

Constructing the Cooperative Niche

Kim Sterelny

Abstract Humans contrast with their great ape relatives in many ways, but one of the most striking is our richly cooperative social lives. The explanation of this difference is complex and multi-factorial. But this paper argues that one central element is niche construction. Hominins are inveterate and extensive niche constructors. Individually and collectively, we have deeply affected our physical and biological environment, and have used technology to filter and transform the selective effects of the changed physical and biology worlds in which we have lived. But members of our lineage have not just acted on physical and biological environments; they have organised their informational environment too. Not just their own, but that of the next generation. While intensive and active teaching is probably a recent phenomenon, teaching itself is not. Furthermore, adults structure the learning environment of the next generation in many other ways: by acting as models of adult life; by providing supervised, safer environments; by providing toys, tools and props that structure and support trial and error learning. So the skills, values, ideas, information, and expected modes of social interaction and behaviour are made accessible to the next generation. This happens in circumstances which have often been adapted to enhance learning. The main theme of this paper is to show that humans cooperate more than other great apes largely because they reconstruct their environment more than other great apes, and one aspect of that reconstruction has been to make a world in which cooperation could survive and expand.

K. Sterelny (✉)

School of Philosophy, Australian National University, Acton, Australia
e-mail: kim.sterelny@anu.edu.au

1 A Puzzling Pattern

The hominin lineage diverged from its *pan* sister group six million years or so ago (Klein 2009a), and for the first half of this period there is little evidence that hominin social life and cognitive capacity varied greatly from great ape sister clades. But by about four million years ago, some hominin species were obligately bipedal (Klein 2009b), and by 3.5 million years ago, we begin to see evidence of increased tool use and a shift to a richer and more meat-based diet (McPherron et al. 2010). The Oldowan lithic industry dates from about 2.3 million years ago (Foley and Lahr 2003), and by then there are clear signs of a major change, with habilines showing a modest increases in relative brain size, reduced teeth, jaws and guts. Our ancestors were changing. Over the next two million years the basic parameters that characterise late hominins evolved: larger brains (especially the neocortex and cerebellum); a longer life span, including both a long period of juvenile dependency and (with women) an intriguingly long period of active competence after menopause; large body size with quite modest sexual dimorphism. Hominins became increasingly technologically adept, with the Acheulian stone industry establishing at about 1.7 mya; fire from perhaps 800 kya; and complex, multi-stage stone tool techniques from perhaps 300 kya (Foley and Gamble 2009). Hominins spread ecologically and geographically. As these ecological and technological changes emerged, hominins also evolved minds and social lives that were very different from those of other great apes.

It is very difficult to specify the changes that lead to the complex and cooperative social lives of late hominins. There is, for example, nothing like consensus on the dates of emergence of language, or of paternal investment in children. That said, it is clear that one change was the evolution of a heavy (ultimately, very heavy) dependence on cooperation, including informational cooperation in social learning and teaching. Great apes will cooperate, and will act prosocially in minor ways without any (obvious) expectation of return benefit. But unlike humans, they appear to be largely blind to one another's informational needs (Warneken et al. 2007; Warneken and Tomasello 2009). Despite these uncertainties, I think it's clear that expanded hominin cooperation has deep roots, dating at least to the erectines (about 1.7 mya) and quite likely to the habilines 2.3 mya. Sarah Hrdy and Kristin Hawkes have argued convincingly that erectine babies and infants were so expensive that erectine life history would not be viable without significant reproductive cooperation (Burkart et al. 2009; Hawkes 2003; Hrdy 2009). It is equally clear that the shift to a meat-based diet depended on ecological cooperation. Hunting large game with short-range, low velocity weapons at acceptable levels of risk depends on cooperation; and hominins have been hunting large game at least since 400 kya and almost certainly much longer (Stiner 2002).

In other work, I have defended a three-stage model of the rise of cooperation in hominin social life (Sterelny 2013a, b; Sterelny forthcoming). The first stage is the transition from the hierarchical and individual world of great apes (for the most part, chimps and other great apes forage individualistically, consuming as

they go) to a world of mutualistic, egalitarian, cooperative foragers. Collective defence, collective hunting, and power scavenging are profitable mutualisms: the rewards of cooperation are produced collectively, but they are divided and enjoyed at the point of production (Tomasello et al. 2012). Mutualism does not depend on mutual tracking and policing over time, and so it is less cognitively and socially demanding than forms of cooperation that depend on reciprocation over time. Erectines were probably mutualist foragers; their larger-brained, large-game hunting successors, the heidelbergians, almost certainly were. Reciprocation-based cooperation ultimately became a central form of forager cooperation, as some mix of technological advance and ecological necessity drove an expansion of the range of resources harvested, an increase in specialization, and a shift to a more dispersed social world. This is my second stage of the evolution of cooperation, and I argue that the emergence of archaeological signals of ritual and ideology between about 120 and 75 kya is an indirect signal of forager economies dependent on reciprocation-based cooperation—it is a sign of the increased conflict risk and cognitive load of that form of cooperation.¹ The final stage is much more recent. Beginning with the Pleistocene-Holocene transition, about 10 kya, many human societies became more sedentary, more complex, and less egalitarian. There was a significant spike in intergroup violence (Seabright 2010). Despite the erosion of face-to-face mechanisms of trust, in many of these societies the social contract survived, and major problems of collective action were solved (Bogucki 1999; Flannery and Marcus 2012). Large scale, perhaps even cross-generation, cooperation had arrived.

