Two Key Steps in the Evolution of Human Cooperation: The Interdependence Hypothesis

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Abstract

Modern theories of the evolution of human cooperation focus mainly on altruism. In contrast, we propose that humans' species-unique forms of cooperation – as well as their species-unique forms of cognition, communication, and social life – all derive from mutualistic collaboration (with social selection against cheaters). In a first step, humans became obligate collaborative foragers such that individuals were interdependent with one another and so had a direct interest in the well-being of their partners. In this context they evolved new skills and motivations for collaboration not possessed by other great apes (joint intentionality), and they helped their potential partners (and avoided cheaters). In a second step, these new collaborative skills and motivations were scaled up to group life in general as modern humans faced competition from other groups. As part of this new group-mindedness, they created cultural conventions, norms, and institutions (all characterized by collective intentionality), with knowledge of a specific set of these marking individuals as members of a particular cultural group. Human cognition and sociality thus became ever more collaborative and altruistic as human individuals became ever more interdependent.

As compared with other primates, human beings are inordinately cooperative, especially with non-relatives. As is well known since Darwin, this creates challenges for evolutionary explanation, since in modern evolutionary theory cooperative behavior must always be grounded in the individual and inclusive fitness of the cooperator.

In this modern context, there are two main theories of the evolution of human cooperation, both of which focus on the most difficult theoretical problem from the point of view of evolutionary theory: altruism. The first theory comes from evolutionary psychology and is often called the Big Mistake Hypothesis (e.g., Burnham & Johnson, 2005). The basic idea is that human altruistic tendencies evolved at a time when humans lived in small groups, comprised mostly of kin. In this setting, altruistic acts would either (a) benefit kin, and so evolve due to kin selection, or else (b) benefit the altruist by enhancing in some way her chances for reciprocity, which is especially critical in small groups in which reputational assessment among familiar interactants is constant. In the modern world, even in the midst of strangers or even when not being observed by others at all, humans nevertheless have some tendency toward altruism (and antipathy toward cheaters) because the proximate mechanism operates as if the ancient, small-group conditions still held.

The second theory is the Cultural Group Selection Hypothesis (e.g., Richerson & Boyd, 2005; Henrich & Henrich, 2007), and it focuses on a later stage in human evolution characterized by larger social groups. The basic idea is that social groups with more altruists will, for various reasons, outcompete other groups. The difference to previous group selection hypotheses is that the main transmission across generations takes place not genetically but culturally. For other reasons, modern humans are built to imitate others (e.g., successful others or the majority), and so if a group has altruists, others will often imitate them and that will lead to group success. As groups become more large-scale, those that create social norms and institutions that better promote altruism will again thrive relative to others. No biological adaptations for altruism are necessarily involved here, but the theory does allow for later gene-culture co-evolution in which individuals biologically adapt to life in a culture characterized by conformist social transmission, group punishment and norms, and group competition.

In what follows we propose an approach to the evolution of human cooperation that begins in a different place. Our starting point is not cooperation as altruistic helping, but rather cooperation as mutualistic collaboration. Our hypothesis, which we call the Interdependence Hypothesis, is that at some point humans created lifeways in which collaborating with others was necessary for survival and procreation (and cheating was controlled by partner choice). This situation of interdependence led inevitably to altruism, as individuals naturally wanted to help the collaborative partners on whom they depended for, for example, foraging success. Moreover, interdependent collaboration also helps to explain humans' unique forms of cognition and social organization, since it is collaboration, not altruism, which creates the many coordination problems that arise as individuals attempt to put their heads together in acts of shared intentionality[1] to create and maintain the complex technologies, symbol systems, and cultural institutions of modern human societies.

Our evolutionary story comprises two distinct steps, the first focusing on small-scale contexts (though we focus on different aspects than the Big Mistake Hypothesis), and the second focusing on group-level contexts (though we focus on different aspects than the Cultural Group Selection Hypothesis). First, small-scale collaboration involving cognitively complex coordination problems took place initially, we will argue, in the context of collaborative foraging. Although

[1] Here we use the term 'shared intentionality' to refer to collaborative phenomena in general. We use the term 'joint intentionality' for the ad hoc, temporary collaborations characteristic of, for example, foraging parties (Step 1 of our story), and the term 'collective intentionality' for the more impersonal yet permanent group-minded practices and modes of collaboration that characterize cultural groups as a whole (Step 2 of our story).

humans' more stable reproductive bonds (Chapais, 2008) and cooperative breeding (Hrdy, 2009) clearly played an important role in establishing the motivational and emotional foundations, the cognitive dimension of human cooperation evolved in contexts in which individuals had to create together various coordination strategies (often involving technologies) in order to acquire food, which they then could communicate cooperatively to others within and across generations (Sterelny, in press). Second, group-level collaboration followed as the entire social group needed to work together interdependently in order to compete with other social groups, leading to such things as group-created conventions, norms, and institutions. This step was undoubtedly followed by something like cultural group selection, but cultural group selection explains why the particular social norms and institutions of particular cultural groups have prevailed, and this assumes species-universal skills and motivations – such as those we will posit - for creating social norms and institutions in the first place.

In support of our hypotheses, we focus on two sources of evidence not common in anthropology. First, we invoke experimental studies, many from our own laboratory, which compare the cognitive and motivational skills of humans, mostly young children, and their nearest great ape relatives (as representative, in a very general way, of the last common ancestor). We show that even young children are adapted for collaborative activities in a way that other great apes are not. Second, we also in some cases invoke human ontogenetic sequences as suggestive of potential phylogenetic sequences, for example, that young children in fact (and possibly of logical necessity) learn to collaborate with other individuals in concrete situations before they construct more abstract group-level phenomena such as social norms and institutions. We invoke observations of modern foragers and some paleoanthropological data, as is more customary in evolutionary theorizing, in a few places as well.

1. First Step: Obligate Collaborative Foraging

The central challenge of social life is often presented as a Prisoner's Dilemma in which the individual must choose between its own well-being and that of the group. But the Prisoner's Dilemma only arises in very special circumstances, and it does indeed tend to block cooperation. A better model for real-life cooperation is the Stag Hunt (Skyrms, 2004). Stag Hunt situations are those in which (i) individuals must collaborate with others to benefit, (ii) the benefits of the collaboration are greater than those of any solo alternatives, and (iii) all solo alternatives must be forsaken (risked) in order to collaborate. In the classic parable, I am hunting alone for hares when I spy a stag - which is much better food but which I cannot capture alone. You are in exactly the same situation, and so it is in both our interests to drop our pursuit of hares and collaborate to capture the stag and then share the spoils. (This general scenario can easily be extended to other foraging activities, including many gathering activities, such as procuring honey collaboratively.)

Human collaborative foraging first occurred, we hypothesize, in Stag Hunt type situations in which all participants had alternatives but anticipated an even greater benefit from successful capturing of the stag (see Alvard, in press). Although much of the foraging of contemporary hunter-gatherers is only loosely collaborative, this is very likely because modern foragers have the kinds of projectile weapons that enable individuals to be successful (from a safe distance) where previously only small groups of individuals working together could attain foraging success (and contemporary foragers also see themselves as part of a group, as in our Step 2 [see below], and so bring the bounty back to the home base for sharing). In stark contrast, nonhuman great apes – and so, by hypothesis, the last common ancestor - were and are almost exclusively individual foragers. Chimpanzees and bonobos may search for food in small social groups, but when they find food each individual procures and consumes it on its own (with sharing only under special circumstances). They do not extract or otherwise obtain food by working collaboratively with others, nor do they, as humans, bring food back to some central location to provision others.

