

Review

Culture and the evolution of human cooperation

Robert Boyd^{1,*} and Peter J. Richerson²

¹*Department of Anthropology, University of California, Los Angeles, CA 90095, USA*

²*School of Environmental Science and Policy, University of California, Davis, CA 95616, USA*

The scale of human cooperation is an evolutionary puzzle. All of the available evidence suggests that the societies of our Pliocene ancestors were like those of other social primates, and this means that human psychology has changed in ways that support larger, more cooperative societies that characterize modern humans. In this paper, we argue that cultural adaptation is a key factor in these changes. Over the last million years or so, people evolved the ability to learn from each other, creating the possibility of cumulative, cultural evolution. Rapid cultural adaptation also leads to persistent differences between local social groups, and then competition between groups leads to the spread of behaviours that enhance their competitive ability. Then, in such culturally evolved cooperative social environments, natural selection within groups favoured genes that gave rise to new, more pro-social motives. Moral systems enforced by systems of sanctions and rewards increased the reproductive success of individuals who functioned well in such environments, and this in turn led to the evolution of other regarding motives like empathy and social emotions like shame.

Keywords: cooperation; culture; coevolution

1. INTRODUCTION

Humans cooperate on a larger scale than most other mammals. Among social mammals, cooperation is mainly limited to relatives. There is little division of labour, no trade and no large scale conflict. Communication is limited to a small repertoire of self-verifying signals. The sick and disabled must fend for themselves. The strong take from the weak without fear of sanctions by third parties. Amend Hobbes to account for nepotism, and his picture of society is not so far off for most other species. In stark contrast, even in foraging societies people regularly cooperate with many unrelated individuals. Division of labour, trade and large scale conflict are prominent features of most known human societies. Human language allows low-cost, generally honest communication of virtually unlimited complexity. The sick and disabled are often cared for, and social life is regulated by shared moral systems that specify the rights and duties of individuals enforced, albeit imperfectly, by third party sanctions.

The scale of human cooperation is an evolutionary puzzle. All of the available evidence suggests that the societies of our Pliocene ancestors were like those of other social primates (Foley & Gamble 2009). Sometime during the last two million years, important changes occurred in human psychology that support larger, more cooperative societies. Given the magnitude and complexity of the changes, the most

plausible hypothesis is that they were the product of natural selection. However, the limited cooperation seen in other mammals fits more comfortably within the received theory of evolution than does human large-scale cooperation among non-kin.

Something makes our species different, and in this paper we argue that something is cultural adaptation. This hypothesis rests on three claims:

- (i) Over the last million years or so, people evolved the ability to learn from each other, creating the possibility of cumulative, non-genetic evolution. These capacities were favoured by ordinary natural selection in the rapidly varying climates of the Middle and Upper Pleistocene, because cumulative cultural evolution allows humans to culturally evolve highly refined adaptations to local environments relatively quickly compared with genetic evolution.
- (ii) Rapid cultural adaptation also vastly increased heritable variation between groups. Systems of reciprocity and reputation can stabilize a vast range of behaviours ranging from ruthless spite to prosocial cooperation. Rapid cultural adaptation can then lead to persistent differences between local social groups, and then competition between groups leads to the spread of behaviours that enhance the competitive ability of groups.
- (iii) Then, in such culturally evolved cooperative social environments, social selection within groups favoured genes that gave rise to new, more pro-social motives. Moral systems enforced by systems of sanctions and rewards

* Author for correspondence (rboyd@anthro.ucla.edu).

One contribution of 16 to a Discussion Meeting Issue 'The evolution of society'.

increased the reproductive success of individuals who functioned well in such environments, and this in turn led to the evolution of other regarding motives like empathy and social emotions like shame.

In the remainder of this paper, we explain the logic behind each of these claims, and sketch the empirical evidence that supports them.

2. CULTURE ALLOWS RAPID LOCAL ADAPTATION

‘Now, if some one man in a tribe, more sagacious than the others, invented a new snare or weapon, or other means of attack or defense, the plainest self-interest, without the assistance of much reasoning power, would prompt the other members to imitate him; and all would thus profit.’

(Charles Darwin, *The Descent of Man* 1871, p. 155)

The human species occupies a wider range of habitats, uses a much greater range of resources, and lives in more diverse social systems than any other animal species. We constitute a veritable adaptive radiation, albeit one without any true speciation. For better or worse, our ability to convert matter and energy into people in almost every terrestrial habitat has made us the Earth’s dominant species.

