. and M. N. Haidle (2012). "Thinking a bow-and-arrow: cognitive implications of Middle Stone Age bow and stone-tipped arrow technology." Cambridge Archaeological Journal **22**(2): 237-264.
- McPherron, S., Z. Alemseged, et al. (2010). "Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia." Nature **466**(12 August): 857-860.

- Noë, R. (2001). Biological markets: partner choice as the driving force behind the evolution of cooperation. Economics in Nature. Social Dilemmas, Mate Choice and Biological Markets. R. Noë, J. van Hooff and P. Hammerstein. Cambridge, Cambridge University Press: 93-118.
- O'Connell, J. F., K. Hawkes, et al. (1999). "Grandmothering and the evolution of Homo erectus." Journal of Human Evolution 36(5): 461-485.
- Okasha, S. (2006). Evolution and The Units of Selection. Oxford, Oxford University Press.
- Richerson, P. (forthcoming). Rethinking Paleoanthropology: A World Queerer Than We Had Supposed. The Evolution of Mind. G. Hatfield. Philadelphia, University of Pennsylvania Press.
- Richerson, P., R. Boyd, et al. (2003). Cultural Evolution of Human Co-operation. Genetic and Cultural Evolution of Cooperation. P. Hammerstein. Cambridge, MIT Press: 373-404.
- Seabright, P. (2010). The Company of Strangers: A Natural History of Economic Life. Princeton, Princeton University Press.
- Seabright, P. (forthcoming). The Birth of Hierarchy. Evolution, Cooperation, and Complexity. B. Calcott, B. Fraser, R. Joyce and K. Sterelny. Cambridge, MIT Press.
- Shenk, M. K., M. Borgerhoff Mulder, et al. (2010). "Intergenerational Wealth Transmission among Agriculturalists: Foundations of Agrarian Inequality." Current Anthropology 51(1): 65-83.
- Shultziner, D., T. Stevens, et al. (2010). "The causes and scope of political egalitarianism during the Last Glacial: a multi-disciplinary perspective." Biology and Philosophy 25(3): 319-346.
- Smith, E. A., K. Hill, et al. (2010). "Wealth Transmission and Inequality among Hunter Gatherers." Current Anthropology 51(1): 19-34.
- Sober, E. and D. S. Wilson (1998). Unto Others: The Evolution and Psychology of Unselfish Behavior. Cambridge, Harvard University Press.
- Sterelny, K. (2007). "Social Intelligence, Human Intelligence and Niche Construction." Proceedings of the Royal Society, London (series B) 362(1480): 719-730.
- Sterelny, K. (2011). The Evolved Apprentice Cambridge, MIT Press.
- Sterelny, K. (2012). The Evolved Apprentice Cambridge, MIT Press.
- Sterelny, K. (forthcoming). Life in Interesting Times: Co-operation and Collective Action in the Holocene. . Evolution, Cooperation, and Complexity. B. Calcott, B. Fraser, R. Joyce and K. Sterelny. Cambridge, MIT Press.
- Stiner, M. C. (2001). "Thirty Years on: The "Broad Spectrum Revolution" and Paleolithic Demography." Proceedings of the National Academy of Sciences 98(13): 6993-6996.
- Stiner, M. C. (2002). "Carnivory, Coevolution, and the Geographic Spread of the Genus Homo." Journal of Archaeological Research 10(1): 1-63.
- Tennie, C., J. Call, et al. (2009). "Ratcheting Up The Ratchet: On The Evolution of Cumulative Culture." Philosophical Transactions of the Royal Society, London, B 364: 2405-2415.
- Tomasello, M. and M. Carpenter (2007). "Shared Intentionality." Developmental Science 10(1): 121-125.
- Tomasello, M., M. Carpenter, et al. (2005). "Understanding and sharing intentions: The origins of cultural cognition." Behavioral and Brain Sciences 28: 675-691.
- Turnbull, C. (2012). The Forest People. New York, Random House.

- Warneken, F. (forthcoming). The Origins of Human Cooperation from a Developmental and Comparative Perspective. The Evolution of Mind. G. Hatfield. Philadelphia, University of Pennsylvania Press.
- West, S., A. Griffin, et al. (2007). "Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection." Journal of Evolutionary Biology **20**: 415-432.
- West, S., C. E. Mouden, et al. (2011). "Sixteen common misconceptions about the evolution of cooperation in humans." Evolution and Human Behavior **32**: 231-262.
- West-Eberhard, M. J. (2003). Developmental Plasticity and Evolution. Oxford, Oxford University Press.
- Woodburn, J. (1982). "Egalitarian Societies." Man **17**(3): 431-451.
- Woodburn, J. (1982). "Egalitarian Societies." Man **17**(3): 431-451.