I have argued that this trajectory has been driven by positive feedback, for at each stage in the evolution of hominin social life there were cooperation profits to be had, just an innovation or two away. The human career is very largely a case study in the profit of cooperation. Hominins began as a minor player in a very rich East African fauna. But our lineage speciated, invaded most terrestrial ecologies, dispersed (even in some earlier forms) over much of the old world, and vastly expanded its total population. Perhaps the hominin cooperation profile is not the whole explanation of that difference, but it is surely central to it. I do not intend to repeat my account of this grand narrative in this paper. Rather, my project here is to identify the resources we need to explain this social revolution and its consequences, and to make explicit the evolutionary mechanisms that underlie it. Like other evolutionary theorists, I see cooperation as puzzling and problematic, but not just because it is hard to understand why cooperation is not undermined by free-riding. Rather, it is because we cannot see cooperation as a feature of individual phenotypes evolving in response to environmental pressure; it is not like salt tolerance in

¹There is a rich archaeological literature on “behavioral modernity,” i.e., on the archaeological signs that ancient foragers resemble those known from ethnography. An important issue is the fact that these signs are about 100,000 years younger than our species (d’Errico 2003; Henshilwood and Marean 2003; Nowell 2010; Sterelny 2011). I interpret many of these signs of modernity as signs that a reciprocation-based economy is replacing a mutualistic economy.

Australian plants, or the sexual dimorphism of many Australian parrots. To explain cooperation, we need to explain the co-construction of individual phenotypes, social structures, and selective environments. In the next section, I identify some of the core cognitive, technological, morphological, and environmental preconditions of the cooperation transition, and sketch some of the ways in which the evolution of cooperation interacts with these enabling factors, leveraging further change. These levers are center stage in Sect. 3. In Sect. 4, I discuss the upshot, showing how these interactions illuminate some puzzling features of human cognition and social life.

2 Cooperation: The Business Plan

In 2003, building on the work of Richard Lewontin, John Odling-Smee, Kevin Laland, and Marcus Feldman published their manifesto on niche construction (Odling-Smee et al. 2003). That work had many threads, but one was to insist that the adaptive fit between organism and environment often depends on organisms, individually or collectively, modifying their environment, not just organisms responding to their environment. This chapter sees hominin cooperation as a particularly important example of this two-way interplay between organisms and environments. Cooperation powers niche construction. But niche construction powers cooperation too, and identifying those links will be a major theme of this chapter. More specifically, to explain cooperation in the hominin lineage, and to explain the contrast between the hominins and the great apes, we have to identify:

- (a) the potential profits cooperation can generate;
- (b) the investment needed to realize those profits; in this case, the cognitive, technical, and social prerequisites of specific forms of cooperation, and the processes by which those prerequisites came to be in place;
- (c) the policing mechanisms that ensure that the profits are not distributed in ways that destabilize cooperation.

These factors will not be constant over the three pulses that characterise the hominin experiment in cooperation: the profit-investment-policing profile of the very large brained, highly social hominins of the last half million years is likely to be very different from that of habilenes or early erectines.

2.1 Profits

As noted above, hominins diverged from the great apes about six million years ago. Orangutans and gorillas, with their dietary specialization, may not be just a social or technical innovation or two away from profitable collective foraging or defence. There are few economies of scale in browsing and fruit-eating, and these are formidable animals living in deep cover. Their ancestors were probably not at

high predation risk. In the typical habitats of these great apes, the seasonal footprint is muted, and the resources they target are abundant, though individually of low value. So these animals do not have to manage risk in the way those that target high value, but rare and scattered resources do. As the classic vampire bat studies show, risk management often rewards cooperation (Wilkinson 1990).

For similar reasons, there is relatively little pressure on these vegetarian great apes for active information-sharing. Gorillas and orangutans experience great botanical diversity, and their young need to learn to identify and exploit edible plants (plants often do not want to be eaten, and protect themselves with spines and thorns) (Byrne 1995, 2000, 2004). But simple, passive social learning probably suffices: young orangutans travel with their mothers, and if her interests and acts are especially salient and interesting to her young, that adaptive bias in trial and error learning probably suffices. There is not much need for active teaching, nor for information sharing and coordination between adults. There are no fruit in Borneo jungles that can be harvested only by orangutans acting together. So perhaps it is no surprise that sustained and active cooperation is not the default for great apes: it needs special explanation.

By contrast, early hominins were probably generalist omnivores living in variable environments (Klein 2009b). In most circumstances, for such animals, in such environments, ecological cooperation is potentially profitable, because collective action, specialization and the division of labor, and cooperative risk management, will all deliver to agents more usable resources at less risk—so long as they can coordinate their activities effectively. So the basic ecological difference between woodland omnivores and forest vegetarians explains why the forest vegetarians never experienced cooperation take-off. However, the *pan* species, like our ancestors, are generalist omnivores. Yet in chimps and bonobos cooperation is limited and (at least in chimps) not very stable. Males form coalitions both to promote their political interest and in defending and extending their territory in conflict with other bands. Males also hunt collectively, though perhaps not cooperatively. So there is some limited ecological cooperation, but almost no informational or reproductive cooperation (de Waal 2008; de Waal and Suchak 2010). So while the basic ecological difference between deep forest herbivores and early hominins might explain the cooperation differences in those lineages, we need an explanation of why the *pan* lineage did not experience cooperation lift-off.

There are some plausible suggestions: (i) chimps, especially males, are extremely strong and dangerous, and hence predation pressure did not select for collective defence, an important early form of cooperation; (ii) early hominins lived in more open habitat, and for that reason, were under stronger selection for collective defense (Foley 1995); (iii) cooperation is linked to bipedality, a morphological and ecological change with profound social and cognitive consequences. Bipedality is important for at least three reasons: first, it frees the hands from the demands of locomotion; second, it indicates a shift to larger and less tree-dominated territories, with their opportunities and dangers; third, it forced our ancestors to sleep on the ground, thus making them more vulnerable to predators at night. If bipedal locomotion was linked to a shift to woodland and grassland environments, it also

exposed hominins to predation, especially if that was coupled with less capacity to shelter in those trees that were available. So this change is a potential cooperation trigger both because fully bipedal apes must sleep on the ground (the predation-cooperation connection again) and because bipedal apes can evolve the capacity to use very simple weapons, which as we will see, may have reduced the costs of controlling defection and free-riding. The problem of understanding the initial divergence of the hominins is real, but because there are a number of plausible scenarios, not because there are none.