Most accounts of human evolution explain our ecological success as the result of superior cognitive abilities (e.g. Tooby & DeVore 1987). While it is probable that individual humans *are* smarter than other animals, we do not think this is the most important cause of our success. Think about what people have to know to survive and prosper in just one habitat where human foragers have flourished, the North American Arctic. They have to know how to make dozens of essential tools—kayaks, warm clothing, toggle harpoons, oil lamps, shelters built of skin and snow, goggles to prevent snow blindness, dog sleds and the tools to make these tools. They also have to know how to use all of this stuff, where and when to hunt and gather, what to seek, how to process it if you succeed, and so on and on. Then they have to decide how to organize their society: how to regulate exchange of resources, how to organize marriage, resolve conflicts and so on and on. If individual intelligence were the key, individuals could create all of this knowledge on their own.

While we are rather clever animals, we cannot do this because we are not close to clever enough. A kayak is a highly complex object with many different attributes. Designing a good one means finding one of the extremely rare combination of attributes that produces a useful boat. The number of combinations of attributes grows geometrically as the number of dimensions increases, rapidly exploding into an immense number. The problem would be much easier if we had a kayak module that constrained the problem, so we would have fewer choices to evaluate (Tooby & Cosmides 1992, pp. 104–108). However, environments are changing far too quickly and are far too variable spatially for selection to shape the psychologies of Arctic populations in this way. The same

learning psychology has to do for all the other knowledge, institutions and technologies necessary to survive in the Arctic. It also has to do for birch bark canoes, reed rafts, dugout canoes, rabbit drives, blow-guns, hxaro exchange and the myriad marvelous, specialized, environment-specific technology, knowledge and social institutions that human foragers have culturally evolved. Our learning and inference mechanisms simply are not up to the task.

Arctic foragers could make and do all the other things that they needed because they could make use of a vast pool of useful information available in the behaviour and teachings of other people in their population. The information contained in this pool is adaptive because combining even limited, imperfect learning mechanisms with cultural transmission can lead to relatively rapid, cumulative adaptation. Even if most individuals imitate most of the time, some people will attempt to improve on what they learned. Relatively small improvements are easier than large ones, so most successful innovations will lead to small changes. These modest attempts at improvement give behaviours a nudge in an adaptive direction, on average. Cultural transmission preserves the nudges, and exposes the modified traditions to another round of nudging. Very rapidly by the standards of evolution by natural selection, many small nudges generate new adaptations. Much theoretical work suggests that this qualitative picture of cumulative cultural adaptation is cogent (Boyd & Richerson 1996, see Richerson & Boyd 2005 for a review)—coupling learning and social transmission allows populations of humans to rapidly varying environments. Culture leverages individual creativity in just the way Darwin imagined. Scraps of individual insight and luck are spread widely to others, recombined with other scraps, and form the basis for additional innovations, all rather quickly.

We have hypothesized (Richerson & Boyd 2005; Richerson *et al.* 2005) that the psychological capacities that allow humans to learn from others evolved during the Middle Pleistocene in response to increased rapid, high amplitude climate variation. Since the mid-Miocene Earth’s mean temperature has dropped several degrees and the amplitude of temperature fluctuations have greatly increased (Lamb 1977; Partridge *et al.* 1995; Bradley 1999; Cronin 1999). Higher resolution data indicate that the period of these fluctuations has decreased over the last 400 000 years or so, and that during the last two glacial periods substantial changes in world temperature have occurred over periods of a few decades. It seems plausible that the capacities that allow cultural adaptation would be strongly favoured in such a chaotic, rapidly changing world.

3. RAPID CULTURAL ADAPTATION POTENTIATES GROUP SELECTION

‘It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense

advantage to one tribe over another... At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.'

(Charles Darwin, *The Descent of Man* 1871, p. 159)

In this paper we use the word *cooperation* to mean costly behaviour performed by one individual that increases the payoff of others. Opportunities for cooperation are omnipresent in social life. Exchange and division of labour increase the efficiency of productive processes for all the reasons given by Adam Smith in *The wealth of nations*. However, in all but the simplest transactions, individuals experience a cost now in return for a benefit later and thus are vulnerable to defectors who take the benefit but do not produce the return. Imperfect monitoring or effort and quality also give rise to opportunities for free riding. The potential for conflict over land, food and other resources is everywhere. In such conflicts larger more cooperative groups defeat smaller less cooperative groups. However, each warrior's sacrifice benefits everyone in the group whether or not they too went to war and thus defectors can reap the fruits of victory without risking their skins. Honest, low-cost communication provides many benefits—coordination is greatly facilitated, resources can be used more efficiently, hazards avoided; the list is long. However, once individuals come to rely on the signals of others, the door is open for liars, flim-flam artists and all the rest. Capital facilities like roads, fortifications and irrigation systems can provide huge benefits. However, the benefits often flow to everyone, whether or not they contributed to the construction.

