
CULTURE-GENE COEVOLUTION, LARGE-SCALE COOPERATION AND THE SHAPING OF HUMAN SOCIAL PSYCHOLOGY

MACIEK CHUDEK
DEPARTMENT OF PSYCHOLOGY
UNIVERSITY OF BRITISH COLUMBIA

WANYING ZHAO
DEPARTMENT OF PSYCHOLOGY
UNIVERSITY OF BRITISH COLUMBIA

JOSEPH HENRICH
DEPARTMENT OF PSYCHOLOGY
DEPARTMENT OF ECONOMICS
UNIVERSITY OF BRITISH COLUMBIA

Evolutionary approaches to understanding human sociality, and in particular to understanding cooperation and altruism, have yielded a wide range of important insights. Noteworthy examples include explorations of how natural selection has shaped our psychological capacities for recognising kin and differentially investing in offspring (e.g., Daly & Wilson 1999, DeBruine 2002). However, canonical evolutionary approaches to cooperation and altruism fail both empirically and theoretically when they aim to explain *larger-scale human cooperation*—that is, cooperation and exchange among hundreds or thousands of unrelated, ephemeral interactants. Empirically, these approaches do not take sufficient note of the peculiarities of human sociality, cooperation and exchange (e.g., Burnham & Johnson 2005), which a proper theory should address. Theoretically, much work from this perspective does not pay sufficiently close attention to what the mathematical evolutionary models of cooperation do, and do not, predict about patterns of altruism and cooperation (e.g., Price et al. 2002).

In this chapter we aim to highlight these deficiencies and provide an alternative approach to human social psychology rooted in culture-gene coevolutionary (CGC) theory. We begin by presenting five challenges to explaining larger-scale human cooperation and sociality, which we argue cannot be met by approaches that fail to explicitly incorporate cultural evolution. In the first half of this chapter, with these challenges in mind, we summarise a large body of theory and evidence that applies the logic of natural selection to developing hypotheses about our psychological capacities for cultural learning, and considers how *cultural evolutionary processes*, unleashed by these newly evolved capacities, interact with genetic evolution to shape our evolved social psychology. Building directly on the formal evolutionary modelling in this arena, we hypothesise that humans may possess a *norm-psychology* that includes default settings, expectations, memory biases and inferential mechanisms that facilitate and influence the acquisition of culturally-transmitted rules

and motivations. This suite of evolved psychological mechanisms allows individuals to adapt to the highly variable local social and physical environments inevitably inhabited by a cultural species. In the second half of this chapter, we consider the canonical evolutionary approaches to larger-scale cooperation (so called *mismatch hypotheses*), and discuss both the theoretical and empirical shortcomings of these approaches. We close by exploring how well each of these approaches meets our five challenges.

THE FIVE CHALLENGES OF HUMAN COOPERATION

Many species both live in social groups and cooperate, often to substantial degrees and in large groups (e.g., bees, ants and wasps). However larger-scale cooperation in humans has a set of interesting patterns that are not found in other species and jointly need to be explained. The five challenges are (Henrich & Henrich 2007):

- 1) **Species differences:** Why is the scale and intensity of human cooperation (at least for some societies) so different from that found among other primates and similar mammals? Any theory that purports to explain larger-scale human cooperation should also be tested against other, similar species where we do not see high levels cooperation. As we discuss below, many primate species live in small-scale stable social groups with lots of repeated interaction among many relatives, but do not cooperate like humans. All-purpose explanations that resort to features like “language” or “intelligence” only make the problem worse (Henrich & Henrich 2007, Lachmann & Bergstrom 2004).
- 2) **Scale and intensity differences:** Why does the scale and intensity of cooperation and sociality vary so dramatically among human societies, from societies entirely lacking collective action beyond the extended family to societies that routinely cooperate on the order of thousands or even millions of individuals, as in modern nation states? That is, explaining human cooperation requires explaining why some societies do NOT cooperate much at all, despite economic and ecological pressures for greater cooperation.
- 3) **Domain differences:** Why do the domains of cooperation vary so much from society to society? Comparative ethnography makes it clear that different social groups inhabiting the same ecology cooperate in different domains. Some cooperate only in warfare and fishing, while others, just downstream, cooperate only in house-building and communal rituals.
- 4) **Rapid intensification:** How can we account for the increasing scale and intensity of human cooperation over the last 12,000 years? Theories of human cooperation need to explain this “scaling-up” as some human populations moved from relatively small-scale communities to vast cities and states on time-scales of only millennia.
- 5) **Non-cooperative and maladaptive sociality:** Why do the sanctioning and other incentive mechanisms that support cooperation, such as those based on punishment, reputation, and signalling, also enforce social behaviour that is unrelated to cooperation, such as ritual practices, food taboos, and clothing choice? Why do these same mechanisms sometimes even sustain maladaptive practices, like the consumption of the brains of dead relatives (Durham 1991), penile subincision, or clitoral infibulations (Mackie 1996)?

Many theoretical efforts to explain larger-scale human cooperation aim only to explain its scale and intensity. However, as our challenges indicate, the puzzle of larger-scale human cooperation is both more difficult, and interesting, than is generally recognised. We next lay out a culture-gene

coevolutionary approach to this puzzle, which we believe provides a framework capable of meeting these five challenges.

BUILDING A THEORY FOR A CULTURAL SPECIES

We begin by recognising that humans are different from other species in a critical way. We are a cultural species. That is, compared to all other species, humans are heavily reliant on large assemblies of socially learned know-how that have accumulated over generations. Even the simplest hunter-gather populations are entirely dependent on these reservoirs of information (including skills, motivations, preferences, and practices) related to such domains as finding water, processing food, making fire, cooking, gathering, medicinal plant use, tool manufacture, tracking, and animal behaviour. Also culturally transmitted, are extensive bodies of social rules, beliefs, and values about rituals, meat sharing, water ownership, community defence, marriage, and kinship relations. Of course, the existence of all this culturally transmitted stuff doesn't diminish the importance of a rich evolved cognitive architecture—to the contrary, this reliance on transmitted information creates selection pressures which might not otherwise exist, for acquiring, storing and organising cultural knowledge about artefacts, foods, animals, plants, and human groups. Nevertheless, it does suggest that any complete account of human behaviour—even for understanding the survival of Palaeolithic foraging bands—requires a rich theory of cultural transmission and cultural evolution (Henrich 2008, Henrich & McElreath 2003).

How do we build an evolutionary theory for a cultural species? Our first step is to deploy the logic of natural selection, aided by formal evolutionary modelling, to generate hypotheses about the *learning strategies* by which individuals – be they toddlers or song birds – can best acquire new behaviours, including forms or elements of social behaviour (Boyd & Richerson 1985). Formal modelling permits researchers to systematically explore what kinds of strategies are favoured by natural selection, and under what conditions (e.g., McElreath & Strimling 2008). In these approaches, alongside direct experience (which, of course, is still important), learning strategies are divided into those that influence the adoption of a novel *cultural variant* (a belief, behaviour or anything else learned from others) based on its (1) *content*, what it actually is or says, or (2) *context*, the number or type of people expressing the variant, and the manner and situations in which they do. These learning strategies evolve because they allow cultural learners to most effectively extract useful information from their social milieu and adapt to their local social and physical environments (Henrich & McElreath 2007). Here are some examples.