So in summary, and focusing on the earliest stages of hominin cooperation take-off, cooperation profits were probably more readily available to our lineage; habitat shifts and phenotype changes brought the first of those profits within, or close to, existing phenotypic variation. As soon as hominins acquired very rudimentary weapons (sticks as clubs or for jabbing; stones as missiles), collective defense and power scavenging opportunities open up. These forms of collective action depend only on the ability to monitor one another's behavior: mobwork is enough to secure some important benefits of cooperation. However, once mobwork became an enduring and important feature of hominin lives, that cooperative foraging practice selected for the expansion of capacities to communicate and coordinate. Hunting and power scavenging required some capacities to share information: in coordination; perhaps in planning; perhaps in recruitment.²

Changes in hominin phenotypes then open up new potential cooperation profits. Sarah Hrdy, Kristin Hawkes, and their colleagues have argued that reproductive cooperation is an important, foundational form of human cooperation, and its profit depends largely on human life history (Hawkes 2003; Hawkes et al. 1998; Hrdy 2009). Cooperation is most likely to evolve if help is cheap to give but very valuable to receive, and with humans, reproductive cooperation sometimes has that fortunate asymmetry. Hominins have long been bipedal, and perhaps by the habilines (about 2.3 mya) and certainly by the erectines (1.7 mya), the characteristics that make sapiens children so expensive had begun to emerge. Ancient human mothers were delivering large-brained, hyper-dependent babies, babies that could not even cling on to their mother. Birth itself was physically challenging; infants were immobile compared to adult range sizes; children were dependent significantly longer than their great ape equivalents. Some forms of aid are quite expensive—actively provisioning children; carrying them significant distances—and help of this kind probably initially depended (and largely continues to depend) on kin selection. But many important forms of help are quite cheap: it costs little to offer a birthing mother help, simple care, and protection; to keep an eye on children for an hour or two at a base camp while she forages (especially if you are already keeping an eye on your own); to carry an infant for a few minutes while the mother attends to some urgent task. If this help comes from near-adult girls in the group, those girls gain valuable experience in return.

²If the group did not forage as a single unit, those who found a major kill or killing opportunity would need to recruit others; power scavenging offers large economies of scale.

Let's briefly step back from detailed conjecture to expose the explanatory strategy: identify significant cooperation profits available to an omnivorous, open-range, bipedal great ape, and show how the exploitation of these profits leads to further changes, both in individual phenotype and environment. These changes establish pull-factors that select for further cooperation, and further phenotypic and environmental change. The strategy, then, is to show how a positive feedback loop is established, and why it was stable over three million years or so.

2.2 *Investment*

It is one thing for there to be cooperation profits in the vicinity, another to be able to exploit them. The opportunities must be recognized; they must be salient to the agents. Cooperative action must be coordinated. Even when agents cooperate to lower risk, by sharing their individual successes to reduce the footprint of luck, or to exploit complementary resources, they depend not just on trust but on coordination: minimally, where and when they will meet to share and exchange. Some forms of profitable collective action require only minimal coordination—that agents assemble at the same time and place, and are focused on the same task. But others demand some division of labor and role specialization. It is for this reason that power scavenging very likely evolved before systematic hunting. For power scavenging requires only minimal coordination: a noisy mob can drive a solitary carnivore from a kill, but systematic hunting often requires planning, coordination, and a division of labor: for example, if prey are spooked into an ambush site, or when prey is exhausted by relays of hunters in endurance hunting.

Hunting is often teamwork, not mobwork, and great apes probably do not have a baseline capacity for teamwork. We owe this insight to Michael Tomasello, who has emphasised the cognitive demands of this more nuanced form of collective action (Tomasello 2009; Tomasello and Carpenter 2007; Tomasello et al. 2005). Teamwork requires both sophisticated theory of mind capacities and the ability to represent the structure of a collective task in an agent-neutral way. Great apes probably have at best a limited form of this capacity, and that is why they struggle with role reversal tasks. Much of the social intelligence literature has focused on the cognitive and informational demands of policing cooperation (Humphrey 1976; Whiten and Byrne 1997). But once we move beyond the profits of mob activity in responding to unplanned opportunities or risks, the cognitive-informational demands of cooperation are very significant. If Tomasello is right, chimps have the cognitive capacity to act in a mob but not in a team.

Collective action depends on motivational preconditions, too. Most obviously, agents need enough tolerance and trust to act in close association with others. That is not trivial: tolerance and trust must be gained despite aversive interactions with some in the group, for no band is free of conflict. A little less obviously, impulse

control is necessary.³ A stag hunt will fail if one of the team is distracted by a passing rabbit, and chases off after it, leaving a hole in the human trap. This is not defection; the distracted hunter would have done better with his share of the stag, even if he caught the rabbit. It is a triumph of the now over the future. The profits of cooperation often require persistence, maintaining focus over time. Once again, we see the same explanatory strategy at work: early forms of hominin cooperation depend only on cognitive, communicative, and motivational capacities at or near great ape baselines. But once these early forms of cooperation become a default form of life, that changes both the selective and developmental environment. Young hominins grow up in a more tolerant and cooperative world, and selection favors those that develop adaptively in that world. Moreover, further cooperation profits are available to those with enough cooperation-coordination-impulse control capacities to inch their way to coordinated collective action and thence to collective action supported by planning and/or role specialisation. Teamwork evolves incrementally, with each increment bringing new activities within reach or reducing the costs and risks of existing activities.

2.3 Policing

Much of the literature on the evolution of cooperation is focused on policing. That focus is driven by an important insight: the profits of cooperation often do not depend on a full contribution from each of those that stand to profit, and this creates a temptation to free-ride. Now suppose, as is plausible, that:

- (a) if free-riding invades, it destabilizes cooperation;
- (b) free-riding will invade, unless active measures are taken to block or deter it;
- (c) active anti-free-rider measures are not cost free.

We then have a puzzle: who pays these costs, and why are they worth paying (see, for example, Okasha 2006). This puzzle is so pressing that many have taken the problem of human cooperation to largely reduce to that of explaining why active measures—punishment costs—are cheap enough to make stable cooperation possible. To take three examples, Don Ross argues that punishment is cheap because of human motivational sensitivity to social rewards and punishments (Ross 2006b); Bowles and Gintis argue that punishment is cheap because it invades as a conditional strategy, triggered only in the presence of sufficient punishers to divide the cost between them (Bowles and Gintis 2011); Paul Bingham argues that the invention of weapons, especially projectile weapons, made punishment cheap by allowing a larger coalition to simultaneously attack a recalcitrant cheat, thus reducing the risk to each individual in the coalition (Bingham 1999, 2000).