However, aside from humans, only a few other taxa, most notably social insects, make cooperation a cornerstone of their adaptation. Those that do are spectacular evolutionary successes. It has been estimated, for example, that termites account for half of the animal biomass in the tropics, and that human biomass exceeds that of all other terrestrial vertebrates combined. Nonetheless, cooperative behaviour does not usually evolve because it is vulnerable to exploitation. Even if everyone benefits by behaving cooperatively, selection usually favours individuals who take the benefits without paying the cost, and, as a result, the immense benefit that can be generated for everyone through cooperation remains untapped.

(a) Reciprocity and reputation can explain the stability but not the evolution of larger scale cooperation

While there is some controversy, the evolution of large scale cooperation in other species (Foster *et al.* 2005) seems to require kinship, perhaps supplemented by policing (Ratnieks & Wenseleers 2005). This explanation obviously does not work for large scale human cooperation among unrelated individuals. Instead, evolutionary thinkers typically explain human cooperation as the resulting from the 'three Rs': reputation, reciprocation and retribution (e.g. Trivers 1971; Alexander 1987; Haley & Fessler 2005;

Nowak & Sigmund 2005). If cheaters are despised by others in their group, and, as a consequence, suffer social costs—lose status, mating opportunities, the benefits of mutual aid when ill or injured—then they may be motivated to cooperate, even though prosocial motivations are entirely absent from their psychology. Of course, punishment may be costly, so we also need to explain why punishers are not replaced by second-order free riders who cooperate, but do not punish. However, there are by now several plausible solutions to this second order free rider problem (Henrich & Boyd 2001; Boyd *et al.* 2003; Panchanathan & Boyd 2004) and so it seems probable that the three Rs can explain why cooperation is evolutionarily stable.

The problem is that the three Rs can stabilize *any* behaviour. If everybody agrees that individuals must do *X*, and punish those who do not do *X*, then *X* will be evolutionarily stable as long as the costs of being punished exceed the costs of doing *X*. It is irrelevant whether *X* benefits the group or is socially destructive. It will pay to do *X*. Thus, the three Rs can explain how cooperative behaviours like participating in group defense can be favoured by evolution, but they can also explain anything else. Since cooperative behaviours are a tiny subset of all possible behaviours, the three Rs do not explain why large-scale cooperation is so widely observed. In other words, the three Rs may sustain large-scale cooperation, but are not sufficient to explain why it evolves in the first place. As was first pointed out by Axelrod & Hamilton (1981), cooperation in very small groups can readily be explained by the combination of the three Rs and the weak kin selection created by low levels of background relatedness typically observed in social groups (e.g. Bowles 2006). However, all of the analysis done so far suggests that the same is not true of larger groups (Boyd & Richerson 1988, 1992; Gardner & West 2004; Panchanathan & Boyd 2004). Something has to be added to the model.

(b) Multiple equilibria plus rapid adaptation = stable variation among groups

So what explains the evolution of large scale human cooperation? We believe that the most probable explanation is that rapid cultural adaptation greatly increased the amount of behavioural variation between groups. We have seen that repeated interactions can stabilize a vast range of alternative behaviours in different groups. A variety of other mechanisms also can lead to multiple stable equilibria (discussed in Boyd & Richerson *in press*). When this is the case, different groups may evolve to different equilibria—one set of practices gets higher reputational benefits in one group, a different set in another group, a third set in a third group and so on. Thus, the social environment varies from group to group, and as a result different behaviours will be favoured by selection or analogous cultural adaptive processes in different groups. Such disruptive selection increases behavioural variation among groups. This tendency will be opposed by the flow of genes or cultural variants between groups due to migration and other kinds of social contact. If local adaptation is rapid compared with mixing,

the variation among groups will persist; if mixing is stronger, all groups will converge to a single genetic or cultural variant.

The following simple model illustrates this idea. There are three independent evolving traits, each with two variants labelled 0 and 1. Each variant is evolutionarily stable when common, and thus there are eight stable equilibria $(0,0,0), (1,0,0), \dots, (1,1,1)$. The selection coefficient for each trait is s . The population is subdivided into 256 subpopulations dispersed in a two-dimensional space. Each subpopulation exchanges a fraction m of its members with its four nearest neighbours. Initial frequencies are assigned at random. In figure 1, the frequencies of the three variants in each subpopulation are represented by the RGB colours, so for example a population with the vector of frequencies $(1,0,0)$ is 100 per cent red, 0 per cent green and blue. When mixing is stronger than local adaptation ($m > s$), evolution proceeds as if there were no groups and evolves toward which ever combination of variants is initially more common. When local adaptation is stronger, mixing and local adaptation balance leading to persistent variation among groups. Stronger local adaptation leads to variation on smaller spatial scales.