Model-biased transmission is a context-based cultural learning strategy in which individuals use cues to figure out who, among their potential models (the people around them), are likely to possess adaptive information, and preferentially learn from these models. Theory suggests, and a wide range of empirical findings have confirmed, that both children and adults preferentially pay attention to and learn from models who are more skilful, competent, successful and prestigious. There is also evidence that learners use cues of ethnic markers (dialect, dress, etc.), sex, and age (Efferson et al. 2008a, Henrich & Gil-White 2001), which further allow learners to selectively acquire the ideas, beliefs, practices and preferences that are most likely to be useful to them later in life (McElreath et al. 2003). These learning strategies emerge early in childhood (Birch & Bloom 2002, Birch et al. 2008, Chudek et al. n.d., Jaswal 2004, Kinzler et al. 2007, Nurmsoo & Robinson 2009) and appear to influence many forms of cultural transmission, including social behaviour,

altruism (Henrich & Henrich 2007: Chapter 2), opinions, economic decisions, food preferences, strategies, beliefs, technological adoptions and dialect (Mesoudi 2008).

Conformist-biased transmission (Boyd & Richerson 1985: Chapter 7, Henrich & Boyd 1998) is another context-based strategy, where learners integrate observations from multiple models¹. By using strategies like 'copy the majority' or 'average what the prestigious individuals are doing' learners can piggyback on the learning costs already paid by many other individuals and reduce transmission errors (misperceptions of any single model's cultural variants), extracting cultural knowledge that is more adaptive, on-average, than anything they could acquire from a single model or figure out on their own (Henrich & Boyd 2002). Some empirical work supports these formal predictions (Carpenter 2004, Coultas 2004, Efferson et al. 2008b, Kohler et al. 2004, McElreath et al. 2005).

Alongside *context* biases, evolutionary approaches to cultural learning suggest a rich set of hypotheses about how learners should evaluate the *content* of cultural variants. The general insight is that learners should pay particular attention to and remember variants likely to contain adaptive information. Specifically, those judged, *ceteris paribus*, to be more (1) fitness relevant, (2) actionable and (3) plausible (that is, compatible with evolved intuitions or existing cultural beliefs; see Henrich 2009a). Such content—including information about meat (Fessler 2003), gossip and social interaction (Chudek et al. In prep., Mesoudi et al. 2006), disgust (Heath et al. 2001), dangerous animals (Barrett 2007), and social norms (O'Gorman et al. 2008)—usually sparks strong emotional responses or greater attention, increasing its likelihood of being stored in memory and recalled later, and may motivate or potentiate adaptive responses, a topic we turn to in our discussion of the internalisation of social norms.

Grounded both theoretical and empirically, these reliably developing features of human cognition generate, as a by-product, cumulative cultural evolution. Cumulative cultural evolution creates *de novo* a whole new set of selection pressures, which open up evolutionary vistas not accessible to non-cultural species.

MANY CULTURAL EVOLUTIONARY ROADS LEAD TO LARGER-SCALE COOPERATION AND SOCIAL NORMS

How do such innate learning strategies help explain larger-scale cooperation? Our next step is to take theoretically and empirically established findings about human cultural learning, and ask what happens when people use these learning strategies to ontogenetically adapt their social behaviour to interactions with others. Specifically, what happens in larger-scale cooperative interactions when people use these individually-adaptive learning strategies?(Panchanathan & Boyd 2004)

¹ A lively debate persists on the evolutionary foundations of conformist transmission (e.g., Guzman et al. 2007, Nakahashi 2007, Wakano & Aoki 2007).

Cultural evolutionary game theory has now repeatedly demonstrated several different ways in which cultural learning can sustain larger-scale cooperation. These approaches all work through some combination of the peculiarities of cultural transmission (vis-à-vis genetic inheritance) combined with incentive mechanisms related to punishment, rewarding, signalling, and reputation (Axelrod 1986, Boyd & Richerson 1992, Gintis et al. 2001, Henrich 2009b, Henrich & Boyd 2001, Kendal et al. 2006, Panchanathan & Boyd 2004). These models demonstrate how culturally transmitted patterns of behaviour can, when common, make prosocial choices more beneficial on-average for individuals than selfish ones. Below we explain why these same mechanisms are unlikely to stabilize cooperation by genetic inheritance alone.

All of these cultural evolutionary models give rise to stable behavioural regularities in social groups, or equilibria, in which deviations do not spread via adaptive learning. That is, stable states that could sensibly be called *social norms* arise as an emergent property of these systems. These stable states can sustain individually costly behaviours, and thus can include highly cooperative norms. However, the same mechanism can also sustain any costly behaviour, even if it does not benefit anyone. In fact, such mechanisms can sustain practices that hurt the group overall. That is, these evolutionary systems all have *multiple stable equilibria*. Stable states typically include those with high levels of cooperation, those with high levels of defection, and many others in which individuals pay costs to perform actions that do not help anyone (e.g., food taboos), and may even hurt the group (e.g., female infibulations).

Below we discuss the question of *equilibrium selection*, how cultural evolutionary processes can “select” among this multiplicity of potential stable equilibria/norms. Some of these processes, cultural group selection in particular, can favour the spread of group beneficial norms, including those that stabilise cooperation. Others may be important as well. Happily, this theoretical situation is looking more and more like the world, with its diverse variety of norms and institutions, recorded by anthropologists and sociologists over the last 150 years. We expect shared, culturally transmitted, behavioural regularities stabilised by either punishment or other incentives (like reputational damage or improvement) that can, but need not be, prosocial or group-beneficial and may even be maladaptive for groups. These theoretical features are crucial, and will help us explain the differences in the scale and intensity of human cooperation across societies (Challenge 2), the variation in domains of cooperation (Challenge 3), and the presence of some neutral or maladaptive (Edgerton 1992) social norms (Challenge 5).

Box 1: Game theoretic evolutionary modelling is a technique for exploring the societal-level consequences of many individual decisions. *Stable equilibria* are situations in which the distribution of an acquired behaviour or practice remains unchanged in a population. In the context of social interactions, these are usually situations where individuals who try to act differently from the equilibrium behaviour (or mix of behaviours) find themselves facing ever worse consequences. For instance, in tipping societies individuals who don't tip may find themselves spurned by their embarrassed friends, while in non-tipping societies, impudent tippers may face similar scorn.

EQUILIBRIUM SELECTION

Three broad theoretical approaches confront the problem of *equilibrium selection* (Henrich 2006). The first, and perhaps the most intuitive, is that rational, forward-looking individuals will recognise the long-term payoffs available at stable cooperative equilibria (i.e. queuing rather than pushing),

assume others are similarly sensible, and choose the prosocial state (Harsanyi & Selton 1988). Though this may be important in some special cases, there are three reasons why it is unlikely to be the main driver of equilibrium selection. First, groups and individuals are usually quite bad at foreseeing the outcome of complex, probabilistic processes (Tversky et al. 2005)— even with the aid of recent mathematical and computer technologies, this can be very hard and even theoretically impossible in sufficiently complex cases. Second, group decisions are often heavily influenced by leaders and coalitions whose interests diverge from the overall group. And third, as one looks across the globe, the world is still full of non-prosocial and even downright anti-social institutions that hurt the group as a whole (Edgerton 1992).

The second mechanism is stochasticity (Young 1998). Over long periods of time, rare accumulations of chance events shock the distribution of behaviours within a society from one equilibrium to another (Kendal et al. 2006). However, since these transits from one stable equilibrium to another are not equally likely, societies will spend more time at some stable states than others. This means that in the long run, some norms will be more common among societies than other norms, on the basis of stochastic fluctuations alone. Different evolved learning strategies can make these random, stochastic shifts more (a prestigious leader) or less (conformity) likely. Stochastic movements can drive interacting societies to different equilibria, providing the raw material for the third mechanism: *cultural group selection*.