³Wynn and Coolidge have long argued that hominin cognitive evolution is largely an expansion of working memory. For them, working memory seems to include executive function skills: planned behaviour and the capacity to resist distraction (Wynn and Coolidge 2004, 2010).

If the three-phase model of Sect. 1 is right, the nature and cost basis of deterrence—of policing free-riding—will almost certainly have changed with changes in the role of cooperation in human social life. Late evolved hominins⁴ do typically care profoundly about how others see them, and they do have formidable capacities to communicate and coordinate. So the mechanisms identified by Ross, Bowles, and Gintis certainly help explain the stability of reciprocity-based forager economies (and cooperation in complex Holocene groups). But the growth of cooperation in the transition from great ape society to egalitarian mutualist foragers cannot depend on such sophisticated cognitive and communicative tools, for these evolved only because hominins had long lived in a cooperative milieu. Bingham's proposal is a more plausible explanation of cheap deterrence (or cheap enough deterrence) in the initial phase of divergence from great ape patterns. But he underestimates the cognitive and motivational prerequisites of coalitional enforcement, even with weapons. For in earlier forms of hominin social life, cooperation was threatened not so much by lazy shirkers but by active and dangerous bullies, by alpha males who simply seize what they want (Boehm 1999, 2012). Great ape societies show that such alphas are aware of the threat posed by coalitions, and attempt to break them up (de Waal 2008). So early forms of coalitional enforcement probably do depend on the extra threat posed by armed coalitions, but they also depend on an enhanced motivational and cognitive platform built by joint activity that is somewhat profitable for all despite a less-than-equitable distribution of profits. Collective defence is one such activity; mob hunting, as in chimpanzee monkey hunting, is another. Monkey hunts do not result in all the chimps getting roughly equal portions of monkey. It is important to recall that coalitional enforcement probably did not evolve from scratch in the hominin lineage; chimps do occasionally lose patience with alphas and collectively hound them (de Waal 2008). What was novel in the hominin lineage was not the existence of coalitions from below, but such coalitions exerting sustained, long-term pressure, flattening social hierarchies in the hominin lineage, perhaps for a couple of million years or more (Boehm 2012). Early hominins learned to tolerate and trust one another more, to act together in more coordinated ways, and to stay on the job. Those added capacities (plus the use of weapons) emerged in ecological contexts, and were then coopted into social ones. The result was a cooperative milieu stable enough to allow selection to build the more complex deterrence mechanisms identified by Ross and others.

3 Trigger and Feedback

I noted above that one of the puzzles in understanding hominin cooperation is identifying the trigger of the initial hominin-pan divergence. My best guess is that that initial trigger was increased predation risk, selecting for shared vigilance

⁴By this I mean sapiens, Neanderthals, and their immediate predecessor: the very large-brained hominins of the last half a million years.

and active collective defence. There is some evidence of stone tool use at about 3.5 million years ago. A group of hominins armed with sticks, throwing stones, and making a loud racket might well deter attack by medium-size predators that would certainly be a threat to an isolated australopithecine; the hominins of three to four million years ago were not especially formidable individuals. Likewise, unless they slept close together and were prepared to respond to danger collectively, they would have been very vulnerable to leopards and other nocturnal predators. If these conjectures are roughly right, we would expect four consequences:

- (i) Tolerance and Coordination. There would be selection for motivational and cognitive changes in the hominin lineage, probably initially just increased tolerance for the proximity of others, and hence somewhat improved impulse control. This would be scaffolded by phylogenetically ancient mechanisms of association and affiliation: the more a group of hominins were successful in the company of one another (in, for example, deterring hyena attack), the more they would like being in one another's presence. Once somewhat cooperative group life became the default hominin experience, there would be positive selection for coordination and the capacity to anticipate others' actions.
- (ii) Developmental Environment. Sarah Hrdy has emphasized the fact that the mother forms the whole social environment of infant apes. In hominins, that changed. If the australopithecines of three million years ago slept and foraged in the immediate company of others, tolerating one another's close presence, even very young hominins would have experienced a social environment of other adults and older juveniles, training the infant from a young age for life in company and giving that infant more opportunity for social learning (Burkart et al. 2009; Hrdy 2009). Moreover, once life in company has become a routine aspect of hominin experience, this is likely to be reinforced by selection on mothers to seek help. Upright mothers have a problem with young infants; they have to be carried, as they cannot ride on their mother's back, holding on themselves, as many infant primates do. Furthermore bipedalism exacerbates the costs of immobile infants, for it almost certainly signals increased range size. Thus there is selection on mothers to seek and give help in carrying and/or creching infants. Helping protect and carry the young is a low-cost, high-value form of aid, and subadult females can learn crucial caring skills by helping mothers. It is also true that the overall mobility of the group is improved if mothers do not have to carry infants the whole time: group members can chase resources more effectively without having to leave exposed the most vulnerable individuals in their cohort. As above, once tolerance is established—once mothers do not fear harm to their infants at the hands of males, and once adults and juveniles tolerate the young and the curious amongst them—a platform is available for a further elaboration of reproductive cooperation.
- (iii) Ecological Opportunity. Intimidating predators by cooperating as a crudely armed mob opens up an ecological opportunity: power scavenging. Initially, armed mobs of australopithecines could probably merely have driven the less

formidable predators and scavengers from their kills—perhaps initially only to get marrow from the large bones of herbivores, or they could use their early skills with stone to break open these bones. But once this opportunity is first seized, it can expand incrementally. For example, hominin bands can learn to recognise the natural signs of a kill: vulture behaviour; the drag marks leopards make when storing a kill in trees, away from hyenas. They can learn to communicate—one foraging group recruiting others, if a really major prize is available. They can become more adept at driving predators from kills by volleys of thrown stones. Leverage and dexterity is one of the payoffs of bipedality, and predators cannot afford serious injury. They must be risk averse.