Cultural adaptation is much more rapid than genetic adaptation. Indeed, if we are correct, this is the *reason* why we have culture—to allow different groups to accumulate different adaptations to a wide range of environments. Thus a shift from genetic adaptation to cultural adaptation should greatly increase the heritable behavioural variation among groups. In other primate species, there is little heritable variation among groups because natural selection is weak compared with migration. Although the strength of selection varies among traits, most selection is relatively weak, and selection coefficients are of the order of 1 per cent. Since one sex leaves at maturity in most primate species, and there are roughly two generations present in a group, migration rates are of the order of 25 per cent per generation. This is why group selection at the level of whole primate groups is not an important evolutionary force. In contrast, there is a great deal of behavioural variation among human groups. And this behavioural variation exists on a wide range of spatial scales. Even neighbouring groups may have very different culturally transmitted languages, marriage systems, and so on.

(c) *Stable variation among groups leads to group selection*

In the *Origin of species*, Darwin famously argued that three conditions are necessary for adaptation by natural selection: first, there must be a ‘struggle for existence’ so that not all individuals survive and reproduce. Second, there must be variation so that some types are more likely to survive and reproduce than others, and finally, variation must be heritable so that the offspring of survivors resemble their parents. As the quote at the beginning of this section illustrates, Darwin thought that the same three postulates apply to groups as well as individuals. Only the first two conditions are satisfied by most other kinds of animal

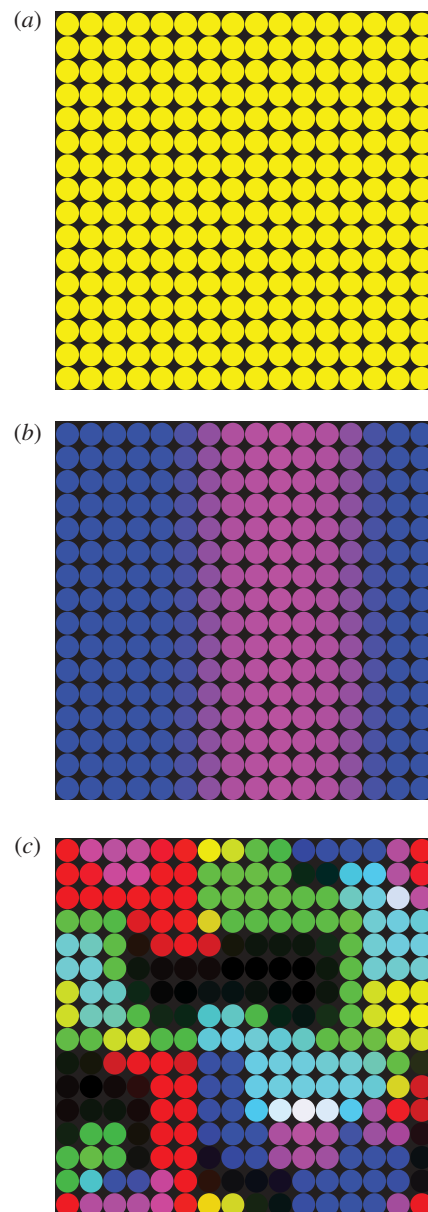


Figure 1. An equilibrium behaviour in a 16×16 array of populations linked by stepping stone migration on a torus is shown. There are three binary traits. Each combination of traits is evolutionarily stable when common, and all basins of attraction are the same. Populations are initialized at random. The vector of frequencies at evolutionary equilibrium is plotted as the RGB colour resulting from that mix of red, green and blue. (a) When migration rates are greater than or equal to selection coefficients ($m \geq s$) all groups have the same behaviour at equilibrium. (b) When migration rates are somewhat less than to selection coefficients ($2m = s$) simple clines often persist at evolutionary equilibrium. (c) When migration rates are much less than to selection coefficients ($10m = s$) complex patterns of small scale variation often persist at evolutionary equilibrium.

groups. For example, vervet monkey groups compete with one another, and groups vary in their ability to survive and grow, but, and this is a big but, the causes of group-level variation in competitive ability are not heritable, so there is no cumulative adaptation. Once rapid cultural adaptation in human societies gave rise to stable, between-group differences, the stage was

set for a variety of selective processes to generate adaptations at the group level.

Different human groups have different norms and values, and the cultural transmission of these traits can cause such differences to persist for long periods of time. The norms and values that predominate in a group plausibly affect the probability that the group survives, whether it is economically successful, whether it expands, and whether it is imitated by its neighbours. For example, suppose that groups with norms that promote patriotism are more likely to survive than groups lacking this sentiment. This creates a selective process that leads to the spread of patriotism. Of course, this process may be opposed by an evolved innate psychology that makes us more prone to imitate, remember and invent nepotistic beliefs than patriotic beliefs. The long run evolutionary outcome would then depend on the balance of these two processes.