The one potential exception is the group hunting of monkeys by some (but not all) groups of chimpanzees (Boesch & Boesch, 1989; Watts & Mitani, 2002). What happens prototypically is that a small party of male chimpanzees spies a red colobus monkey somewhat separated from its group, and they proceed to surround and capture it (normally one individual begins the chase and others scramble to the monkey's possible escape routes). One individual actually captures the monkey, but all participants usually end up getting at least some meat. Chimpanzee group hunting can be reasonably modeled as a Stag Hunt situation, since it is difficult for individuals to capture monkeys on their own, and they always have other, less exciting alternative foods potentially available.

If the many collaborative foraging activities of humans and the one collaborative foraging activity of great apes represent Stag Hunt type situations, we may compare humans and their nearest great ape relatives in terms of their proximate mechanisms, both cognitive and motivational, for operating in such situations. We may best do this by telling a very general evolutionary story (supported by comparative experimental data) about how humans developed new strategies to meet the three main challenges to Stag Hunt collaboration as an evolutionarily stable subsistence strategy:

- Sharing the Spoils: individuals had to find some way to divide the spoils at the end of the collaboration such that there was no destructive fighting, and such that everyone was incentivized for future stag hunting.
- Coordination: individuals had to find some way to make a confidence-inspiring "group decision" about whether to go for the stag, given that each of them had to relinquish their "hare in the hand" to do so.
- Temptations to Free Ride: individuals had to solve the problem that if there were more people present than were needed to capture the stag (but all could

eat), then everyone had an incentive to let the others do the hard and risky work of stag killing - resulting in inaction from everyone.

In their group hunting of monkeys, chimpanzees have ways of meeting all three of these challenges. But humans have come to meet them in some demonstrably different ways, using species-unique proximate mechanisms.

1.1. Sharing the Spoils

Chimpanzees, like most primates, are mostly herbivorous (and insectivorous). They forage in small social parties mainly for ripe fruit and some insects, consuming other vegetation as backup. When the party finds a patch of fruit, typically everyone gets some by scrambling, which works well because the fruit is at least moderately spread out in the tree or on the ground. If they encounter monopolizable food, the ensuing contest-competition will go to the dominant individual in typical mammalian fashion.

The consequences of this way of doing business for collaboration may be clearly seen in a recent experiment. Melis et al. (2006a) presented pairs of chimpanzees with out-of-reach food on a platform that could be obtained only if both individuals pulled simultaneously on the two ends of a rope. When there were two piles of food, one in front of each individual, the pair often collaborated successfully. However, when there was only one pile of food in the middle of the platform, pulling it in often resulted in the dominant individual monopolizing all of the food. This naturally demotivated the subordinate for future collaboration with this individual, and so cooperation fell apart over trials. Chimpanzees' predominant solution to food competition in general, namely, dominance, tends to destabilize collaborative foraging over time.

So why does not dominance undermine chimpanzees' group hunting of monkeys? The answer is twofold. First, dominant chimpanzees do not normally take small parcels of food away from subordinates who already have it in their grasp. So if the captor of the monkey is subordinate, he nevertheless is typically able to eat his fill. Second, even if the captor is dominant he cannot monopolize the carcass himself because it is too big. As with social carnivores like lions and wolves, trying to protect a large carcass with other hungry individuals approaching is a losing battle. After the kill, non-captors harass the captor (no matter his dominance) and obtain pieces of meat from the too-big-to-monopolize carcass, with those who harass most getting the most meat (Gilby, 2006). Although there is some favoritism in "meat sharing" toward coalitionary partners (Mitani & Watts, 2001), the most important factor in non-captors' obtaining of meat is, not surprisingly, dominance (Boesch, 1994).

Humans share their spoils differently. Contemporary hunter-gatherers routinely share the spoils of their collaborative foraging on the scene, without harrassment, and large packets of food are almost always brought back to some central location and shared with non-participants (Gurven, 2004). Different cultural groups may do this differently, and it may work differently with particular resources, but there are no human groups who behave like other great apes in simply scrambling for food competitively in most situations, with dominants taking all that they can regardless of others. And unlike great apes, humans actively provision their children with food for many years, with human children being well into their teens in most cases before they actually pull their own weight (Hill, 1993).

In experiments, humans are much more generous with food than are chimpanzees, and they expect their conspecifics to be more generous (even fair) as well. Thus, in economic games humans routinely take into account the needs and desires of others, whereas this is not the case for chimpanzees. For example, humans routinely give a significant portion of some windfall resource to an unknown individual in dictator games, whereas no one has ever performed a dictator game with chimpanzees because the outcome - that they would actively give none of their windfall to others - is already known. In ultimatum games, humans typically expect their playing partner to expect a reasonable offer (with "reasonable" depending on general cultural norms; Henrich et al., 2006), whereas chimpanzees in the ultimatum game seem not to take into account the needs or expectations of their playing partner at all (Jensen et al., 2007).

But it is not until the second step of our account (in Section 2) that we include such things as group-wide social norms of fairness and the like, and so for now a better representative of the human species would be children - before they have become fully normative beings. Nevertheless, even without internalized norms, human children are more generous with valued resources than are their great ape relatives. In one fairly direct comparison, both Silk et al. (2005) and Jensen et al. (2006) found that when pulling in food for themselves, chimpanzees did not care whether this also resulted in a companion getting food. In contrast, Brownell et al. (2009) found that even 2-year-old children - well before they self-govern through social norms - chose to pull food to themselves more often when that also meant food for their companion. Chimpanzees will in some situations help others gain access to food (Warneken et al., 2007; Melis et al., 2011), but only if the helper has no possibility of obtaining the food herself.

Perhaps of most importance for the current account, human children share the spoils after collaboration in species-unique ways. Thus, Warneken et al. (2011) presented pairs of 3-year-old children with the same task presented to chimpanzees by Melis et al. (2006a): a board they had to pull in together, with food either (i) pre-divided on the two ends of the board, or else (ii) clumped in the middle. Unlike the apes, children collaborated together readily in both of these situations. Even more striking, in a direct comparison of species Hamann et al. (2011) found that 3-year-old children shared resources more equitably if those resources resulted from their collaborative efforts, rather than from parallel work or no work at all, whereas chimpanzees "shared" (allowed the other to take) to the same degree (and infrequently) no matter how the spoils were produced (see also Melis, Schneider, & Tomasello, 2011).

How might we account for an evolutionary transition from the way that other great apes treat food to the way that humans treat food - especially after a collaboration? One especially plausible transitional context is scavenging. Thus, as the genus *Homo* was emerging some two million years ago, a global cooling and drying trend created an expansion of open environments and a radiation in terrestrial monkeys, who would have competed with *Homo* for many plant foods. Scavenging large carcasses killed by other animals would have been one possible response. Such scavenging would have required multiple participants, as other carnivores would be competing for those carcasses as well.