- (iv) Morphology, Life History and Social Learning. A shift to power scavenging (perhaps with opportunistic small game hunting) adds more meat and fat to the diet, easing energetic constraints on brain size, reducing the mechanical demands on teeth and jaws, and allowing gut mass (also expensive tissue) to shrink (Roebroeks 2007). By two million years ago, there had clearly been a major change in hominin diets, for hominin skeletons show a marked reduction in tooth and jaw size: Richard Wrangham hangs his hypothesis of the early evolution of cooking on this morphological transformation (Carmody and Wrangham 2009; Wrangham 2001, 2009). I noted above that great apes are extractive foragers, using resources that require skill and knowledge to harvest (Byrne 2002, 2004). Add three ingredients from above to this extractive foraging basis, and we see how positive feedback can drive the expansion of hominin cooperation. First: bipedalism opens potentials for cognitive, behavioural, and morphological specializations, supercharging extractive foraging. Second: hominins develop in an intimate environment that makes social learning more reliable. Third: cooperation adds the potentials of collective action, teamwork, and specialization to the existing baseline of skilled extractive foraging. There is positive feedback between information sharing, ecological cooperation, and reproductive cooperation.

Social learning and information sharing support effective foraging by giving hominins access to new resources and by helping them extract more from their existing resource base. Power scavenging depends on understanding the local environment and animal behavior, both in locating scavengers' kills, and knowing how and when to drive a dangerous animal from its own kill. Hunting, once it moves beyond opportunistically seizing anything small or vulnerable a party might by chance come across, even more obviously depends on the ability to read the landscape and to understand animal behaviour. Kim Shaw-Williams has shown that one consequence of going bipedal is that, first, physical tracks become more perceptually salient, and scent trails less salient, and that (second) physical tracks are much more information-rich than scent trails. Hominins became the first primate, almost certainly the first animal, to exploit this rich source of information (Shaw-Williams 2011).

Power scavenging and hunting were supported by technology, though to the extent that we can tell this from the physical record, the human toolkit remained

fairly simple until the last few hundred thousand years. Even so, almost certainly its manufacture and use depended on social transmission, perhaps including active teaching (Csibra and Gergely 2011; Stout 2011). But technology and technique was important not just in capturing resources but in preparing them. For the last decade, Richard Wrangham has shown the importance of cooking, and of food processing more generally. Cooking increases food value, and reduces the time and effort of eating. Chimps spend three or four times longer in eating than do typical humans, because they have to chew their food intensively, just to make it edible. Cooking improves our time budget, not just our energy budget (Wrangham 2009). In addition, and perhaps still more importantly, food preparation makes a whole new source available. Many plants that live in seasonal environments develop underground storage organs (“USOs”). These are rich sources of starch, but they are often difficult to find and dig out, so good botanical skills are needed. Moreover, most are protected chemically, and they cannot be eaten until they are processed, by one or more of soaking, washing, and cooking (O’Connell et al. 1999).

In all probability, early hominin social learning was richer and more reliable than great ape social learning only as a passive by-product of changes in adult activity patterns. If adults stay together in cohesive bands, while making simple tools or using them to process challenging resources in their environment, juvenile learning environments change. They are exposed to more adult models, and adult ecological choices shape their environment of exploration learning. Once social learning and information flow becomes more deliberate and bi-directional, further opportunities open up. Specialist tool kits and an expanded material technology are relatively recent, dating to perhaps 100 kya (McBrearty 2007; McBrearty and Brooks 2000). On the other hand, large game hunting requires coordination and communication, not just cooperative intent in an armed mob, and there is clear evidence of systematic large game hunting much earlier—perhaps as early as 1.7 mya, and certainly at about 400 kya (Boehm 2012; Jones 2007). And while the technological base of the Middle Stone Age of 200 kya is not varied, there is evidence of compound tools and the use of adhesives (Wadley 2010). So although the flow of technical skill between the generations might not have required rich communicative capacities until perhaps the last 200,000 years or so, large game hunting shows that active communication and collaboration—a deliberate, two way flow of information exchange—is half a million years old, perhaps much older.

In short, then, more reliable and more extensive social learning makes foraging more profitable. But equally, profitable foraging supports more reliable and extensive social learning. Successful cooperative foraging supports longer childhoods—one very important life history difference between the hominins and the great apes—thus giving young hominins longer to acquire critical skills. Kaplan, Gurven and their colleagues place great weight on this factor, providing data suggesting that foragers do not become fully self-sufficient until they are almost 20 but, once they are competent, produce more than they consume for decades (Gurven et al. 2006; Kaplan et al. 2009). So an intergenerational subsidy supports social learning, but that social learning supports skills which in turn makes the subsidy possible. Profitable foraging supports larger groups, which makes social learning

more reliable in the short run, by giving the young more models to learn from, and in the medium run, by making it less likely that skills will be lost through the unlucky death of a few key individuals. Recent modelling has revealed that small populations are surprisingly vulnerable to the loss of information by unlucky accident (Powell et al. 2009). And it also helps explain longer hominin life expectancies—sapiens life expectancy is a couple of decades longer than that of chimps. Cooperation reduces the risk of predation, and even very simple care makes many illnesses and accidents survivable; animals without social support are desperately at risk if seriously hurt or ill. The take-home message remains the same: an initial ecological trigger builds an adaptive platform, which is then elaborated through positive feedback.

4 The Peculiarities of the Beast

So far in this chapter I have outlined a picture of the incremental evolution of human cooperation, and provided a framework for that trajectory. I have attempted to make explicit some of the preconditions—both internal and external preconditions—of cooperation take-off, and sketched some of the feedback loops through which those enabling factors themselves changed with changes in hominin cooperation. In this final section, I focus on the upshot. In understanding this trajectory we understand some of the very strange features of human life and cognition.