The simplest mechanism is intergroup competition. The spread of the Nuer at the expense of the Dinka in the nineteenth century Sudan provides a good example. During the nineteenth century each consisted of a number of politically independent groups (Kelly 1985). Cultural differences in norms between the two groups meant that the Nuer were able to cooperate in larger groups than the Dinka, and as a consequence defeated their Dinka neighbours, occupied their territories and assimilated tens of thousands of Dinka into their communities. This example illustrates the requirements for cultural group selection by intergroup competition. Contrary to some critics (Palmer *et al.* 1997), there is no need for groups to be strongly bounded, individual-like entities. The only requirement is that there are persistent cultural differences between groups, and these differences must affect the group's competitive ability. Losing groups must be replaced by the winning groups. Interestingly, the losers do not have to be killed. The members of losing groups just have to disperse or to be assimilated into the victorious group. Losers will be socialized by conformity or punishment, so even very high rates of physical migration need not result in the erosion of cultural differences. This kind of group selection can be a potent force even if groups are very large.

Group competition is common in small scale societies. The best data come from New Guinea, which provides the only large sample of simple societies studied by professional anthropologists before they experienced major changes due to contact with Europeans. Joseph Soltis assembled data from the reports of early ethnographers in New Guinea (Soltis *et al.* 1995). Many studies report appreciable intergroup conflict and about half mention cases of social extinction of local groups. Five studies contained enough information to estimate the rates of extinction of neighbouring groups. The typical pattern is for groups to be weakened over a period of time by conflict with neighbours and finally to suffer a sharp defeat. When enough members become convinced of the group's vulnerability to further attack, members take shelter with friends and relatives in other groups, and the group becomes socially extinct. At these rates of group extinction, it would take between 20 and

40 generations, or 500 to 1000 years, for an innovation to spread from one group to most of the other local groups by cultural group selection. This might seem slow, but the history of the rise of ever larger and more complex societies in the Holocene does have a millennial time scale.

A propensity to imitate the successful can also lead to the spread of group beneficial variants. People often know about the norms that regulate behaviour in neighbouring groups. They know that we can marry our cousins here, but over there they cannot; or anyone is free to pick fruit here, while individuals own fruit trees there. Suppose different norms are common in neighbouring groups, and that one set of norms causes people to be more successful. Both theory and empirical evidence suggest that people have a strong tendency to imitate the successful (Henrich & Gil-White 2001; McElreath *et al.* 2008). Consequently, behaviours can spread from groups at high payoff equilibria to neighbouring groups at lower payoff equilibria because people imitate their more successful neighbours. A mathematical model suggests that this process will result in the spread of group beneficial beliefs over in a wide range of conditions (Boyd & Richerson 2002). The model also suggests that such spread can be rapid. Roughly speaking, it takes about twice as long for a group beneficial trait to spread from one group to another as it does for an individually beneficial trait to spread within a group.

Selective migration is a third mechanism that can lead to the spread of some kinds of group beneficial traits. In the modern world streams of migrants flow between societies. The extensive literature on this topic (e.g. Borjas 1994; Alba & Nee 2003; Martin 2005) supports two generalizations: (i) that migrants flow from societies where immigrants find their prospects poor to ones where they perceive them to be better, and (ii) most immigrant populations assimilate to the host culture within a few generations. Ethnographic evidence suggests that selective immigration is not limited to complex modern societies, and thus is likely to be an ancient phenomenon (Knauff 1985; Cronk 2002). The spread of cultural institutions associated with ancient complex societies, such as China, Rome and India supports the idea that this process is not new. Ancient imperial systems often expanded militarily but the durable ones, such as Rome, succeeded by assimilating conquered peoples and by inducing a flow of migrants across their boundaries. Although the Roman Empire as a political entity eventually faded, its most attractive institutions were adapted by successor polities and persist in modified form to this day. Rome, India, China and Islamic civilization stand in stark contrast to pure conquest empires like that of the Mongols, which expanded but did not assimilate.

A simple mathematical model of this process (Boyd & Richerson 2009) indicates that it has two qualitatively different evolutionary outcomes. The model assumes that there are two possible evolutionary equilibria in an isolated population, and one equilibrium leads to higher average welfare than the other. The population is subdivided into two subpopulations linked by migration. There is more migration from

low payoff to high payoff subpopulations than the reverse. When local adaptation is strong enough compared with migration to maintain cultural variation among subpopulations, the population as a whole evolves toward a polymorphic equilibrium at which the variants that produce higher average welfare are more common, but the lower payoff variant also persists. Initial subpopulation size and the sizes of the basins of attraction play relatively minor roles. When migration is stronger, however, initial population sizes and sizes of the basins of attraction predominate. The variant that is common in the larger of the two populations tends to spread and the other variant tends to disappear even it yields a higher payoff.