Individuals would be especially well suited for scavenging if they were tolerant of conspecifics co-feeding on a carcass with them. An important finding in this regard is that when experimenters pair together chimpanzee individuals who are especially tolerant with one another in the context of food (established by an independent food tolerance test) they are much more likely to collaborate successfully and share the spoils at the end than are intolerant partners (Melis et al., 2006a). And bonobos show both more tolerance around food and more cooperation in obtaining and sharing monopolizable food than do chimpanzees (Hare et al., 2007). These findings suggest that variation in tolerance around food among individuals of the last common ancestor to *Homo* and *Pan* might have served as the raw material on which natural selection worked on the way to a species that actively shared the spoils of collaboration (Hare & Tomasello, 2005).

It is also likely that at some point individuals who attempted to hog all of the food at a scavenged carcass would be actively repelled by others, and perhaps shunned in other ways as well - a first step toward what Boehm (2001) calls "counter-dominance". Chimpanzees already engage in social selection of collaborative partners, preferentially choosing a partner with whom they have had past success over one with whom they have previously had difficulties (Melis et al., 2006b). Scavenging *Homo* would thus have already had a tendency to avoid dominants who tried to monopolize the carcass. Moreover, a small coalition attacking a greedy dominant to drive him away would have been a simple extension from driving other species away from the carcass (and of course chimpanzees already form small social coalitions in intragroup conflicts). The outcome of socially selecting against dominants is of course that good cooperators get selected "for" by being chosen more often as collaborative partners.

As humans became ever more dependent on collaborative foraging - and so ever more interdependent with others in the social group - additional factors contributed to their tendency to share resources with others relatively generously and even fairly. But for now we are interested only in the early steps (perhaps in combination with cooperative breeding), and our proposal is that in the context of scavenging, the individuals who did best were those who (1) were tolerant of others peacefully co-feeding on the same carcass, and (2) did not attempt to hog the spoils and so be socially selected against by others for selfish behavior.

1.2. Coordination

Boesch and Boesch (1989) describe chimpanzees' group hunting of monkeys in very human-like terms, with participants having a shared goal and well-defined roles. Focusing on the chimpanzees of the Tai Forest (since in more open environments chimpanzees use more solo and less coordinated strategies), they posit that all of the chimpanzees have the shared goal of capturing the monkey. Then a 'driver' begins chasing a monkey, while 'blockers' prevent lines of escape, and an 'ambusher' attempts to make the kill. However, it is also possible that what the chimpanzees are doing is something less cooperative, that is, the initiating chimpanzee is attempting to capture the monkey for itself since the captor gets most meat (or else he knows from experience that once he initiates the chase a group kill will often ensue and he will get at least some meat), and then the others go to places where they expect to maximize their chances of capturing the fleeing monkey, which also increases the group's chances as an unintentional by-product (Tomasello et al. 2005; Tomasello, 2008).

It is not that each chimpanzee is scrambling for the monkey on its own ignoring the others. In deciding what to do, each participant takes into account the position of the others and their behavior, and how these might influence the monkey's flight. The coordination is therefore an emergent property generated by individual decision-making not aimed at that coordination. Thus, Melis et al. (2006b) found that in situations in which a chimpanzee could pull in a board with food by itself, that is what they did (in preference to opening a door for a potential partner). But if pulling in the board required two individuals, then they would either wait for their partner or even open a door for her to join. The chimpanzees were mainly interested in their own acquisition of food, but they understood when they needed a partner for success. Similarly, Bullinger et al. (in press a) and Rekers et al. (in press) found that when chimpanzees were given the choice to obtain food by collaborating with a partner or acting alone, they most often chose to act alone, whereas human children most often chose to collaborate.

Nevertheless, even though chimpanzees will go and open a door for a necessary partner, they do not actively communicate about the collaboration much or at all. In the wild, chimpanzees do vocalize their excitement at various points throughout the hunt. But chimpanzee vocalizations, as virtually all primate vocalizations, are hardwired to particular stimulus and motivational states; and so what is being expressed is general excitement (with the same vocalizations used when excited about other things) and not anything about the content of what is happening or what the vocalizer wants to happen. There are no reported vocalizations (or gestures) specifically associated with hunting or coordination. Indeed, in the laboratory, several investigators have reported a striking lack of communication among chimpanzees as they engage in collaborative tasks (e.g., Povinelli & O'Neil, 2000; Melis et al., 2009), including in tasks in which they had previously communicated with humans (Hirata & Fuwa, 2007).

This overall picture may be clearly seen in a recent experiment constructed as a Stag Hunt for pairs of chimpanzees (Bullinger et al., in press b). Each individual had access to a less preferred "hare" food, which she would lose for good if she left it. Then a highly preferred "stag" food appeared that required the pair to work together for access (which they knew from previous experience). Because of the risk involved, communicating with the partner, or at least checking on the partner before forsaking the hare in hand, would seem to be called for. But what chimpanzees did in this situation was almost always bolt for the stag (90% of the time when a partner was present) without communicating or checking, presumably optimistic that the partner would be coming also (leader-follower strategy). They did this even in a condition in which they could not see what the partner was doing unless they looked around a barrier (which they did not do). If an individual arrived at the stag first she sometimes banged on things to induce the other to join her; but there was no communication or systematic checking of the partner ahead of time as a way of coordinating their decisions.

Humans, in contrast, coordinate and communicate about their decision-making in such situations to form a joint goal. To form a joint goal, we must know together that each of us has the goal of working with the other (Bratman, 1992). Knowing together means engaging in some form of recursive mindreading (we each know that the other knows, etc.), which is the basic cognitive ability that enables humans to engage in all forms of joint and collective intentionality (Tomasello, 2008; 2009), including joint attention, common conceptual ground, and all "public" knowledge and activities. And once they have formed a joint goal, humans are committed to it. Thus, when their collaborative partner stops interacting with them, even 18-month-old infants expect her to be committed, and so they attempt in various ways to reengage her - as opposed to human-raised chimpanzees, who do not (Warneken et al., 2006). Slightly older children understand and respect their own commitment, such that they keep pursuing the joint goal until both partners have received their reward even if they have already received theirs (Hamann et al., in press) - which, again, is not true of chimpanzees (Greenberg et al., 2010). And when 3-year-olds need to break away from a joint commitment with a partner, they even "take leave" through some form of implicit or explicit communication - as a way of acknowledging and asking to be excused for breaking the commitment (Graefenhain et al., 2009).

Young children also understand the role of the partner in the collaborative activity in a way that chimpanzees do not, and they communicate about roles as well. Thus, when they are forced to switch roles in a collaborative activity, young children already know what to do from having observed their partner earlier from the "other side" of the collaboration - whereas chimpanzees seemingly do not (Tomasello & Carpenter, 2005). And even prelinguistic children communicate with others to help them play their role in a joint activity, for example, by using a pointing gesture to direct them to the part of an apparatus they should be acting on - whereas, once more, human-raised chimpanzees do not (Warneken et al., 2006; and of course human adults communicate about their collaboration with language). One possible explanation for this different understanding of the roles in the collaborative activity is that humans, but not chimpanzees, comprehend joint activities and their different roles from a "bird's eye view" in which all roles are interchangeable, that is, conceptualized in an agent-neutral manner in a single representational format. This conceptual organization enables everything from bi-directional linguistic conventions to social institutions with their publicly created joint goals and individual roles that can in principle be filled by anyone.

This brings us again to the evolutionary question. How did early humans move from a chimpanzee mode of initiating and coordinating Stag Hunt activities - based either on a leader-follower strategy or on a kind of naïve optimism about the other's actions - to the modern human mode in which individuals coordinate their decision-making through some kind of implicit or explicit communication, resulting in a joint commitment to follow through until everyone gets their reward, with a coordination of interchangeable, agent-neutral roles?