4.1 *Individuals and Groups*

Great apes are typically social, and hominins inherited this trait; we are social too. But because humans cooperatively modify their environment, including their social environment, human social life is very different from great ape social life. Human groups are not mere aggregates or heaps. At least since the evolution of reciprocity-based forager bands, and obviously since the emergence of the much larger and more complex societies of the Holocene, human groups are more like systems than populations. (i) Humans do not just belong to bands (and the like); they identify with the groups of which they are a part; they and others recognise their membership, especially as individuals often display insignias of group identity (as in gang patches and the like); individuals often have strong emotions of affiliation and loyalty to the groups to which they belong. (ii) Individuals within groups often have stable, distinctive roles, roles that shape their actions in predictable ways. (iii) Groups often have significant internal structure. In small traditional societies, this structure often takes the form of genealogical groupings: families, clans, moieties (Barnard 2011). But economic units exist as well, in stable hunting partnerships. In the Holocene, with its larger cultures, economic and other institutions became increasingly important (Seabright 2010). So even in traditional small-scale societies, human groups are complex, with vertical complexity and horizontal differentiation.

(iv) Groups sometimes engage in planned, coordinated activity with a collective product. Quite often, that product is not physical or biological but informational or representational. The legal system of a culture is clearly the collective product of that culture, and is a characteristic of the culture as a whole rather than of the individuals within the culture. The same is true of much of the normative and ideological life of a group: its norms, customs, religious rituals, and representations.

These collective products challenge the project of developing an evolutionary account of hominin social life. To a reasonable approximation, great ape social life can be explained by explaining the cognition and behaviour of individual apes; patterns in great ape social life are mostly simple statistical patterns in the summed behavior of individual agents. It is far from obvious that the same is true of human social life, in even the simplest of human societies. One response is to treat the groups themselves as units of selection (Bowles and Gintis 2011). Cultural group selection models probably do explain some features of human social life, but the conditions under which groups themselves are selected are quite restrictive: only a few features of groups are selectable, and that only in a rather narrow range of circumstances.

An alternative and more general approach is to see human social life as a more elaborated version of something seen quite often in the animal world. Think, for example, of swarming or flocking behaviour: functionally co-ordinated collective behavior that is the result of individual agents following simple local rules, typically in response not to any perception of the group as a whole but to the actions of their immediate neighbours. Just as flocks and swarms are the collective product of individual decision for individual benefit, human social life is the collective product of individual decision for individual benefit, but with the following important added features. (i) The collective phenomenon is not just an aggregate of individual decision, because of the ways human groups are structured—with stable individual roles, and persisting levels of organization between the individual and the group as a whole. (ii) In part because human groups are highly structured, these collective products are stable and persisting. Human social life is characterised by repeated patterns of interaction and a stable, organized informational environment. Local skills, customs, norms, and habitual patterns of interaction are on display, and this makes both coordination between adults and the enculturation of the next generation more reliable and predictable.⁵ Human groups do not hide their norms, expectations, and customs from each other or the next generation. (iii) As a consequence of the stability of the collective phenomena, the collective character of the group influences individual phenotype, in both ontogeny and development. (iv) This mutual causal influence can result in positive feedback; we have already seen the example of

⁵Don Ross goes further, arguing that humans shape one another's psychology and habits, creating in one another stable and relatively public intentional profiles, making longer term collaboration and coordination possible. Our unshaped brains would leave us with much less stable world views and preference functions, and hence make our moment-by-moment decision making far less predictable (Ross 2006a).

the connection between effective group size and innovation. There is persuasive modelling (with some archaeological support) to indicate that once a threshold is reached, humans are able to retain informational resources much more reliably, and innovate more frequently. Size gives redundancy in retaining critical information (small groups can easily lose rare skills through unlucky accident), offers the next generation more and more diverse models in social learning, and affords more opportunities for specialization. Once the retention-innovation cycle takes off, groups extract more resources more efficiently from their environment, thus making it more likely that they can support or expand their population base. In sum, seeing humans as collective niche constructors helps explain the fact that the collective features of human groups can drive an evolutionary trajectory, transforming individual phenotypes, without the group itself being a unit of selection.

4.2 *Cognitive Perversity*

It is obvious that humans are far more intelligent (admittedly, in ways that are difficult to make precise) than other great apes. Individually and collectively we understand far more about our environment—physical, biological, social, psychological—than do other great apes. Individually and collectively, we are good at putting this information to use in making long-term plans (we do not just live in the present); in organizing collective action; and in making and using physical and social tools. Our capacities for efficient reason are far more highly developed than those of the great apes. But a strikingly large fraction of the representational and informational resources of the human mind is not devoted to efficient reason—to representing our environments and their latent possibilities, opportunities, and risks. A sizable fraction is devoted to (i) fictions, narratives (and other depictions known not to be veridical), and myths, quasi-fictional, quasi-historical narratives of special importance and affective power; (ii) religions, which typically involve stories and claims about the history and workings of the world that are presented as true, and which seem to be taken as true, despite the fact that efficient cognition would show them to be profoundly implausible and without evidential support; (iii) norms—humans typically represent themselves as living in a world of prohibitions and obligations, not just in a world of natural facts.

In sum: we think normatively; we represent the world in religious and magical terms; we consume and produce stories and other fictions, often knowing that they are fictions, perhaps enjoying them because they are fictions. There is much more to human minds than information-gathering and efficient instrumental reasoning about our actual environment. It has often been argued that there is a crucial connection between these apparently perverse features of the human mind and our propensity to cooperate (see for example (Joyce 2006; Kitcher 2011; Wilson 2002)). I think this idea is right, and that it is an increasingly important factor stabilizing human cooperation over the last 100,000 years: that is, cooperation in reciprocity-based forager economies and the farming economies that succeeded

them. Sapiens hominins (and perhaps earlier ones) have invented a set of social or cultural tools—ways of organizing their social environment to enhance cooperation. Those tools are an utterly pervasive feature of contemporary environments: legal and institutional frameworks coordinate markets and other systems of social interaction to minimise conflict costs and increase their predictability and efficiency.⁶ In my view, these social tools have a deep history: they date back in time to the mid-Pleistocene, 100 kya, and perhaps earlier. (I have argued for this elsewhere (Sterelny 2012b); since my main focus in this chapter has been on early phases of hominin cooperation, it is not front and center here.)