(d) *This argument is consistent with an evolved, genetically adaptive psychology*

The claim that cultural evolution can give rise to forms of novel cooperation is vulnerable to an obvious objection: Cultural evolution can lead to the spread of cooperation in large, weakly related groups only if computational and motivational systems existed in the human brain that allowed people to acquire and perform the requisite behaviours. Given that such behaviours were not favoured by natural selection, why should these systems exist?

Like living primates, our ancestors were large brained mammals capable of flexibly responding to a range of biotic and social environments. Natural selection cannot equip such organisms with fixed action patterns; instead it endows them with a complex psychology that causes them to modify their behaviour adaptively in response to environmental cues (Tooby & Cosmides 1992). Cultural evolution can generate novel behaviours by manipulating these cues. For example, cooperation among relatives requires (among other things) a means of assessing costs and benefits, and of identifying relatives and assessing their degree of relatedness. Such systems can be manipulated by culturally transmitted input. Individuals have to *learn* the costs and benefits of different behaviours in their particular environment. Thus people who learn that sinners suffer an eternity of punishment may be more likely to behave morally than those who only fear the reprisals of their victims. Individuals have to *learn* who their relatives are in different environments. So the individual who learns that members of his patrilin are brothers may behave quite differently from one who learns that he owes loyalty to the band of brothers in his platoon. Once activated, such computational systems provide input to existing motivational systems which in turn generate behaviour.

This account raises an obvious question: If cultural inputs regularly lead to what is, from the genes point of view, maladaptive behaviour, why has not selection modified our psychology so that it is immune to such maladaptive inputs. This is a crucial question, and we have dealt with it at length elsewhere (Richerson & Boyd 2005, ch. 5). In brief, we believe that cumulative cultural evolution creates a novel evolutionary tradeoff. Social learning allows human *populations* to accumulate adaptive information over many

generations, leading to the cultural evolution of highly adaptive behaviours and technology. Because this process is much faster than genetic evolution, human populations can evolve cultural adaptations to local environments, an especially valuable adaptation to the chaotic, rapidly changing world of the Pleistocene. However, the same psychological mechanisms that create this benefit *necessarily* come with a built-in cost. To get the benefits of social learning, humans have to be credulous, for the most part accepting the ways that they observe in their society as sensible and proper, and such credulity opens up human minds to the spread of maladaptive beliefs. This cost can be shaved by tinkering with human psychology, but it cannot be eliminated without also losing the adaptive benefits of cumulative cultural evolution. Culture is a little like breathing. One could reduce the chances of respiratory infections by breathing less, but the costs of doing so would curtail other essential activities. One could learn less from other people in order to avoid getting bad ideas from them. In humans, the optimum in these tradeoffs has led to lots of breathing and lots of cultural transmission.

4. NATURAL SELECTION IN CULTURALLY EVOLVED SOCIAL ENVIRONMENTS MAY HAVE FAVOURED NEW TRIBAL SOCIAL INSTINCTS

In regard to the moral qualities, some elimination of the worst dispositions is always in progress even in the most civilized nations. Malefactors are executed, or imprisoned for long periods, so that they cannot freely transmit their bad qualities.

(Charles Darwin, *The Descent of Man* 1871, p. 166)

We hypothesize that this new social world, created by rapid cultural adaptation, led to the genetic evolution of new, derived social instincts. Cultural evolution created cooperative groups. Such environments favoured the evolution of a suite of new social instincts suited to life in such groups including a psychology which ‘expects’ life to be structured by moral norms, and that is designed to learn and internalize such norms. New emotions evolved, like shame and guilt, which increase the chance the norms are followed. Individuals lacking the new social instincts more often violated prevailing norms and experienced adverse selection. They might have suffered ostracism, been denied the benefits of public goods, or lost points in the mating game. Cooperation and group identification in inter-group conflict set up an arms race that drove social evolution to ever-greater extremes of in-group cooperation. Eventually, human populations came to resemble the hunter-gathering societies of the ethnographic record. We think that the evidence suggests that after about 100 000 years ago most people lived in tribal scale societies (Kelly 1995). These societies are based upon in-group cooperation where in-groups of a few hundred to a few thousand people are symbolically marked by language, ritual practices, dress and the like. These societies are egalitarian, and political power is diffuse. People are quite ready to punish others for transgressions of social norms, even when personal interests are not directly at stake.