The main thing to note is that given the normal feeding ecology of chimpanzees, their approach to Stag Hunt situations makes imminently good sense - and indeed is successful. Their main food sources are fruits and other vegetation, and monkeys are an addition. A chimpanzee on its way to a fig tree is only sacrificing a small amount of time and energy to participate in an unsuccessful monkey hunt.[2] With humans, the hypothesis is that at some point their scavenging turned into active collaborative hunting and gathering (perhaps with the emergence of *Homo heidelbergensis* some 800k years ago; Dubreuil, 2010), with evidence for bringing large prey back to a home base from at least 400-200k years ago (Stiner et al., 2009). The key point in the transition from chimpanzees, from a psychological point of view, would have been when the decision-making became more challenging, and in particular when the risk became such that just optimistically leaving the hare in hand (as chimpanzees seemingly do) was no longer an effective strategy. That is to say, the situation was such that giving up the hare was no longer so cheap that one should just go for the stag without attempting to coordinate decisions with other potential hunters.

As in the case of sharing the spoils, social selection based on reputation almost certainly played a role in all of this as well - but in this case not for individuals who were tolerant around food and fair at sharing the spoils but rather for competent coordinators and communicators who would increase the likelihood of success. Clearly humans' skills of coordination and communication increased continuously after their initial emergence - from pointing and pantomiming to conventional languages - and the hypothesis is simply that better coordinators and communicators were chosen as collaborative partners more often. In general, as humans went from more passive scavenging to more active collaborative foraging they were faced with ever more challenging coordination situations and decisions, and this provided the selective context for the evolution of ever greater skills of coordination and communication.

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[2] This may help to explain the surprising fact that chimpanzees hunt more frequently for monkeys in the rainy season when their fruit and other options are actually *more* plentiful (perhaps because the cost of unsuccessful monkey hunting is lower; Watts & Mitani, 2002).

1.3. Temptations to Free Ride

In Stag Hunt situations with no excess of labor available (all individuals present are needed for success), free riding is not possible: if I don't participate then I (and everyone else) get nothing. The proposal is thus that the earliest manifestations of human collaborative foraging were not so vulnerable to free riding because they involved very small numbers of collaborators, each of whom believed their participation to be necessary. Interestingly, contemporary children seem to have virtually no interest in free riding, as participating in collaborations seems to be rewarding in itself (Graefenhain et al., 2009).

So how does it work in chimpanzee hunting of monkeys, when there are often excess participants around? As noted above, the main factor in acquiring meat in chimpanzee hunts is being the captor. But, in addition, Boesch (1994) reports that individuals get more meat when they are actually in the hunt than if they are either bystanders or latecomers to the party - suggesting the possibility that meat is divided based on participation. But bystanders still get plenty of meat (83% of bystanders in Tai get at least some meat) and they get more than latecomers. This suggests that the main variable in obtaining meat is proximity to the kill at the key moment, with the captor getting most, those in the immediate vicinity getting next most, and latecomers getting least – an hypothesis receiving strong support from a recent experiment (Melis et al., 2011). Boesch also reports that of the hunters who are not captors the one who obtains the most meat is the one who best anticipates the monkey's escape route - but they tend to be both close to the kill site and also older individuals who command more meat in general. Interestingly, in Boesch's (1994) similar analysis of the hunting of the Gombe chimpanzees, bystanders actually get more meat than hunters. So, overall, hunting chimpanzees would seem to have either no, or very poor, mechanisms for controlling free riders, leading Boesch (1994, p. 660) to ask: "Why do so many individuals cheat, and why are they so readily accepted by hunters?"

Another interesting situation is that the individual who begins chasing the monkey is not the one most likely to capture it (Boesch, 1994). This could easily undermine group action altogether, as each individual lags to avoid being the first chaser. But it does not, and this is instructive of the process. The key is that at least one individual would rather be the dispreferred first chaser than for there to be no hunt at all. That is, some individual must reason that if I don't act soon noone will get anything - and I would prefer to get something, even if it is less than maximal (and even a small amount of meat is valuable because it contains vital micro-nutrients; Tennie et al., 2009a). In game theory this is the Snowdrift situation, with as many equilibria as participants who reason in this way. Interestingly, in the Tai chimpanzees, it is most often youngsters who begin the chase, perhaps because they have yet to learn that the first chaser is disadvantaged (whereas the older individuals know this, and so lag a bit). But it also might be because youngsters are typically more impulsive, impatient, and risk-prone than are adults.

So what do humans do about free riders? The answer is of course social selection by means of reputation. Humans have evolved extremely sensitive "cheater detection" mechanisms of a type never observed in chimpanzees or other great apes (no studies have investigated apes' partner choice with respect to free riders) - which lead them not only to shun free riders but sometimes even to punish them (Cosmides, 1989). Because everyone knows this to be the case, individuals are very concerned that others not think them to be laggards, and so they have developed a concern for self-reputation, something also never observed in other great apes. Many experiments clearly demonstrate that humans' concern for their own reputation is an important incentive for cooperation in many situations in which free riding would otherwise be beneficial (Milinski et al., 2002). In general, to the degree that collaborative foraging becomes obligate for survival, a reputation as a good collaborative partner becomes obligate as well.

A mechanism related to reputation and self-reputation is punishment. So far we have simply assumed that individuals choose partners with good reputations and avoid those with bad reputations. But there is also the possibility of punishing those who do not cooperate (or rewarding those who do), presumably both to encourage their cooperation on the spot and also to improve their behavior for future collaborations - and indeed such punishment has been shown to be effective in helping to enforce cooperation in various economic games (Boyd, 2006). Humans sometimes even mete out third-party punishment against those harming others (when they themselves are not being harmed), whereas chimpanzees - even though they retaliate against those who harm them directly (Jensen et al., 2007b) - do not (Riedl et al., submitted)[3]. When humans are punishing a non-cooperator, they typically experience resentment or moral anger, which goes beyond normal anger because it seems "justified".

And so, lagging or free riding would not have been much of a problem for early humans foraging together in pairs or trios where the participation of all is necessary for success and where lack of participation would be easily noted and count against reputation. When the collaboration is obligate, the stakes are raised to the degree that there may be even competition for partners, and in this case a concern for self-reputation would be especially important. Note that by this point reputation means both (i) a more motivated collaborator who will not cheat by either monopolizing the food at or by lagging, and (ii) a more skillful collaborator who is better able to form joint goals and coordinate roles. What enables good collaborators to find one another is thus not reputation for altruism or anything else external, but simply reputation for being a good collaborator - which is, with actual partners and direct observers, impossible to fake.

1.4. Interdependence and Altruistic Helping

Helping one's partner during a mutualistic collaborative activity pays

[3] Chimpanzees sometimes intervene in the fights of others (so- called policing; Flack et al. 2006). But they are not in these interventions punishing particular individuals for bad behavior, but only attempting to keep a dangerous (for them) situation of conflict from escalating.

direct dividends. If my partner has dropped or broken his spear, it is in my interest to help him to find or repair it, as this will improve our chances for success toward our joint goal (and he has no incentive to now suddenly defect, as the mutualistic situation is still operative). Mutualistic collaboration thus provides a "safe" context within which basic tendencies to help others could evolve (cf. Silk, 2009). It is thus not surprising that when Ache foragers are hunting, they do such things for their partners as giving them weapons, clearing trails for them, carrying their child, repairing their weapon, instructing them in best techniques, and so forth (Hill, 2002). Interestingly, young children, but not chimpanzees, help others more readily in the context of collaborative activities than outside of such activities (Hamann et al., in press; Greenberg et al., 2010).