4.3 *Niche Construction*

Let me end by returning to the overarching theme of niche construction. Many organisms (and groups of organisms) act on their environment in ways that significantly alter that environment; significantly enough to affect the intensity and direction of selection; significantly enough so that organism-environment effects help explain the adaptive fit between the organism's phenotype and its environment. Hominins, and especially recent hominins, are major league niche constructors. Holocene humans have transformed their physical and biological environment: over the last 10,000 years, an increasing fraction of our species have lived in built environments and eaten from intensively managed biological resources. In doing so, we have almost certainly exerted transforming effects on our symbionts, parasites, pathogens, and commensals, and living in these constructed environments has had effects on humans, too. While Pleistocene humans did not transform their physical and biological environment quite so profoundly, shelters, clothes, fire, and resource management have deep histories. But humans do not just intervene on their physical and biological environment; they organize their informational environment too, and not just their own, but that of the next generation. Intensive, prolonged active teaching is probably an artefact of contemporary environments. This is not the case for teaching more generally: while social learning is found in many species, active teaching is rare (Hewlett et al. 2011). Moreover, adults structure the learning environment of the next generation in many other ways: by providing supervised, safer environments; by providing toys, tools, and props that structure and support trial-and-error learning; by merely being tolerant of the curiosity of the young. So ideas, information, and skills are made available to the next generation in a physical environment that is often physically and biologically modified to enhance learning (Sterelny 2012a). The extent and transforming character of human niche

⁶That is not all they do, of course, and while these contemporary social mechanisms do coordinate and regularize interaction, making forms of cooperation possible that would be otherwise inconceivable, they also distribute the profits of those interactions very unequally, while often at the same time entrenching those inequalities.

construction is far from unique. Termites, for example, live in worlds that are almost entirely termite-constructed, and their entire phenotypes are adapted to a world they have made (Turner 2000). But human niche construction is unique for a primate, for a great ape. Other great apes modify their environments: for example, chimps build nests in which they sleep. But these modifications are fairly minor: to a reasonable approximation, great apes live in the world as they find it, rather than the world as they reconstruct it. Humans do not. Part of the reconstruction that humans have engaged in has been the making of a world that enabled cooperation to survive and expand.

References

- Barnard, Alan. 2011. *Social anthropology and human origins*. Cambridge: Cambridge University Press.
- Bingham, Paul. 1999. Human uniqueness: A general theory. *Quarterly Review of Biology* 74: 133–169.
- Bingham, Paul. 2000. Human evolution and human history: A complete theory. *Evolutionary Anthropology* 9: 248–257.
- Boehm, Chris. 1999. *Hierarchy in the forest*. Cambridge, MA: Harvard University Press.
- Boehm, Christopher. 2012. *Moral origins: The evolution of virtue, altruism and shame*. New York: Basic Books.
- Bogucki, Peter. 1999. *The origins of human society*. Oxford: Blackwell.
- Bowles, Sam, and Herbert Gintis. 2011. *A cooperative species: Human reciprocity and its evolution*. Princeton: Princeton University Press.
- Burkart, Judith, Sarah Blaffer Hrdy, and Carel van Schaik. 2009. Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology* 18: 175–186.
- Byrne, R. 1995. *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
- Byrne, Richard. 2000. Evolution of primate cognition. *Cognitive Science* 24: 543–570.
- Byrne, Richard. 2002. Seeing actions as hierarchically organized structures: Great ape manual skills. In *The imitative mind*, ed. Andrew Meltzoff and William Prinz, 122–140. Cambridge: Cambridge University Press.
- Byrne, Richard. 2004. The manual skills and cognition that lie behind hominid tool use. In *Evolutionary origins of great ape intelligence*, ed. Anne Russon and David R. Begun, 31–44. Cambridge: Cambridge University Press.
- Carmody, Rachael, and Richard Wrangham. 2009. The energetic significance of cooking. *Journal of Human Evolution* 57: 379–391.
- Csibra, Gergely, and György Gergely. 2011. Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of the Royal Society B* 366: 1149–1157.
- d’Errico, F. 2003. The invisible frontier: A multiple species model for the origin of behavioural modernity. *Evolutionary Anthropology* 12: 188–202.
- de Waal, Franz. 2008. *Chimpanzee politics: Power and sex among apes*, 25th anniversary ed. Baltimore: John Hopkins University Press.
- de Waal, Franz, and Malini Suchak. 2010. Prosocial primates: Selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B* 365: 2711–2722.
- Flannery, Kent, and Joyce Marcus. 2012. *The creation of inequality*. Cambridge, MA: Harvard University Press.
- Foley, Robert. 1995. *Humans before humanity*. Oxford: Blackwell.