These new tribal social instincts did not eliminate ancient ones favouring self, kin and friends. The tribal instincts that support identification and cooperation in large groups, are often at odds with selfishness, nepotism and face-to-face reciprocity. People feel deep loyalty to their kin and friends, but they are also moved by larger loyalties to clan, tribe, class, caste and nation. Inevitably, conflicts arise. Families are torn apart by civil war. Parents send their children to war (or not) with painfully mixed emotions. Criminal cabals arise to prey upon the public goods produced by larger scale institutions. Elites take advantage of key locations in the fabric of society to extract disproportionate private rewards for their work. The list is endless.

Some of our colleagues in evolutionary psychology have complained to us that this story is too complicated. Wouldn't it be simpler to assume that culture is shaped by a psychology adapted to small groups of relatives? Well, maybe. But the same people almost universally believe an equally complex co-evolutionary story about the evolution of an innate language acquisition device (Pinker 1994, pp. 111–112). Such innate language instincts must have *coevolved* with culturally transmitted languages in much the same way that we hypothesize that the social instincts coevolved with culturally transmitted social norms. Initially, languages must have been acquired using mechanisms not specifically adapted for language learning. This combination created a new and useful form of communication. Those individuals innately prepared to learn a little more proto-language, or learn it a little faster, would have a richer and more useful communication system than others not so well endowed. Then selection could favour still more specialized language instincts, which allowed still richer and more useful communication, and so on. We think that human social instincts constrain and bias the kind of societies that we construct, but the details are filled in by the local cultural input (Steward 1955; Kelly 1995). When cultural parameters are set, the combination of instincts and culture produces operational social institutions.

5. CONCLUSION

The model described above gives a cogent Darwinian explanation for why human societies are so cooperative, and why human psychology seems to include prosocial motivations. The theory of cultural group selection is fairly well worked out, and there are a number of convincing examples of the process at work. We believe that work in this area can profit from two kinds of researches: first, there has been little systematic quantitative empirical work that allows an assessment of the relative importance of cultural group selection compared with other processes that shape cultural variation. We need quantitative empirical estimates of rates of group extinction, and of rates of spread of cultural variants due to differential imitation and differential migration. Quantitative estimates of cultural variation would also be useful. Second, this model predicts that societies should exhibit design at the group level, that we should be able to

understand the structure and variation of norms in terms of how they enhance group welfare. Of course there is a long tradition of functionalist explanation in the social sciences, but for the most part this work takes the form of group-level just so stories. What is needed are sharp, testable hypotheses about how group functional behaviours, especially group functional norms, should vary with ecology, group size, and other measurable variables.

REFERENCES

- Alba, R. & Nee, V. 2003 *Remaking the American mainstream: assimilation and the new immigration*. Cambridge, MA: Harvard University Press.
- Alexander, R. D. 1987 *The biology of moral systems*. New York, NY: Aldine de Gruyter.
- Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)
- Borjas, G. J. 1994 The economics of immigration. *J. Econ. Lit.* **32**, 1667–1717.
- Bowles, S. 2006 Group competition, reproductive leveling, and the evolution of human altruism. *Science* **314**, 1569–1572. (doi:10.1126/science.1134829)
- Boyd, R. & Richerson, P. J. 1988 The evolution of reciprocity in sizable groups. *J. Theor. Biol.* **132**, 337–356. (doi:10.1016/S0022-5193(88)80219-4)
- Boyd, R. & Richerson, P. J. 1992 Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13**, 171–195. (doi:10.1016/0162-3095(92)90032-Y)
- Boyd, R. & Richerson, P. J. 1996 Why culture is common, but cultural evolution is rare. *Proc. Br. Acad.* **88**, 77–93.
- Boyd, R. & Richerson, P. J. 2002 Group beneficial norms spread rapidly in a structured population. *J. Theor. Biol.* **215**, 287–296. (doi:10.1006/jtbi.2001.2515)
- Boyd, R. & Richerson, P. J. 2009 Voting with your feet: payoff biased migration and the evolution of group beneficial behavior. *J. Theor. Biol.* **257**, 331–339. (doi:10.1016/j.jtbi.2008.12.007)
- Boyd, R. & Richerson, P. J. In press. Transmission coupling mechanisms: cultural group selection. *Phil. Trans. R. Soc. B*.
- Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. 2003 The evolution of altruistic punishment. *Proc. Natl Acad. Sci. USA* **100**, 3531–3535. (doi:10.1073/pnas.0630443100)
- Bradley, R. S. 1999 *Paleoclimatology: reconstructing climates of the quaternary*, 2nd edn. San Diego, CA: Academic Press.
- Cronin, T. M. 1999 *Principles of paleoclimatology*. New York, NY: Columbia University Press.
- Cronk, L. 2002 From true Dorobo to Mukogodo Masai: contested ethnicity in Kenya. *Ethnology* **41**, 27–49.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
- Foley, R. & Gamble, C. 2009 The ecology of social transitions in human evolution. *Phil. Trans. R. Soc. B* **364**, 3267–3279. (doi:10.1098/rstb.2009.0136)
- Foster, K. R., Wenseleers, T. & Ratnieks, F. L. 2005 Kin selection is the key to altruism. *Trends Ecol. Syst.* **21**, 57–60. (doi:10.1016/j.tree.2005.11.020)
- Gardner, A. & West, S. 2004 Cooperation and punishment, especially in humans. *Am. Nat.* **164**, 753–764.
- Ghiselin, M. T. 1974 *The economy of nature and the evolution of sex*. Berkeley, CA: University of California Press.
- Haley, K. & Fessler, D. 2005 Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evol. Hum. Behav.* **26**, 245–256.