But humans help one another outside of collaborative activities as well. Indeed, in experimental settings infants as young as 14 months of age will help adults with all kinds of problems from fetching out-of-reach objects to opening doors to stacking books (Warneken & Tomasello, 2006; 2007). Perhaps surprisingly, chimpanzees also help conspecifics with their problems in some similar ways (Warneken et al., 2007; Melis et al., 2011). But humans would seem to do it much more frequently and in a much wider array of contexts, including actively sharing resources and information more freely (e.g., informing others of things helpfully and even teaching them things; see Warneken & Tomasello, 2009, for a review). Why might this be the case?

Our proposal is that obligate collaborative foraging produces interdependence among members of a group, and this interdependence makes it in my direct interest to help others who might be my future partners. If I can acquire food only with the help of a partner, then when potential partners are in trouble I should help them - even outside of any collaborative activity. The logic is exactly the same as Hamilton's equation for kin, as worked out by Roberts (2005) in his Stakeholder Model: I should sacrifice to help potential partners when:

$$sB > C$$

In this equation, as in Hamilton's, *B* represents ultimate reproductive benefits, and these must exceed costs, *C*, when the benefits are conditioned by the "stake", *s*, I have in the particular partner (analogous to Hamilton's coefficient of relatedness). The variable *s* in the case of collaborative foraging simply represents how important it is for me that an individual currently in trouble be alive and well and ready to collaborate with me in the future.[4] To be a bit fanciful, if a particular individual's survival will lead to me to be successful in foraging to the tune of 1.3 more offspring in the future (e.g., because it will help me to live longer), then it will pay for me to sacrifice for her to the tune of 1.2 fewer offspring for me in the future. The same logic holds for many other behaviors in social groups, of course, so that if an alarm caller benefits my reproductive fitness I should help her when needed. Clutton-Brock (2002) proposes a generalized version of this mechanism called group augmentation: if my prosperity depends on my social group (for defense against predators, etc.), then it is in my interest to keep them alive and prosperous as well.

The process is then a form of social selection: I help others who do things that benefit me (more than my help costs me). But the scenario we are proposing here is special. It is special because if I have a stake in an alarm caller and so help her, then what I am socially selected for is better alarm callers (who have keen perception, loud vocalizations, etc.). But when the target domain is collaboration, then what is being socially selected for is good collaborators - who are tolerant of others in co-feeding situations, skillful at coordination and communication, have a tendency to shun or punish free riders, help their partners, and so forth.

Of course this account still has a problem of free riding because one can lag on the helping: my highest preference is that someone else help my potential collaborative partner or alarm-calling groupmate so that I do not have to bear the

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[4] The process is thus similar to what has been called "pseudoreciprocity" (e.g., Bshary & Bergmüller, 2008) in which one individual "invests" in another, who does nothing contingent in return but just what she normally would do in such circumstances.

costs. But as Zahavi (2003) points out, the same is true of kin selection: it is in my interest to help my sibling because he shares my genes, but my first preference is that someone else help him so that I do not have to bear the costs. The point is not that interdependence as described by the stakeholder model solves the problem of altruism; but, using the same logic as kin selection, it changes the math because my selfish benefits depend on the well-being of selected others.

Obligate collaborative foraging thus creates a logic of interdependence, which leads to the selective helping of those who will be needed as collaborative partners in the future. It is noteworthy that whereas almost all other accounts of the evolution of human altruism rest on one or another form of reciprocity, reciprocity cannot explain uncontingent acts of altruistic helping. The current account, in contrast, does not depend on reciprocity because I am "repaid" for my altruistic acts not by reciprocated altruistic acts from others, but rather by their later mutualistic collaboration, which costs them nothing (actually benefits them). Indeed, it has recently been demonstrated experimentally that humans will actually compete with one another to be more altruistic so that observers will later choose them to engage in a mutualistic collaboration (Sylwester & Roberts, 2010).[5]

1.5. Summary

Bonobos, gorillas, and orangutans do not collaboratively forage at all. Only some chimpanzees do so and then in only one of their many foraging activities. And the data we have presented suggest that when chimpanzees do hunt in small groups for monkeys, they do this with cognitive and motivational mechanisms not specifically evolved for the task, that is, they somehow manage to be successful quite often in spite of their tendencies toward dominance in solving food disputes. In contrast, humans, as already evident in young children, have

[5] Note that if two thieves are totally interdependent – the first needs the second to pick the lock and the second needs the first to crack the safe – and this is the only way they can get resources for food, then when the police question them there is no Prisoner's Dilemma. Neither wants to be set free on his own while the other stays in jail because this would mean starvation.

evolved a suite of cognitive and motivational mechanisms for sharing food cooperatively, coordinating and communicating toward joint goals with complementary roles, and engaging in various kinds of reputation-based social selection (including a concern for self-reputation as a cooperator); what we have called skills and motivations for joint intentionality. They seem evolved for the task. Table 1 summarizes the basic mechanisms involved.

	APES/CHIMPANZEES	*HUMANS*
SHARE SPOILS	• dominance • harassment + reciprocity • partner choice	• cooperative food sharing • share more in collaboration • social selection against "hogs"
COORDINATION	• leader-follower (risk taking) • no coordination by communication	• joint goals & attention • agent-neutral roles • cooperative communication
SOCIAL SELECTION	• free riders not punished • dominance	• selection against free riders • third-party punishment • self-reputation
ALTRUISTIC HELPING	• helping • reciprocal sharing • no informing	• help more in collaboration • cooperative sharing • informing and teaching

Table 1. Basic mechanisms used by great apes and humans to solve the three main problems of Stag Hunt foraging (Step 1).

Our evolutionary story so far has been highly selective. As noted at the outset, we have backgrounded the important role of kinship, as humans evolved more stable reproductive bonds (resulting in an increase in male tolerance), which obviously played an important role in the attitudes of individuals toward one another in small groups (Chapais, 2008). Further in this context, humans also became cooperative breeders, regularly providing child care for offspring who were not their own, and this clearly would have affected emotions and motivations for collaboration and altruism as well (Hrdy, 2009). Most likely, both of these processes played a key role in the earliest stages of the story we are telling here as humans were becoming more tolerant with one another around food. But, as also argued at the outset, these kinds of processes, important as they are, would not help us to explain the more cognitive aspects of coordinating and communicating toward joint goals, nor would they explain humans' tendency to socially select others with regard to their cooperative behaviors. To explain these, we need not just prosocial tendencies, but joint intentional skills and motivations for various kinds of collaboration.

And so a big first step in the evolution of uniquely human cooperation is one in which the usual suspects - kin selection, sexual selection, direct reciprocity, and indirect reciprocity - play only minor roles. The heroes of our story are: (1) mutualistic collaboration and the logic of interdependence; and (2) social selection based on reputation as a good collaborator. But still, the collaboration we are talking about here was only small-scale and ad hoc, in the sense that it existed only during the collaboration itself; when the foraging trip was over, so was the special "we" it had engendered. There was still some way to go to get to human large-group cooperation and its complex conventions, norms, and institutions.