At equilibrium the individuals within a group have reached a certain harmony; however groups at different equilibria also interact. This competition among groups with different stable norms will favour the spread of norms that best facilitate success and longevity in competition with other groups (Boyd & Richerson 1990, Henrich 2004). Competition among groups can take the form of warfare (with assimilation or extinction), demographic production, or more subtle forms in which individuals learn by observing more successful individuals from groups at more group-beneficial equilibria. This can lead to a differential flow of decisions, strategies, and even preferences from higher to lower payoff groups (Boyd & Richerson 2002), or to differential migration from high payoff groups to lower payoff groups (Boyd & Richerson 2009).²

Building on this foundation of formal modelling, there are now several lines of empirical evidence to support cultural group selection, including data from laboratory studies, ethnography, archaeology, and history. In the laboratory, Gurerk et. al. (2006) has shown how individuals migrate from lower payoff institutions to higher payoff ones, and adopt the local norms of that group (Henrich 2006). Ethnographically and ethno-historically, Atran et. al. (1999) has shown how conservation-oriented ecological beliefs spread from locally prestigious Itza Maya to Ladinos in Guatemala, and how highland Q'eqchi' Maya, with tightly bound cooperative institutions and commercially-oriented economic production, are spreading at the expense of both Itza and Ladinos. Soltis et al. (1995), using quantitative data gleaned from New Guinea ethnographies, has shown that even the slowest forms of cultural group selection (conquest) can occur in 500 to 1000 year time scales. Kelly (1985) has demonstrated how differences in culturally acquired beliefs about bride-price fuelled the Nuer expansion over the Dinka, and how different social institutions, underpinned

² Recent theoretical work by Lehman et. al. (2008, 2008, 2007) has sought to challenge some of these theoretical conclusions. Their models, however, make quite different assumptions (which are buried deep in the mathematics) about the (1) strength of cultural learning relative to the forces of mixing among group and (2) presence of multiple stable equilibria. Their efforts are not critiques but rather alternative hypotheses based on empirically difficult-to-support assumptions about human cultural transmission and social norms (Boyd et al. forthcoming).

by cultural beliefs about segmentary lineages, provided the decisive competitive advantage. Sahlins (1961) has argued that cultural beliefs in segmentary lineages facilitated both the Nuer and Tiv expansions. Using archaeological data, anthropologists are increasingly arguing for the importance of cultural group selection in prehistory (Flannery & Marcus 2000, Spencer & Redmond 2001), including competition among foragers (Bettinger & Baumhoff 1982, Young & Bettinger 1992). At the global level, Diamond (1997) has made a cultural group selection case for the European expansion after 1500AD, as well as for the Bantu and Austronesian expansions.

There is little doubt that in the real world, equilibrium selection likely mixes all the mechanism we have discussed above, along with some we have not thought of. While competition between groups (cultural group selection) spreads cooperative norms that can sustain internal harmony, conflict among interest groups within a society can shift them towards less harmonious outcomes, as predatory elites and other self-interested subgroups establish equilibria/norms that disproportionately benefit themselves (Henrich & Boyd 2008). Ideologically motivated groups with coercive power may even sustain equilibria at mad extremes.

In closing this section, we briefly address three interrelated questions about this approach. To begin, why are these processes unlikely to work for genetic evolution? There are three reasons. First, some of the mechanisms discussed rely on forms of transmission (e.g., conformist transmission) that do not exist for genes. Second, for those that do not rely on such mechanisms, genetic evolution might be able to produce stable equilibria, but equilibrium shifting (or searching the space of possible equilibria via stochastic shocks) and genetic group selection among stable equilibria are extremely slow—too slow given the time available for human evolution. Finally, and most importantly, assuming away these theoretical problems doesn't lead to a world that meets the five challenges. Even if cooperation can evolve genetically via one of the mechanism, it does not produce a world that fits with what we observe—it would not address the five challenges.

Next question: assuming we start in a world of defectors (who never cooperate), how did culturally-transmitted cooperation ever become common in that first group? It can spread once it is established in one group, but how can it spread when initially rare in all groups? As just noted, cultural transmission is noisier than genetic transmission, and for a variety of reasons, more subject to stochastic “peak shifting”. For example, the evolved learning strategies reviewed above can help explain how punishment norms might initially spread: at first they are championed by prestigious individuals (model-bias) and then preferentially learned because they're held by the majority (conformist-bias), or they become linked with other content-biased ideas, for instance: successful religions typically have potent, moralising deities (Atran & Henrich forthcoming, Henrich 2009b).

Finally, we are assuming these equilibria are stable against most shocks, and that there is not gradual deterministic movement away from cooperation. But, what if there is? What if all that these mechanisms of cultural transmission, punishment, reputation and signalling do is slow down an inevitable decay to full defection within groups? Some modelling work suggests that even this is not a devastating problem, if competition among cultural groups is strong enough. Boyd and his collaborators (2003, forthcoming) have shown that adding costly punishment to a model with intergroup competition and extinction can still dynamically sustain high levels of cooperation and punishment. This occurs even though *within a single isolated group* both cooperative and punishing strategies will decline to zero in the long run. Pursuing a similar strategy, Bowles and Choi have combined models involving warfare and altruism with empirical data on conflict and mortality rates from foraging populations. They show that, especially if one assumes the inheritance is

cultural, actual rates of intergroup competition are sufficient to spread and sustain altruistic behaviour (Bowles 2006, Choi & Bowles 2007). More generally, comparisons of genetic variation to cultural variation show that there is much more cultural variation among human groups than genetic variation, indicating that we should expect cultural group selection to be substantially more important in humans than genetic group selection (Bell et al. 2009).

So, to summarise our Culture-Gene Coevolutionary (CGC) account so far: The learning strategies which benefit individual members of a cultural species, when employed by many individuals, lead to stable group-wide patterns of behaviour: norms. Groups with more cooperative norms outcompete others by the various mechanisms of cultural group selection, spreading their cooperative norms.

CULTURE-GENE COEVOLUTION AND A NORM-PSYCHOLOGY

Recent investigations have documented many examples of the human genome responding and adapting to our cultural environment (for a review, see Laland et al. 2010). If norms are a ready by-product of a species heavily reliant on cultural learning, then social norms have likely been a ubiquitous and enduring part of our social environment. How might genetic evolution have adapted to their presence? We saw that *stable* means that, on average, those deviating from norms do worse than those who abide by them. Though the content of the norms themselves may change frequently, and even evolve to be more cooperative via cultural group selection, the need to figure them out and follow them (at least sometimes) has remained a stable feature of our social environments. It's plausible that these conditions selected for a *norm-psychology*: a suite of genetically evolved cognitive mechanisms that rapidly perceive the local norms of one's social group and acquire them.

Such a norm-psychology should include the capacity to learn and be motivated to follow a large range of norms, including those pertaining to the sanctioning of norm violations. In highly cooperative societies, individuals display prosocial behaviour even on occasions when a selfish act would be advantageous. One mechanism that can achieve this efficiently is via affect: norm-adherence just "feels" right because the motivation to comply with norms has been *internalised*. Punishment and reputation-based mechanisms can stabilise cooperative equilibria, but are effortful and costly: both for individuals to calculate payoffs and delay gratification, and for punishers to identify violators, track reputations and to carry out punishment. By internalising the motivation to behave in a norm-consistent manner, the culturally acquired affective shorthand does the work of deciding between alternative courses of action in recurring situations, reducing the need for external enforcement and costly deliberation. What is true of cultural transmission is also true of internalisation: learning from others, if done wisely, can often yield better results than trial and error. Natural selection uses internalisation to this end in other circumstances. For instance, people internalise food preferences merely by observing others enjoying something (Addessi et al. 2005, Birch 1980, 1987) presumably because this is usually an accurate indicator of what's good to eat. Similarly, at equilibrium, a group's norms are usually a good marker of the most individually advantageous behaviour, on average.