- Henrich, J. & Boyd, R. 2001 Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *J. Theor. Biol.* **208**, 79–89. (doi:10.1006/jtbi.2000.2202)
- Henrich, J. & Gil-White, F. J. 2001 The evolution of prestige—freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)
- Kelly, R. C. 1985 *The Nuer conquest*. Ann Arbor, MI: University of Michigan Press.
- Kelly, R. L. 1995 *The foraging spectrum: diversity in hunter-gatherer lifeways*. Washington, DC: Smithsonian Institution Press.
- Knauff, B. M. 1993 *South coast New Guinea cultures: history, comparison, dialectic*. Cambridge studies in social and cultural anthropology, no. 89. Cambridge, UK: Cambridge University Press.
- Lamb, H. H. 1977 *Climatic history and the future*. Princeton, NJ: Princeton University Press.
- Martin, P. 2005 Migrants in the global labor market, pp. 1–57. Global Commission on International Migration. See <http://www.gcim.org/attachements/TP1.pdf>.
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J. & Waring, T. 2008 Beyond existence and aiming outside the laboratory: estimating frequency-dependent and payoff-biased social learning strategies. *Phil. Trans. R. Soc. B* **363**, 3515–3528. (doi:10.1098/rstb.2008.0131)
- Nowak, M. A. & Sigmund, K. 2005 Evolution of indirect reciprocity. *Nature* **437**, 1291–1270. (doi:10.1038/nature04131)
- Palmer, C. T., Fredrickson, B. E. & Tilley, C. F. 1997 Categories and gatherings: group selection and the mythology of cultural anthropology. *Evol. Hum. Behav.* **18**, 291–308. (doi:10.1016/S1090-5138(97)00045-7)
- Panchanathan, K. & Boyd, R. 2004 Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* **432**, 499–502. (doi:10.1038/nature02978)
- Partridge, T. C., Bond, G. C., Hartnady, C. J. H., deMenocal, P. B. & Ruddiman, W. F. 1995 Climatic effects of Late Neogene tectonism and vulcanism. In *Paleoclimate and evolution with emphasis on human origins* (eds E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 8–23. New Haven, CT: Yale University Press.
- Pinker, S. 1994 *The language instinct: the new science of language and mind*. New York, NY: Penguin.
- Ratnieks, F. & Wenseleers, T. 2005 Policing insect societies. *Science* **307**, 54–56.
- Richerson, P. J. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- Richerson, P. J., Boyd, R. & Bettinger, R. L. 2005 Evolution on a restless planet: were environmental variability and environmental change major drivers of human evolution? In *Handbook of evolution*, vol. 2 (eds F. M. Wuketits & F. J. Ayala), pp. 223–242. Weinheim, Germany: John Wiley & Sons.
- Steward, J. 1955 *Theory of culture change*. Urbana, IL: University of Illinois Press.
- Soltis, J., Boyd, R. & Richerson, P. J. 1995 Can group-functional behaviors evolve by cultural group selection? An empirical test. *Curr. Anthropol.* **36**, 437–494.
- Tooby, J. & Cosmides, L. 1992 The psychological foundations of culture. In *The adapted mind: evolutionary psychology and the generation of culture* (eds J. H. Barkow, L. Cosmides & J. Tooby), pp. 19–136. New York, NY: Oxford University Press.
- Tooby, J. & DeVore, I. 1987 The reconstruction of hominid behavioral evolution through strategic modeling. In *The evolution of primate behavior: primate models* (ed. W. G. Kinsey), pp. 183–237. New York, NY: SUNY Press.
- Trivers, R. L. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57.