2. Second Step: Group-Mindedness

Small-scale obligate collaborative foraging would seem to be a stable form of cooperation: it is in the enlightened self-interest of individuals to collaborate well with others and to help their collaborative partners. But, apparently, at some point it was not stable, as evidenced by the fact that contemporary humans possess a whole other level of mechanisms for cooperation, including social conventions, norms (internalized into guilt and shame), and institutions, along with a strong in-group bias. Why did these become necessary?

We think there were two, essentially demographic, factors: population growth within groups, and competition between groups. These factors probably began playing a role with the emergence of behaviorally modern humans. Thus, Foley and Gamble (2009) argue and present evidence (mostly from palaeo- and modern genetics) that in the Middle Pleistocene hominin groups (characteristic of the first step of our story) had relatively small effective population sizes. In contrast, Hill (2009) argues and presents evidence that a transition to larger social groups with central place foraging – and comprising a hierarchical structure in which "bands" coalesce into "tribes" or "societies" - took place basically with modern humans and the advent of behavioral modernity (i.e., at the time of our second step). The result was two new sets of challenges to human cooperators:

- Large-Group Coordination: as groups became larger, at least partly in competition with other groups, individuals needed to be able to coordinate with relative strangers - while still knowing that they were from within the group (and so had the requisite skills and trustworthiness).
- Large-Group Social Selection: as groups became larger, again due partly to competition with other groups, incentives for cooperation diminished (each individual was less needed and reputational information was more difficult to obtain; Olson, 1965), and so free riding - and even active cheating - proliferated, and needed to be controlled.

With these large-group processes, we have pretty much left the domain of factors important in the lives of nonhuman great apes. But still, a comparison of humans' and great apes' proximate mechanisms for meeting these two challenges is instructive for the question of origins. Also instructive is the fact that human children do not participate in group-minded things such as social norms and institutions until some time after they have learned to collaborate effectively with others in concrete tasks – giving at least some indirect support to our hypothesized evolutionary sequence of collaboration before group-mindedness.

2.1. Large-Group Coordination: Cultural Practices and Group Identification

If collaboration is the horizontal dimension of human culture, as adults interact with one another for mutual benefit, then cultural transmission is its vertical dimension, as adults pass along things to children across generations. Cultural transmission was very likely an important part of human social life from the beginning of the genus *Homo*, as subsistence activities became more complex and the use of tools became more important. Being a good social learner was thus good for individual fitness, and indeed, even chimpanzees and orangutans socially learn from others in ways that create behavioral traditions that persist across generations (Whiten et al., 1999; van Schaik et al., 2003).

But when social groups become larger, and the target of social learning is collaborative activities in which each participant must have some skills and trustworthiness to be a good partner, a new set of issues arise. The problem for the individual is to know who has the requisite skills and trustworthiness, and, reciprocally, to make sure that others know that I myself possess these qualities. This is accomplished by individuals displaying various markers of group identity that indicate to all that I grew up in this tribe and share its cultural practices and values. Contemporary humans have many diverse ways of doing this, but one can imagine that the original ways were mainly behavioral: people who talk like me, prepare food like me, and net fish in the conventional way - i.e., those who share my cultural practices - are very likely members of my society. And I know that others are scrutinizing my cultural practices in this same manner.

Cultural practices are different from behavioral traditions because their practitioners understand them as "shared" in the group; that is, they understand them as conventional. We have all “agreed” to do them in a particular way, even though we all know that there are other ways we could do them. It is thus common ground in the society that everyone expects everyone else both to behave in the conventional way and to expect others to behave in the conventional way (Lewis, 1969). Conventions thus require some kind of recursive mindreading or common ground as the basis of the “agreement”, and this basic ability evolved initially, as argued above, as a skill for forming joint goals and joint attention in collaborative activities.[6] Our hypothesis is that because of this cognitive requirement other great apes do not have human-like conventions or cultural practices as such (only behavioral traditions; Tomasello, 2008; 2011).

Conventions generate the conformity characteristic of cultural practices because it is in the individual's interest to do things the way that others do them so that they can effectively coordinate - and this is especially important if one wishes to be able to coordinate with anyone in the larger society including strangers. I can immediately net fish effectively and efficiently with an in-group stranger if we both do it in the conventional way and can expect the partner to do it in the conventional way as well. In this connection, it is interesting that human children are much more conformist than are other great apes. Thus, two decades of experimental research have shown that human children have a much stronger tendency than do other apes to copy the actual actions they observe (Tennie et al., 2009b). This tendency is so strong that both adults and children conform to others even when they know better themselves (Asch, 1956; Haun & Tomasello, in press; see also Lyons et al., 2007, on children's tendency to "over-imitate"). Most directly, when individuals solve some task on their own and then see other individuals demonstrating a different solution, apes tend to go with their own experience over the demonstration (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008)[7], whereas human children follow the demonstration

In addition to pressure from growing population sizes to conform to cultural practices, competition with other groups helped to engender group identification. In the face of group competition, group life in general becomes one big collaborative activity, both directly for agonistic conflicts with competitor

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[6] Problems with the proper formulation of mutual knowledge and similar constructs are well-known. Here we simply adopt the terminology of Clark (1996), *common ground*, to indicate the various forms of joint attention, mutual expectations, mutual knowledge, etc.

[7] Whiten et al. (2005) claimed that in their study individuals of a chimpanzee group shifted their problem-solving strategy as a result of observing demonstrators. A close inspection of the data, however, shows that this was true of only one individual. Moreover, a subsequent study with a different chimpanzee group failed to replicate this result (Hopper et al., 2007).

groups and indirectly in competing for resources with competitors in the same geographical area. To compete, the society as a whole - especially as population increased and there was increasing division of labor - had to scale up its small-scale collaboration to form collective, society-wide goals, plans, and collective knowledge of things in the face of outside threats. And individuals again had to help their collaborative partners for these group enterprises - who at this point comprised essentially everyone in the society including some strangers.

Under these conditions - within-group population growth and between-group competition - group identification thus became critical. Group identification may seem a fuzzy concept, but many phenomena confirm its reality, most especially, the many in-group biases that modern humans show (helping in-group more than out-group members, caring more about reputation with in-group rather than out-group members, etc.). Even more striking, people feel collective guilt, pride, or shame when some member of their group does something especially praiseworthy or blameworthy - as if they themselves had done it (see Bennet & Sani, 2008, for this phenomenon in young children). Although the process may not be so well understood, the idea is that group identification is a scaled up version of the "we" intentionality that small-scale groups of foragers might have experienced previously as they hunted or gathered collaboratively toward a joint goal. "We" are all in this together, and are interdependent with one another, as we compete for food with the barbarians from across the river. This psychological attitude may be called group-mindedness - underlain by skills and motivations of not just joint intentionality with other individuals in the moment, but of collective intentionality with the society as a whole (Tomasello & Rakoczy, 2003).[8]

As far as we know, great apes do not have this same kind of group identity

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[8] Interestingly, social psychologists often distinguish two broad types of group formation in humans: *interpersonal interdependence* (corresponding to our small-group interdependence) and *shared identity* (corresponding to our large-group group-mindedness) (e.g., Lickel et al., 2007).

or group-mindedness. Chimpanzees live in spatially segregated groups, and are hostile toward chimpanzee strangers they meet on their borders. But this hostility is not, as far as we know, directed at other groups qua groups, based on their different appearance or behavioral practices.