In some situations, reputation and punishment can actually make prosocial actions better for the individual, but in highly cooperative societies many individuals act prosocially even when anonymity ensures that these mechanisms don't apply (i.e. returning a stranger's wallet, anonymous charitable giving). Our CGC model of norm-psychology helps account for such phenomena. Internalising societal norms rather than deliberating each decision is better for an

individual *on average*, as it saves time and processing costs and minimises the risk of being punished when (error-prone and effortful) rational deliberation misfires. Such misfires include, for instance, being rationally tempted by decisions that yield short-term gains, without factoring in the diffuse long-term costs they bear as a result of the complex reputational system in which actors are embedded. But internalisation also has a cost (out-weighed by its benefit): norm-adherence in situations where it's *not* the individually best choice. Once stable cooperative norms have emerged, perhaps by cultural group selection, norm-psychology can turn *rationally* cooperative societies (where defection usually doesn't pay) into *highly* cooperative ones (where people cooperate even when it does not).

EMPIRICAL SUPPORT FOR NORM-PSYCHOLOGY

The above approach makes a number of empirical predictions about our evolved psychology. Here, we have only space to briefly present each prediction and sketch the available evidence.

Human should possess an intuitive ontology that scaffolds the acquisition of norms. That is, individuals intuitively assume that social rules exist, that these rules influence people's behaviour, that others ought to follow these rules, and that failure to adhere to these rules can have negative consequences. People assume such rules exist even when they do not know yet what the specific rules are. Recent work with younger children shows that (1) children spontaneously infer the existence of social rules, in one trial learning, (2) react negatively to deviations by others to a rule learned in one trial, and (3) spontaneously sanction norm violators (Rakoczy et al. 2008).

Because cultural group selection has selectively favoured mostly prosocial norms over tens of thousands of years, part of our intuitive scalding should include prosocial default content and related learning biases. Recent work by Hamlin and colleagues indicates that three-month-old preverbal infants are able to evaluate actions as either helpful or hurtful to another's goal. By six-months, and possibly earlier, they use this information as a basis for their own desire to interact with these helping or hindering individuals (Hamlin et al. 2007, Hamlin et al. 2010).

Humans should readily acquire costly social norms via cultural learning. An extensive body of research demonstrates that children acquire context-specific prosocial norms by observing others perform actions consistent with such norms. Children also spontaneously enforce prosocial norms on other children, suggesting that merely observing a costly prosocial act being modelled induces normative inferences. The effects of such inferences persist in re-tests weeks or months after initial learning (Bryan 1971, Bryan et al. 1971, reviewed in Henrich & Henrich 2007, Mischel & Liebert 1966, Rushton 1975, Rushton & Campbell 1977).

Both adhering to social norms and punishing norm violators should be intrinsically or internally rewarding. The evidence supporting this comes from economic games (Camerer 2003). Converging lines of evidence now indicate these games tap social norms for dealing with ephemeral interactants (those with whom the actor lacks any relationship, based on kinship, status, reciprocity, etc.) in situations involving money (Henrich et al. 2010). First, findings in these experiments vary dramatically across human populations in ways that correlate with the relevant norms (Henrich et al. 2005, Herrmann et al. 2008). Second, in the U.S. and Europe the costly prosocial behaviour measured in such experiments develops slowly over the life course and does not hit its adult plateaux until a person's mid-twenties (Carter & Irons 1991, Harbaugh et al. 2002, Henrich 2008, Sutter & Kocher 2007). Third, results can be influenced by re-framing the game in

ways that tap other social norms (Heyman & Ariely 2004, Pillutla & Chen 1999, Ross & Ward 1996), and the same framing effects operate differently in different places (Hayashi et al. 1999). Fourth, chimpanzees—lacking the relevant norms—do not show any prosociality when placed in parallel experiments (Jensen et al. 2007, Jensen et al. 2006, Silk et al. 2005, Vonk et al. 2008). Adult chimpanzees, unlike any human population ever studied including four-year olds, actually behave according to game theoretic predictions that assume pure self-interest.

Using these behavioural games, work in neuroeconomics shows that behaving according to acquired social norms—by cooperating, contributing to public goods or charity, and punishing in locally prescribed ways—activates the brain’s rewards or reward anticipation circuits in the same manner as does obtaining a direct cash payment (de Quervain et al. 2004, Fehr & Camerer 2007, Rilling et al. 2004, Sanfey et al. 2003, Tabibnia et al. 2008). These studies variously show that: complying with norms “feels good” to brains in the same way that personally getting money does; punishing by really hurting defectors (physically or monetarily) activates these reward circuits more than punishing symbolically. Activations of the brain’s reward circuitry in these experiments predict behavioural outcomes.

Once internalised, norm adherence should be automatic such that norm violations require a cognitive override. Violating norms (not adhering to norms), such as breaking promises or inflicting harm on an individual for utilitarian reasons, requires deliberately overriding more automatic responses by brain regions responsible for cognitive control and abstract reasoning (Baumgartner et al. 2009, Greene et al. 2004).

ALTERNATIVES: THE MISMATCH HYPOTHESES

Many evolutionary researchers resist the centrality of both cultural evolution and the emergence of social norms to understanding almost any aspect of human evolution, psychology, or behaviour. Instead, mainstream evolutionary approaches build primarily from the assumption that humans are well adapted to an ancestral, small-scale, nomadic lifestyle. Consequently, they argue that the high levels of human cooperation, fairness and trust observed in contemporary societies, as well as corresponding findings from behavioural experiments, arise from a (mis)application of cognitive heuristics evolved according to the logic of kinship and reciprocity (direct and indirect) for survival in ancestral small-scale societies. These misfires lead people, even in genuinely anonymous situations, to overestimate their relatedness to interactants, the likelihood of future interactions, and/or the possibility of reputation damage. These mechanisms “misfire”, the story goes, because they are adapted to cues present in ancestral societies and cannot fully recalibrate to either modern society (using modern cues) or to the artificial worlds of behavioural experiments. Below, we compare such *mismatch hypotheses* against our CGC approach, in light of the available empirical evidence. While misfire hypotheses are quite popular among evolutionary researchers, they are typically offered only in abbreviated form (Dawkins 2006, Johnson et al. 2003, Levitt & Dubner 2009, Nowak et al. 2000, Trivers 2004), and usually off-handedly. They have not, to our knowledge, been systematically presented or defended, with two possible exceptions (Burnham & Johnson 2005, Hagen & Hammerstein 2006).

We want to emphasise that we are not taking issue with mismatch hypotheses in general, only with those mismatch hypotheses related to human sociality. Mismatch hypotheses related to, for example, explaining why modern diets are so high in fat and sugar seem perfectly plausible to us.

Just because some mismatch hypotheses fit the data, does not mean all mismatch hypotheses are correct. Hereafter, when we write “mismatch hypotheses” we are concerned specifically with those explaining human cooperation and sociality.