- Foley, Robert, and Clive Gamble. 2009. The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B* 364: 3267–3279.
- Foley, Robert, and Marta Mirazon Lahr. 2003. On stony ground: Lithic technology, human evolution, and the emergence of culture. *Evolutionary Anthropology* 12: 109–122.
- Gurven, Michael, Hillard Kaplan, and Maguin Gutierrez. 2006. How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of Human Evolution* 51: 454–470.
- Hawkes, Kristin. 2003. Grandmothers and the evolution of human longevity. *American Journal of Human Biology* 15: 380–400.
- Hawkes, K., J.F. O’Connell, N.G. Blurton Jones, H. Alvarez, and E. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America* 95: 1336–1339.
- Henshilwood, Christopher, and Curtis Marean. 2003. The origin of modern behavior. *Current Anthropology* 44: 627–651 (includes peer commentary and author’s responses).
- Hewlett, Barry, Hillary Fouts, Adam Boyette, and Bonnie Hewlett. 2011. Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society B* 366: 1168–1178.
- Hrdy, Sarah Blaffer. 2009. *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge, MA: Harvard University Press.
- Humphrey, Nicholas. 1976. The social function of intellect. In *Growing points in ethology*, ed. P.P.G. Bateson and R.A. Hinde, 303–317. Cambridge: Cambridge University Press.
- Jones, Martin. 2007. *Feast: Why humans share food*. Oxford: Oxford University Press.
- Joyce, Richard. 2006. *Evolution of morality*. Cambridge, MA: MIT Press.
- Kaplan, Hilliard, Paul Hooper, and Michael Gurven. 2009. The evolutionary and ecological roots of human social organization. *Philosophical Transactions of the Royal Society B* 364: 3289–3299.
- Kitcher, Philip. 2011. *The ethical project*. Harvard: Harvard University Press.
- Klein, Richard G. 2009a. Darwin and the recent African origin of modern humans. *Proceedings of the National Academy of Sciences of the United States of America* 106: 16007–16009.
- Klein, Richard G. 2009b. *The human career: Human biological and cultural origins*, 3rd ed. Chicago: University of Chicago Press.
- McBrearty, Sally. 2007. Down with the revolution. In *Rethinking the human revolution: new behavioural and biological perspectives on the origin and dispersal of modern humans*, ed. K. Paul Mellars, Bar-Yosef O. Boyle, and C. Stringer, 133–151. Cambridge: McDonald Institute Archaeological Publications.
- McBrearty, S., and A. Brooks. 2000. The revolution that wasn’t: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39: 453–563.
- McPherron, Shannon, Zeresenay Alemseged, Curtis Marean, Jonathan Wynn, Denné Reed, Denis Geraads, René Bobe, and Hamdallah Béarat. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466: 857–860.
- Nowell, April. 2010. Defining behavioral modernity in the context of Neandertal and anatomically modern human populations. *Annual Review of Anthropology* 39: 437–452.
- O’Connell, J.F., K. Hawkes, and N.G. Blurton Jones. 1999. Grandmothering and the evolution of *Homo erectus*. *Journal of Human Evolution* 36: 461–485.
- Odling-Smee, F. John, Kevin Laland, and Marcus Feldman. 2003. *Niche construction: The neglected process in evolution*, Monographs in population biology. Princeton: Princeton University Press.
- Okasha, Samir. 2006. *Evolution and the units of selection*. Oxford: Oxford University Press.
- Powell, Adam, Stephen Shennan, and Mark Thomas. 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324: 1298–1301.
- Roebroeks, Will (ed.). 2007. *Guts and brains: An integrative approach to the hominin record*. Leiden: Leiden University Press.
- Ross, Don. 2006a. The economic and evolutionary basis of selves. *Cognitive Systems Research* 7: 246–258.

- Ross, Don. 2006b. Evolutionary game theory and the normative theory of institutional design: Binmore and behavioral economics. *Politics, Philosophy and Economics* 5: 51–80.
- Seabright, Paul. 2010. *The company of strangers: A natural history of economic life*. Princeton: Princeton University Press.
- Shaw-Williams, Kim. 2011. *The triggering track-ways theory*. M.A. thesis, Victoria University of Wellington.
- Sterelny, Kim. 2011. From hominins to humans: How sapiens became behaviourally modern. *Philosophical Transactions of the Royal Society B* 366: 809–822.
- Sterelny, Kim. 2012a. *The evolved apprentice*. Cambridge, MA: MIT Press.
- Sterelny, Kim. 2012b. Morality's dark past. *Analyse and Kritik* 34: 95–116.
- Sterelny, Kim. 2013a. Cooperation in a complex world: The role of proximate factors in ultimate explanations. *Biological Theory* 7: 358–367.
- Sterelny, Kim. 2013b. Life in interesting times: Cooperation and collective action in the Holocene. In *Cooperation and its evolution*, eds. Kim Sterelny, Richard Joyce, Brett Calcott, and Ben Fraser, 89–108. Cambridge, MA: MIT Press.
- Sterelny, Kim. Forthcoming. Signals, symbols and norms. *Biological Theory*.
- Stiner, Mary C. 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* 10: 1–63.
- Stout, Dietrich. 2011. Stone toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society Series B* 366: 1050–1059.
- Tomasello, Michael. 2009. *Why we cooperate*, Cambridge, MA: MIT Press.
- Tomasello, Michael, and Malinda Carpenter. 2007. Shared intentionality. *Developmental Science* 10: 121–125.
- Tomasello, Michael, Malinda Carpenter, Josep Call, Tanya Behne, and Henrike Moll. 2005. Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences* 28: 675–691.
- Tomasello, Michael, Alicia P. Melis, Claudio Tennie, Emily Wyman, and Esther Herrmann. 2012. Two key steps in the evolution of human cooperation: The interdependence hypothesis. *Current Anthropology* 53: 673–692.
- Turner, J. Scott. 2000. *The extended organism: The physiology of animal-built structures*. Cambridge, MA: Harvard University Press.
- Wadley, Lyn. 2010. Compound-adhesive manufacture as a behavioral proxy for complex cognition in the Middle Stone Age. *Current Anthropology* 51: S111–S119.
- Warneken, Felix, and Michael Tomasello. 2009. Varieties of altruism in children and chimpanzees. *Trends in Cognitive Science* 13: 397–402.
- Warneken, Felix, Brian Hare, Alicia Melis, Daniel Hanus, and Michael Tomasello. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* 5: e184. doi:[10.1371](https://doi.org/10.1371/journal.pbio.0184).
- Whiten, A., and R. Byrne (eds.). 1997. *Machiavellian intelligence II: Extensions and evaluations*. Cambridge: Cambridge University Press.
- Wilkinson, Gerald S. 1990. Food sharing in vampire bats. *Scientific American* 262: 64–70.
- Wilson, David Sloan. 2002. *Darwin's cathedral: Evolution, religion and the nature of society*. Chicago: University of Chicago Press.
- Wrangham, Richard. 2001. Out of the pan, into the fire: How our ancestors' evolution depended on what they ate. In *Tree of life*, ed. Franz de Waal, 121–143. Cambridge, MA: Harvard University Press.
- Wrangham, Richard. 2009. *Catching fire: How cooking made us human*. London: Profile Books.
- Wynn, Thomas, and Frederick Coolidge. 2004. The expert Neanderthal mind. *Journal of Human Evolution* 46: 467–487.
- Wynn, Thomas, and Frederick Coolidge. 2010. How Levallois reduction is similar to, and not similar to, playing chess. In *Stone tools and the evolution of human cognition*, ed. April Nowell and Iain Davidson, 83–103. Boulder: University of Colorado Press.