2.2. Large-Group Social Selection: Social Norms and Institutions

Cultural practices are thus conventionalizations (standardizations) of the small-scale collaborative (and other) activities of Step 1 humans. Similarly, the acts of social selection by Step 1 humans were also conventionalized, leading, at Step 2, to social norms. Social norms are conventionalizations (standardizations) of the specific acts of social judgment that Step 1 individuals meted out to collaborative partners. Social norms are mutual expectations in common ground that people behave in certain ways, where the expectations are not just statistical but rather normative, as in you are *expected* to do your part (or else!).

Social norms have two key aspects. First is their force. Social norms have force over human behavior because, first of all, individuals know that to participate effectively in the collaborative activities of the group they must conform to the group's ways of doing things. Even young children enter new situations in their culture looking for "What am I supposed to do here? How do I do it?" (Kalish, 1998). In addition, of course, individuals do not want to suffer the consequences of norm violations in the form of shunning or punishment. These punitive aspects of social selection were already a part of collaborative activities at Step 1 of our story, but now, with their conventionalization, everyone knows with everyone else in common ground that conforming to cultural practices and social norms is necessary for group coordination - so that group members may view nonconformity in general as potentially harmful to group life in general. Moreover, if conforming to social norms also displays my group identity (which again we all know in common ground) my nonconformity expresses my disdain for the opinion of this group and for being considered a member of this group -

which makes me potentially dangerous.

Social norms can thus channel human behavior quite strongly in certain directions. The theoretical problem is that social norms can, in principle, channel human behavior in any direction, including group detrimental directions (Boyd, 2006). But this potential multi-directionality is only a problem if we envision social norms emerging in a vacuum. In our view, because of humans' already existing cooperative lifeways and interdependence as evolved in Step 1, social norms could not have emerged as directionally arbitrary, but only as encouraging collaboration and helping and discouraging their opposites - since, to repeat, social norms are nothing more than conventionalizations of the more particular acts of social selection for cooperative behavior (and against uncooperative behavior) of Step 1 individuals. Under conditions of group competition, social norms may be scaled up to the level of societal life in general.

The second key aspect of social norms is their generality. They are general, first, because they imply an objective standard against which an individual's behavior is evaluated and judged. These objective standards come from the fact that we all know in common ground how the different roles in particular cultural practices need to be performed for everyone to reap the anticipated benefit. Thus, if it is common ground in the group that when collecting honey the person smoking out the bees must do it in this particular way, and that if she does not we will all go home empty-handed, then everyone's behavior may be evaluated relative to this mutually known behavioral standard. Social norms are general, second, because they emanate not from individual opinion but from group opinion. Thus, if dominance is not an important part of the social interaction of the beings we are talking about here, then the punishment of the laggard needs to be by the group as a whole - so that when an individual enforces a social norm, she is doing so, in effect, as an emissary of the group as a whole (with even further objectification of the norm coming if the enforcer is supposedly a representative of a deity). The third source of generality of social norms is that the group disapproval involved is aimed in an agent-neutral way at, in principle, all individuals equally (including the self), that is, all who know with us in common ground the social norm and identify with our group's lifeways. Social norms are thus group expectations and judgments, with respect to group-known standards, that all group members mutually expect one another to respect.[9]

It is thus easy to see why people follow social norms - following social norms coordinates their behavior with the normative expectations of the group so as to collaborate better and avoid punishment and/or shunning. But the reason why people enforce social norms is not as straightforward. One reason is again a natural tendency to want to help and protect one's collaborative partners and, in the spirit of group-mindedness, the smooth functioning of the group. When we enter into a joint commitment to a social norm, group-minded thinking means that we commit not only to follow it but to see that others do too - for the benefit both of ourselves as well as those with whom we are interdependent (Gilbert, 1989). Thus, when 3-year-old children observe someone doing something that violates a previously established conventional norm, they often object, using normative language about what people *should* or *ought* to be doing (Rakoczy et al., 2008). Non-conformists are not doing things the way that "we" in this group do them, and this is, in a sense, a threat to our group.

Nevertheless, there is still the problem that punishing others on behalf of the group is costly and risky, and so there is the problem of free riding: why not let someone else do it? One solution would be to punish those who do not punish others as they should. This of course leads to an infinite regress if followed to its logical conclusion: individuals punishing non-punishers of non-punishers and so forth. And this is where social norms help: recent mathematical models show that when it is a group that is punishing, costs to the individual punisher may be negligible (Boyd et al., 2010). Another part of the solution is that we do not

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[9] The common ground assumption exempts from the force of our social norms individuals from another social group, or young children or mentally incompetent persons.

sanction people who fail to enforce norms in the same way that we sanction norm violators themselves. If you see me trying to steal some honey, you will either try to stop me or punish me. But if a third person watches you not trying to stop me or punish me, her attitude toward you, the non-enforcer, while negative, is not nearly so severe - and may not call for punishment at all. In the model of Ellickson (2001) we punish norm violators, but we simply avoid or shun non-punishers, which is potentially cost free (a mathematical treatment of the problem that goes in this general direction is presented by Panchanathan & Boyd, 2004).

Moreover, in practice enforcing social norms is mostly not necessary because individuals have already internalized them and naturally want to conform to them. And if individuals do violate a norm, they often punish themselves. Thus, if, in a moment of weakness, I take some honey that is needed by others, I will very likely feel guilty. The feeling of guilt is a kind of self-punishment that functions to prevent me from doing it again in the future, lessening the chances of actual punishment (or shunning) from others. In addition, displaying guilt to others, if caught, signals that I know the norm, that I know I should have followed it, and that I am punishing myself for its violation already (hopefully evoking your empathy) - which all means that I am indeed a cooperative group member and norm-follower who just had a momentary lapse (see Vaish et al., in press, for evidence that even young children prefer individuals who display guilt for their transgressions). Shame is not bound up with harm in the same way as guilt, but it is also a form of self-punishment (Fessler, 2004, emphasizes its appeasement function). I am ashamed that I wore the wrong clothing to the wedding, and my blushing displays that I know the norm and that I should have followed it, so you don't have to shun or punish me, and you can trust me to do better in the future.

Guilt, shame, and pride are thus internalized versions of the kind of moral indignation and approbation that humans mete out to others who violate social norms. These norm-related emotions thus demonstrate with special clarity that the judgment being made is not my personal feeling about things but rather the group's. I am sanctioning myself or praising myself as an emissary of the group. I stole the honey because I wanted it, and I still like having it, but I feel guilty. I, as a representative of the group's values, am judging myself, as an individual, negatively. It is almost certainly the case that the individuals of no other animal species judge and evaluate themselves in this way. And, as noted above, collective guilt and pride for the group (based on the behavior of individuals as representatives of the group) are perforce uniquely human as well.

Pretty much all of the cooperative mechanisms characteristic of humans at this second step in our evolutionary story come together in the creation of social institutions. Social institutions are collaborative cultural practices with joint goals and standardized roles, with social norms governing how rewards are dispensed, how cheaters and free riders are treated, etc. What is new about institutions is that they create new statuses for individuals playing particular roles that everyone must respect; for example, we give individuals the rights and obligations to be group 'chief', and we give 'police' the rights and obligations necessary to keep within-group peace. These new statuses exist because and only because everyone agrees in common ground that they do; and because institutions are especially clearly public, no one may ignore the new statuses by pleading ignorance of them (Chwe, 2003). These status functions (as Searle, 1995, calls them) are essentially entitlements: the group has, in essence, agreed that an individual can and indeed should do certain specified things immune from punishment via "normal" social norms. These statuses are typically symbolically marked with all kinds of official markers, and their ontological status is prefigured ontogenetically in young children pretending socially that, for example, this stick is a bird that can fly through the air as it pleases (Rakoczy & Tomasello, 2007).