This section proceeds in three steps. First, we clarify several common misconceptions regarding our criticisms of these mismatch hypotheses. Second, we delineate several theoretical problems for mismatch hypotheses. In short, mathematical models of cooperation reveal basic conceptual problems for mismatch intuitions such that it is difficult to even get them off the ground as cogent evolutionary hypotheses—despite their superficial plausibility. Third, we compare the claims about human ancestral social life required by mismatch theories to the available empirical evidence regarding human evolutionary history. While the data is thin, and the inferences necessarily substantial, there is little empirical reason to suspect that ancestral human social life was characterised by a lack of fitness-relevant interaction with (1) non-kin, (2) short-term interaction partners, or (3) situations without reputational repercussions. Nothing we know from studies of primates, paleoanthropology, or small-scale societies suggests our psychology should be insensitive or poor at recalibrating to *these three features* of modern social environments. Finally, we review recent experimental findings from both human and non-human primates that challenge mismatch hypotheses, while remaining consistent with our CGC approach. We close by examining how well both our approach and mismatch hypotheses do against the five challenges of human cooperation.

CLARIFICATION AND THEORETICAL PROBLEMS

Before we lay out our theoretical concerns with this approach, let’s clarify a common misconception. Though CGC also takes as its point of departure that humans possess evolved psychologies associated with kinship, status competition, and reciprocity, available mathematical evolutionary theory is not consistent with the claim that *these mechanisms alone* can explain the scale of human cooperation, let alone the other four challenges. We argue (1) that cultural evolution can harness and extend aspects of our *ancient social psychology* (e.g., kinship, status) to expand to the sphere of human cooperation, and (2) that this process may be sufficiently old and important that genetic evolution has responded, with the result that we possess a coevolved *tribal psychology* (Richerson & Boyd 1998), including norm-psychology, built on top of those ancient social instincts. Thus, the debate at hand is not a question of “evolved psychologies” vs. “culture”. It is a question of “only ancient evolved psychologies” (mismatch hypotheses) vs. “ancient evolved psychologies plus cultural evolution plus gene-culture coevolved psychologies” (CGC hypotheses: Henrich & Henrich 2007).

KINSHIP

Sociality mismatch hypotheses come in three distinct flavours – kinship, reciprocity and reputation; all are purely verbal extensions of formal modelling results. Kinship-mismatch builds on work by W.D. Hamilton (1964). Hamilton and his successors (West et al. 2007), with the aid of a few simplifying assumptions, translated formal models of complex evolutionary dynamics into a simpler, tractable insight that explains when kinship will promote cooperation: whenever $rb > c$, where b and c represent the benefits and costs of cooperation. Hamilton’s r is a key quantity which, *given some simplifying assumptions* is well-approximated by the probability that two individuals’ genes are identical by common descent. This value, sometimes called *relatedness*, can be readily calculated: for full siblings, parents and children, $r=.5$, for half-siblings $r=.25$, for cousins $r=.125$.

Testing the prediction that kinship promotes cooperation produces a very good fit – many species really do seem to recognise and preferentially help their kin, or at least avoid hurting them, including humans (Daly & Wilson 1982).

Given just this, the kinship-mismatch hypothesis seems plausible: ancestral humans lived in much smaller groups that probably consisted of numerous kin. If fitness interactions with non-kin were rare or inconsequential enough, couldn't our genome have evolved a reliable, cognitive-load-sparing heuristic of always assuming some minimum (non-zero) relatedness to interaction partners? Today those same cognitive heuristics may still drive us to cooperate with strangers, even when we could profit by defecting.

This argument is flawed. Even in communities of relatives, evolutionary theory predicts that individuals should try to accurately estimate how related they are to any particular interactant and moderate the degree of cooperation accordingly. Still, a mismatch theorist might argue that what's mismatched isn't our ability to gauge relatedness, but our capacity to calibrate to interactants for whom $r=0$; we heuristically always assume some relatedness. This reveals a deeper problem: claiming ancestral humans interacted in isolated kin groups violates one of the assumptions used to derive the simplified form of Hamilton's rule: that competition is global. If we assume individuals interact exclusively with local kin, Hamilton's rule becomes $\frac{r-\bar{r}}{1-\bar{r}} b > c$, where \bar{r} is a group's average relatedness (McElreath & Boyd 2007). In such societies, individuals should selectively cooperate only with *closer kin* than average (i.e. where $r - \bar{r} > 0$). In such a world, individuals would not cooperate with relatives who were less related than average and would in fact be *less* cooperative than if interaction (and competition) were global and included strangers (Boyd 1982, Gardner & West 2004).

If anything, kin selection predicts that animals like humans will *almost never* cooperate unconditionally with *all* the members of their local group; they will reserve cooperation for those they are *more* related to. Even if ancestral humans interacted exclusively with kin, they would not have evolved default heuristics for cooperating with just anyone, least of all strangers, and—in fact—we might predict spite toward distant relatives and strangers.

DIRECT RECIPROCITY

The reciprocity-mismatch hypothesis extends important formal results about the ability of reciprocity to sustain cooperation (Axelrod & Hamilton 1981, Boyd & Lorberbaum 1987, Trivers 1971). With some simplifying assumptions these too can boil down to a rule: cooperation can be sustained when $\omega b > c$, where ω is the probability of an individual interacting again with the same partner (Henrich & Henrich 2007). When this is true, pairs of cooperators can enjoy the benefits of continued cooperation, while unremitting defectors, whose past behaviours reveal their ill-intent, soon find their partners turning against them.

Reciprocity-mismatch theories claim that our psychology mistakenly promotes cooperation in historically anomalous, modern one-shot interactions because it was calibrated to cooperate by ancestral environments in which interactions were almost exclusively with long-term partners. This betrays a misunderstanding. Reciprocity theory predicts that reciprocators should always estimate their probability of future interactions and compare it to their cost/benefit ratio and that for any interactant, there is always a cost/benefit ratio at which one should defect. Whether “one-shot” interactions existed over human evolutionary history is *completely irrelevant*.

Again mismatchers might fall back on a subtler argument, that humans can estimate the expected number of future interactions, but since interactions with a very low probability of continuing rarely existed, natural selection calibrated a non-zero floor on our estimates. Thus sometimes we continue cooperating even when the actual likelihood of continuing interaction drops below b/c . One reason to be skeptical of this reasoning is that a recurrent feature of ancestral environments was the likelihood of death increasing with age. Survivorship curves for modern foragers (Gurven & Kaplan 2007) approach zero as individuals enter their 70s, and their peers repeatedly face interactions with a very low probability of continuing. Aging alone, exacerbated by disease and injury, generates ample need to calibrate for low-frequency interactions whose probability of continuing approaches zero.

Further, mismatch fans often point to early work by Axelrod (1984) indicating that successful strategies are generally “nice”, meaning they cooperate on the first round of an interaction. This finding, however, is based on an assumption of independent pairing. Releasing this assumption, which was made purely for analytical convenience, by modelling the emergence of more realistic networks of reciprocators yields the opposite conclusion: successful strategies are only “nice” until they establish a core set relationships, which is constrained by many factors, then they begin defecting on everyone else immediately (Hruschka & Henrich 2006). The logic of direct reciprocity does not predict *broad* cooperation or prosociality with new partners (repeated or not) under more plausible assumptions. Mismatch hypotheses built on an artefact of the early reciprocity models.

Even if we ignore these concerns, modelling work also indicates that direct reciprocity cannot sustain cooperation as groups get larger (Boyd & Richerson 1988, Joshi 1987). That is, if we take the available evolutionary theory seriously, we should predict that individuals will be keenly sensitive to the size of the cooperative group, defecting as soon as it rises above a handful of individuals, and that most reciprocity-based cooperation should be limited to dyads (Henrich & Henrich 2007). This means that direct reciprocity cannot sustain larger-scale cooperation even if we accept the typical image of ancestral human societies as small groups (unless one believes these groups were limited to size two).

In short, the available models of reciprocal altruism suggest selection will favour individuals who attend to costs, benefits, group size and the likelihood of future interactions, as well as to the costs of monitoring and sustaining their current relationships and to their current strategic ecology. No pure strategy is stable, even in the simplest models, so reciprocal altruists must consistently adjust their strategies (Henrich & Henrich 2007). This is perhaps why reciprocity is so rare in nature (Clutton-Brock 2009). Overall, we think there is little doubt that human behaviour and psychology are influenced by direct reciprocity, but theoretically speaking, there is no reason to suspect that this mechanism alone can sustain larger-scale cooperation—even if we assume a mismatch in social environments.

INDIRECT RECIPROCITY

Indirect reciprocity extends direct reciprocity by showing that cooperators can thrive if they withhold benefits from anyone who has a *reputation* for defecting on others, irrespective of whether they’ll interact with them again personally (Leimar & Hammerstein 2001, Ohtsuki & Iwasa 2004). Perhaps, the mismatch argument runs, cooperation in ancestral environments was sustained by reputation and groups were small enough that reputations were well known and accurate. Since reputations ensured negative consequences usually followed non-cooperative behaviour, we

evolved a cognitive heuristic for cooperation that misfires in anonymous modern interactions where reputation damage is unlikely.

There are two central problems with this version of the mismatch hypothesis. First, as with direct reciprocity and for the same reasons, indirect reciprocity works best for interactions involving pairs of individuals—not larger-scale cooperation (say, interactions of 30 people building a house, or raiding a nearby village). As the number of interactants increases, the chances for stable cooperation rapidly collapse because the poor reputations of one or two individuals penalise the whole cooperative group (Henrich & Henrich 2007).

Second, indirect reciprocity can only sustain cooperation when high quality (both accurate and complete) reputational information is available (Taylor & Nowak 2007). There are two forms of reputation in indirect reciprocity. The simpler version proposes that individuals directly observe interactions and judge the interactants (i.e. give them reputations) based on their behaviour. This is only plausible for very small groups, and only for some limited types of interactions. On this account, when groups become large enough that many interactions aren't witnessed directly by most individuals (and even foraging bands are this large), well-adapted indirect reciprocators should stop cooperating. The more complex form of reputation involves using language to spread reputational information. Unfortunately invoking this form simply introduces another cooperative dilemma, arguably even more pernicious than the one it solves (Lachmann & Bergstrom 2004). You cannot just “assume language” to get cooperation. Communication, the sharing of valuable, abstract information, is itself a challenging cooperative dilemma, which cannot be solved by simply assuming language.

There are models which extend indirect reciprocity via reputation to stabilise larger-scale cooperative dilemmas (Panchanathan & Boyd 2004). This modelling work, mentioned above, shows that these mechanisms produce multiple stable equilibria, including non-cooperative equilibria. Unless mismatch theorists invoke genetic group selection or (like CGC theorists) cultural group selection, there's no theoretical reason why indirect reciprocity should produce *cooperative* equilibria involving larger groups that spread across the species.

SOCIAL LIFE IN ANCESTRAL SOCIETIES

Let's now consider how mismatch hypotheses stack up against the empirical evidence, particularly the claims they make about ancestral environments. Kinship-mismatch requires not only that we lived in closely related groups (substantial coefficient of relatedness), but that those groups had sufficiently few non-kin members that any selective pressures to distinguish non-kin would have been trivial. The reciprocity (direct and indirect) versions require that (1) low-frequency interactions were fitness *irrelevant*, such that insufficient selection pressure existed for the evolution of an ability to calibrate one's expectation of future interactions to be near zero, and (2) interactions with individuals without reputations were similarly fitness irrelevant, such that humans have evolved an implicit assumption that costly reputational consequences always exists.

There are three kind of evidence that anthropologists typically use to reconstruct the nature of ancestral environments: data from (1) non-humans primates, (2) ethnographically known foraging populations, and (3) paleoanthropology (the stones and bones of ancestral societies).

Non-human primates like chimpanzees live in small-scale foraging societies, just as human ancestors did. How related are individuals in these groups? This question has been answered by long-term field observation and molecular genetics techniques. The average relatedness between pairs of individuals in three different chimpanzee societies in Tai National Park in West Africa range from 0.012 to 0.15 for males and -0.003 to 0.045 for female (Vigilant et al. 2001). Over 92% of all the dyads in these foraging groups have r -values less than 0.2. For an East African chimp community, values were even lower: males at $\bar{r} = -0.22$ and females at $\bar{r} = -0.082$, though not statistically significantly different. A recent study of chimps in an unusually large community in Kibale National park, Uganda (Langergraber et al. 2007) found the same pattern; average relatedness was about 0.02. This leaves little doubt that chimpanzees absolutely need to be able to calibrate to an r of zero, even when interacting with members of their own sex in their own group.

What about the reciprocity versions of the mismatch hypothesis: Do chimpanzees have infrequent interactions, perhaps with strangers, that have fitness relevant consequences? Absolutely. When chimpanzees from one group encounter chimpanzees from another group, violence is generally only avoided if the two groups are evenly matched. If a solitary male chimpanzee encounters a group of five stranger-chimpanzees, he'd best flee for his life, as the strangers are likely to try to kill him. During one 3.5 year study period in Kibale National Park in Uganda, researchers observed 95 boundary patrols by male coalitions; twelve resulted in intergroup violence and five in fatalities, along with four further fatal intergroup encounters in the months immediately following the study (Watts et al. 2006). Such coalitional, intergroup violence has also been observed in wild populations in Gombe National Park, Tanzania (Wilson et al. 2004) and Budongo forest, Uganda (Newton-Fisher 1999). Both strangers and non-relatives are a fitness-relevant, even potent, component of the small-scale societies of our closest relative.

This is consistent with interactions between unfamiliar chimpanzees at research facilities; chimpanzees go ape at the mere sight of a stranger-chimp, and experimental interactions cannot be performed with stranger-chimpanzees. Thus, despite living in more kin-based groups of mostly repeat interactions, selection appears to have favoured in chimpanzees a keen psychological ability to distinguish both strangers and non-kin.

Another source of data on ancestral human societies comes from ethnographically and historically known foraging populations. How closely related are the smallest scale foraging bands? Not very. In the most detailed study of pre-contact foraging band composition, data from 58 Ache (Paraguay) bands involving 980 adults and 20,614 dyadic relationships reveal an average degree of relatedness of 0.05. More importantly, about a quarter of a band were entirely unrelated, not even linked through marriage ties. Data from the Gebusi, a very small-scale population of forager-horticulturalists from New Guinea, shows that 28% of community coresidents are non-relatives (Knauff 1985). Less detailed data from 31 other foraging societies are consistent with the Ache picture (Hill et al. n.d.). These patterns are not surprising, given the importance of exogamy, band fluidity and bilocality among hunter-gathers (Marlowe 2003, 2004).

So the kinship version of mismatch hypothesis is a non-starter, but what about the reciprocity and reputation versions: are there fitness relevant interactions with low-frequency interactants and individuals for whom reputational information is unavailable? Are there interactions with strangers or individuals unlikely to be seen again? Fehr and Henrich (2003) have summarised the ample evidence for these kinds of interaction. Here are three highlights:

1. Life histories gathered from Australia foragers—living on a continent of hunter-gatherers—who had not seen a white man until their 60’s show frequent journeys across vast territories, often on “walkabout”, in which these foragers would encounter and briefly live with all manner of peoples they had never seen before and would never encounter again.
2. The earliest European explorers found that both Australian and Fuegian (South American) foragers had special rituals designed for bringing strangers into camp—implying that encounters with strangers were sufficiently frequent and the strangers themselves sufficiently different to drive the emergence of special rituals.
3. Among Kalahari foragers, periods of drought that hit approximately once in a person’s lifetime brought distant bands together at shared waterholes. Suddenly people needed to interact with many strangers with whom they were unlikely to interact again.