2.3. Summary

The dynamics of small-scale collaboration worked fine for foraging in dyads and triads of the moment. But as groups became larger, eventually turning into tribal societies, and groups started competing with one another for resources, new challenges to cooperation arose. The solution was a suite of new proximate mechanisms that we may summarize with the term "group-mindedness". Behavioral traditions were conventionalized into cultural practices that everyone knew and that everyone expected everyone else to know and conform to, which facilitated individuals' coordination with in-group strangers. Social selection was conventionalized into group-wide social norms, which were also part of the common ground of the group, as was the group-wide obligation to enforce these norms. People used conformity to the cultural practices and social norms of the society as markers of group identity, and everyone favored and trusted members of their own society over others, especially as group competition heightened. The result was a new kind of interdependence and group-mindedness that went well beyond the joint intentionality of small-scale cooperation to a kind of collective intentionality at the level of the entire societal, that is, cultural, group (Tomasello & Rakoczy, 2003). Interestingly and importantly, young children do not begin to show this kind of group-mindedness and collective intentionality – in particular they do not enforce social norms on others – until after three years of age, which is considerably after they are capable of collaborating with other individuals toward joint goals as in Step 1 of our story (Rakoczy et al., 2008).

Cultural group selection may have played an important role at this point as well, as some groups created cultural practices, norms, and institutions that enabled them to collaborate better among themselves and so to outcompete other groups. But, as noted at the outset, cultural group selection explains why the particular social norms and institutions of particular cultural groups prevailed, and this assumes species-universal skills and motivations for creating social norms and institutions in the first place. We thus view cultural group selection as a critically important component in the process leading to modern human cooperation in large-scale societies, but only fairly late in the process, that is, after our second step in which human groups began their truly cultural life in larger societies. In any case, a summary of the specific proximate mechanisms and group processes involved in Step 2 of our account, and some of their possible evolutionary precursors in other great apes, is presented in Table 2.

	Apes/Chimpanzees	*Humans*
Large-group Coordination	• behavioral traditions • social learning • hostility to strangers	• cultural practices • teaching & conformity • group markers/identification • institutions
Large-group Social Selection	• retaliation, intervention • general social emotions for affiliation, retaliation, etc.	• self-reputation • social norms • norm-related emotions
Cultural Group Selection	• conformity not strong enough for coherent cultural groups	• selection of best functioning (most cooperative) groups

Table 2. Basic mechanisms used by humans (plus ape precursors) to solve the main problems of cooperative social life in large cultural groups (Step 2).

3. Conclusion

Modern theories of the evolution of human cooperation tend to focus either on small-scale cooperation early in human evolution or else on group-level cooperation later in the process with the advent of modern humans (or even later with agriculture). We believe, however, that the full story will require an account that incorporates both of these levels and evolutionary periods.

Small-group collaboration, in our account, is not solely about kinship and reciprocity, as in most accounts, though these undoubtedly played some role. Kinship and reciprocity are important in the lives of almost all primates, and so if they were the whole story, it is hard to see how humans came to their distinctive lifeways and social organization. Kinship and reciprocity do not get you culture.

Instead, we have hypothesized a change of ecology that led humans to an interdependent lifestyle, especially collaborative foraging, which resulted in the evolution of new skills and motivations for collaborating with others (joint intentionality) and which gave individuals special incentives for helping their partners altruistically as well. The emergence of more stable reproductive bonds and cooperative breeding undoubtedly played important roles in the emotional-motivational side of things at this early period as well, but contrary to what is implied by Burkhardt and van Schaik (2010), we do not believe that if chimpanzees became cooperative breeders human-like social-cognitive skills and shared intentionality would automatically result. What is needed in addition is new cognitive challenges such as those presented by collaborative foraging: the need to coordinate with others toward joint goals, the need to master with others complex skills and technologies, the need to communicate these skills and technologies to others within and across generations. In our view, cooperative childcare fits in very well with a lifestyle of collaborative foraging, and so the cooperative breeding and cooperative foraging accounts go very well together.

Group-level cooperation was then built upon the cognitive and motivational foundations of small-scale collaboration. Creating cultural conventions, norms, and institutions at the level of the social group as a whole requires a new way of thinking in which there is a "we" that constitutes not just my current partners in a collaborative enterprise, but all of us in this society. This new way of thinking – that we are a "we" - very likely evolved in response to group competition, as each group had to "circle its wagons". Group-mindedness thus relies on a kind of collective intentionality in which all members of the group participate, both following and enforcing the norms that define the group and stabilize its cooperative activities. At this point, cultural group selection undoubtedly played an important role as well. But it could only play that role after humans had evolved the kind of group-mindedness that is the mark of human cultural organization in the first place. Thus, cultural group selection cannot help us much with the cognitive dimension of human collaboration - which at this level means the creation of cultural conventions, norms, and institutions - which are the targets of cultural group selection not its creations.

And so, for us, it is all about the evolution of a distinctively new, un-chimp-like lifestyle that required both emotional-motivational and cognitive adaptations. The key ecological change was one that made individual human beings interdependent with one another for subsistence, which led naturally to helping those on whom one was dependent. This required the development of cognitive skills for putting one's head together with others in acts of mutualistic collaboration and communication. It also required individuals suppressing certain selfish tendencies, for example, for hogging all the spoils or for free riding on the efforts of others. The ability to suppress selfishness resulted, we would argue, from another aspect of the logic of interdependence, social selection, in which there arises a kind of market for collaborative partners such that anyone with a poor reputation will be avoided. In order to be chosen one needs to appear to others to be a good partner, and the best way to do that is to actually be a good partner - which means good cognitive skills for coordination and communication, sharing the spoils peacefully with others, shunning and punishing non-cooperators, concerns for self-reputation as a cooperator, and so forth. This logic of interdependence and resulting social selection scales up to the level of the whole society, if all of its members are interdependent because they are in competition with other groups and so have become group-minded.

This account is of course speculative. Ethnographies of modern-day foragers may not be representative of the earlier periods in human evolution in which we are interested, and the paleoanthropological record is far from definitive on any of the important issues. We have thus supplemented these traditional anthropological forms of evidence with comparative experimental data on similarities and differences in the skills and motivations for cooperation between contemporary human children and other great apes. Here the data are quite clear that contemporary humans have some specific skills and motivations for collaboration and cooperative communication not possessed by other great apes, at least not in the same way. And importantly, these can be theoretically connected to the specific challenges presented by collaborative foraging – as represented by the Stag Hunt from game theory – which provides further evidence for collaborative foraging as a key context for the evolution of uniquely human skills and motivations for cooperation and shared intentionality.

In any case, what the current account makes abundantly clear is just how difficult it is to establish and maintain cooperation in complex social organisms. Humans have all kinds of species-unique skills and motivations specifically designed to support cooperation, but still we are very, very far from perfect cooperators. Cooperation is really difficult.

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