Based on ethnographic and ethno-historical observations, interactions with strangers and ephemeral interactants are neither uncommon nor fitness irrelevant in human foraging societies. This is true even if one puts aside the massive evidence for intergroup conflicts, raids, rapes, ambushes and theft by strangers and anonymous others (Bowles 2006, Keeley 1997). As noted previously, the mere fact that people get old, contract deadly diseases and suffer mortal wounds means there is no shortage of selection pressures to recognise slim chances for future interactions.

One basis for the reputational mismatch hypothesis is the view that ancestral societies were so closely knit that no actions could be anonymous or secret. Without even considering intergroup interactions, the ethnography of small-scale societies is full of clandestine actions within groups, in particular theft and adultery.³ Consistent with this, Table 1 shows two populations of foragers and two of forger-horticulturalists that have indigenous words for “secret” in their languages. There are no (indigenous) words for “computer” or “phone” in these languages, but they do have word(s) for “secret”.

Overall, the ethnographic and ethno-historical record does not provide support for the notion that ancestral foraging societies lacked fitness-relevant interactions with non-kin, low-frequency or short-term

interactants, strangers, or situations with low probabilities of reputational damage. Instead, it suggests that people should be keenly able to distinguish kin from non-kin, strangers

Group	Location	Word(s)
Hadza	Africa, Tanzania	chiki chikia
Ju (!Kung)	Africa, Kalahari	dcaa = to steal love secretly; have an affair. kaahn = secretly (adverb) g=om = to keep one’s mouth shut (keep a secret)
Tsimane	Amazonia, Bolivia	jumve, camin
Machiguenga	Amazonia, Peru	maireni

from frequent partners, and opportunities for action without reputational consequences.

³ Much work in evolutionary psychology is based on the assumption that extra-pair copulations (adultery) and copulations with different males in relatively short periods of time were not only possible, but a serious factor in the lives of our foraging ancestors (Buss 2007). If true, secrets and anonymity (like about paternity) were indeed possible, and individuals could avoid reputational damage and revenge while engaging in clandestine activities. We think this fits well with ethnography, but not with the assumptions of some mismatch hypotheses.

⁴ Thanks to Frank Marlowe, Glenn Sheppard, Mike Gurven, and Polly Weissner for this information.

We have presented a series of theoretical problems for mismatch hypotheses, showing that such hypotheses are actually inconsistent with the available theoretical work, and provided empirical evidence from both non-human primates and human foragers that challenge the assumptions required by mismatch hypotheses about the nature of ancestral environments. Now let's put all this aside and consider how mismatch hypotheses stack up against CGC theory in meeting the five challenges of human cooperation.

MEETING THE FIVE CHALLENGES

In this closing section we review each of the five challenges and briefly consider how mismatch hypotheses and CGC hypotheses address them.

- 1) **Species differences:** Why is the scale and intensity of human cooperation so different from that found among other primates? *CGC* hypothesises a long-term interaction between genetic and cultural evolution, initiated when a species becomes sufficiently dependent on cultural learning. Thus, the theory applies only to highly cultural species, which rules out all primates and most mammals. In contrast, *mismatch hypotheses* purport to explain larger-scale human cooperation using evolutionary models that are equally applicable to other primate species (among many other species). Short of nodding to something vague like “language” or “cognitive capacities,” there is little room in this approach to even account for differences in cooperation between human and chimpanzee foragers.
- 2) **Scale and intensity differences:** Why does the scale and intensity of cooperation and sociality vary so dramatically among human societies? *CGC* proposes that larger-scale cooperation depends on local, culturally-evolved norms. Different intensities of competition on different continents or in different regions, and in different ecologies, have favoured the proliferation of norms that vary in the nature and degree of prosociality they sustain. Mismatch hypotheses have not addressed this issue. One approach might be to invoke the jukebox analogy (Tooby & Cosmides 1992), and suggest that different environmental cues evoke different degrees of cooperation based on local affordances. Of course, we know that similar groups have revealed quite different degrees of cooperation even while inhabiting identical environments (Henrich et al. 2003).
- 3) **Domain differences:** Why do the domains of cooperation vary so much from society to society? For *CGC*, this is a prediction that follows directly from the notion that larger-scale cooperation is linked directly to local norms. Mismatch theorists have not tackled this one. They might again deploy the jukebox analogy, emphasising varying costs and benefits across different domains.
- 4) **Rapid intensification:** How can we account for the increasing scale and intensity of human cooperation over the last 12,000 years? *CGC* explains this with cultural group selection. Climatic changes at the beginning of the Holocene created conditions favourable to agriculture and larger societies (Henrich et al. 2010, Richerson et al. 2001). Those societies with norms and institutions best suited to sustaining ever expanding cooperative populations engaged in mutually beneficial transactions and spread at the expense of other groups. Mismatch theorists have not addressed this issue.
- 5) **Non-cooperative and maladaptive sociality:** Why do the sanctioning mechanisms that enforce cooperation also sustain social behaviour that is unrelated to cooperation, such as ritual practices, food taboos, and clothing choice? For *CGC*, this prediction emerged unexpectedly from mathematical models of larger-scale cooperation—punishment,

reputation and signalling can all sustain any costly action, not merely cooperation. Mismatch theorists might try to deny this claim, and instead propose distinct explanations for each non-cooperative phenomenon.

REFERENCES

- Addressi, E., Galloway, A. T., Visalberghi, E. & Birch, L. L. (2005) Specific social influences on the acceptance of novel foods in 2-5-year-old children. *Appetite* 45: 264-271.
- Atran, S. & Henrich, J. (forthcoming) The Evolution of Religion: How Cognitive By-Products, Adaptive Learning Heuristics, Ritual Displays, and Group Competition Generate Deep Commitments to Prosocial Religions. *Biological Theory* 5(1): 1-13.
- Atran, S., Medin, D. L., Ross, N., Lynch, E., Coley, J., Ek, E. U. & Vapnarsky, V. (1999) Folkecology and commons management in the Maya Lowlands. *Proc. Natl. Acad. Sci.* 96: 7598-7603.
- Axelrod, R. (1984) *The Evolution of Cooperation*, Basic Books.
- Axelrod, R. (1986) An Evolutionary Approach to Norms. *American Political Science Review* 80(4): 1095-1111.
- Axelrod, R. & Hamilton, W. D. (1981) The evolution of cooperation. *Science* 211(1): 390-396.
- Barrett, H. C. (2007). *Evolved developmental systems and prepared learning about dangerous animals in children*. Unpublished manuscript, Los Angeles.
- Baumgartner, T., Fischbacher, U., Feierabend, A., Lutz, K. & Fehr, E. (2009) The Neural Circuitry of a Broken Promise. *Neuron* 64(5): 756-770.
- Bell, A. V., Richerson, P. J. & McElreath, R. (2009) Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences of the United States of America* 106(42): 17671-17674.
- Bettinger, R. L. & Baumhoff, M. A. (1982) The Numic Spread: Great Basin Cultures in Competition. *American Antiquity* 47(3): 485-503.
- Birch, L. L. (1980) Effects of Peer Model's Food Choices on Eating Behaviors on Preschooler's Food Preferences. *Child Development* 51: 489-496.
- Birch, L. L. (1987) Children's Food Preferences: Developmental Patterns and Environmental Influence. *Annals of Child Development* 4: 171-208.
- Birch, S. A. J. & Bloom, P. (2002) Preschoolers Are Sensitive to the Speaker's Knowledge When Learning Proper Names. *Child Development* 73(2): 434-444.
- Birch, S. A. J., Vauthier, S. A. & Bloom, P. (2008) Three- and four-year-olds spontaneously use others' past performance to guide their learning. *Cognition: International Journal of Cognitive Science* 107(3): 1018-1034.
- Bowles, S. (2006) Group competition, reproductive leveling, and the evolution of human altruism. *Science* 314(5805): 1569-1572.
- Boyd, R. (1982) Density-dependent mortality and the evolution of social interactions. *Animal Behaviour* 30(4): 972-982.
- Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. (2003) The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences of the United States of America* 100(6): 3531-3535.
- Boyd, R. & Lorberbaum, J. (1987) No pure strategy is evolutionarily stable in the repeated Prisoner's Dilemma game.
- Boyd, R. & Richerson, P. (1988) The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology* 132: 337-356.

- Boyd, R. & Richerson, P. (1992) Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups. *Ethology & Sociobiology* 13(3): 171-195.
- Boyd, R. & Richerson, P. (2002) Group Beneficial Norms Can Spread Rapidly in a Structured Population. *Journal of Theoretical Biology* 215: 287-296.
- Boyd, R. & Richerson, P. J. (1985) *Culture and the Evolutionary Process*, University of Chicago Press.
- Boyd, R. & Richerson, P. J. (1990) Group Selection Among Alternative Evolutionarily Stable Strategies. *Journal of Theoretical Biology* 145: 331-342.
- Boyd, R. & Richerson, P. J. (2009) Voting with your feet: Payoff biased migration and the evolution of group beneficial behavior. *Journal of Theoretical Biology* 257(2): 331-339.
- Boyd, R., Richerson, P. J. & Henrich, J. (forthcoming) Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral Ecology and Sociobiology*.
- Bryan, J. H. (1971) Model Affect and Children's Imitative Altruism. *Child Development* 42(6): 2061-2065.
- Bryan, J. H., Redfield, J. & Mader, S. (1971) Words and Deeds about Altruism and the Subsequent Reinforcement Power of the Model. *Child Development* 42(5): 1501-1508.
- Burnham, T. C. & Johnson, D. D. (2005) The Biological and Evolutionary Logic of Human Cooperation. *Analyse and Kritik* 27: 113-135.
- Buss, D. (2007) *Evolutionary Psychology: The New Science of the Mind*, Allyn & Bacon.
- Camerer, C. (2003) *Behavior Game Theory: Experiments in Strategic Interaction*, Princeton University Press.
- Carpenter, J. (2004) When in Rome: Conformity and the Provision of Public Goods. *Journal of Socio-Economics* 4(4): 395-408.
- Carter, J. R. & Irons, M. D. (1991) Are Economists Different, and If So, Why? *Journal of Economic Perspectives* 5(Spring): 171-177.
- Choi, J.-K. & Bowles, S. (2007) The coevolution of parochial altruism and war. *Science* 318(5850): 636-640.
- Chudek, M., Heller, S., Birch, S. & Henrich, J. (n.d.). *Prestige-Bias: Developmental Evidence for Biased Cultural Learning*. Unpublished manuscript, Vancouver.
- Chudek, M., Mesoudi, A., Collard, M. & Henrich, J. (In prep.) Social Recall Bias: An Influence on the Evolution of Cultural Information?
- Clutton-Brock, T. (2009) Cooperation between non-kin in animal societies. *Nature* 462(7269): 51-57.
- Coultas, J. (2004) When in Rome... An Evolutionary Perspective on Conformity. *Group Processes & Intergroup Relations* 7(4): 317-331.
- Daly, M. & Wilson, M. (1982) Homicide and kinship. *American Anthropologist*: 372-378.
- Daly, M. & Wilson, M. (1999) *The truth about Cinderella: a Darwinian view of parental love*, Yale University Press.
- Dawkins, R. (2006) *The God delusion*, Houghton Mifflin Co.
- de Quervain, D. J., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A. & Fehr, E. (2004) The Neural Basis of Altruistic Punishment. *Science* 305: 1254-1258.
- DeBruine, L. (2002) Facial resemblance enhances trust. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 1307-1312.
- Diamond, J. M. (1997) *Guns, Germs, and Steel: The Fates of Human Societies*, W.W. Norton & Co.
- Durham, W. H. (1991) *Coevolution : genes, culture, and human diversity*, Stanford University Press.
- Edgerton, R. B. (1992) *Sick societies : challenging the myth of primitive harmony*, Free Press.
- Efferson, C., Lalive, R. & Fehr, E. (2008a) The coevolution of cultural groups and ingroup favoritism. *Science* 321(5897): 1844-1849.
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R. & Lubell, M. (2008b) Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior* 29(1): 56-64.

- Fehr, E. & Camerer, C. F. (2007) Social neuroeconomics: the neural circuitry of social preferences. *Trends in Cognitive Sciences* 11(10): 419-427.
- Fehr, E. & Henrich, J. (2003) Is Strong Reciprocity a Maladaptation? In: *Genetic and Cultural Evolution of Cooperation*, ed. P. Hammerstein, MIT Press.
- Fessler, D. M. T. (2003) Meat Is Good to Taboo: Dietary Proscriptions as a Product of the Interaction of Psychological Mechanisms and Social Processes. *Journal of Cognition and Culture* 3(1): 1-40.
- Flannery, K. V. & Marcus, J. (2000) Formative Mexican chiefdoms and the myth of the 'Mother Culture'. *Journal of Anthropological Archaeology* 19(1-37).
- Gardner, A. & West, S. (2004) Spite and the scale of competition. *Journal of Evolutionary Biology* 17(6): 1195-1203.
- Gintis, H., Smith, E. A. & Bowles, S. (2001) Costly signaling and cooperation. *Journal of Theoretical Biology* 213(1): 103-119.
- Greene, J., Nystrom, L., Engell, A., Darley, J. & Cohen, J. (2004) The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44(2): 389-400.
- Gurerk, O., Irlenbusch, B. & Rockenbach, B. (2006) The Competitive Advantage of Sanctioning Institutions. *Science* 312: 108-111.
- Gurven, M. & Kaplan, H. (2007) Longevity among hunter-gatherers: A cross-cultural examination. *Population and Development Review* 33(2): 321-365.
- Guzman, R. A., Rodriguez-Sickert, C. & Rowthorn, R. (2007) When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation. *Evolution and Human Behavior* 28(2): 112-117.
- Hagen, E. H. & Hammerstein, P. (2006) Game theory and human evolution: A critique of some recent interpretations of experimental games. *Theoretical Population Biology* 69(3): 339-348.
- Hamilton, W. D. (1964) The genetical evolution of social behavior. *Journal of Theoretical Biology* 7: 1-52.
- Hamlin, J. K., Wynn, K. & Bloom, P. (2007) Social evaluation by preverbal infants. *Nature* 450(7169): 557-U513.
- Hamlin, J. K., Wynn, K. & Bloom, P. (2010) Three-month-olds show a negativity bias in their social evaluations. *Developmental Science*: 1-7.
- Harbaugh, W. T., Krause, K. & Liday, S. G. (2002). *Bargaining by Children*. Unpublished manuscript.
- Harsanyi, J. C. & Selton, R. (1988) *A General Theory of Equilibrium Selection in Games*, MIT Press.
- Hayashi, N., Ostrom, E., Walker, J. & Yamagishi, T. (1999) Reciprocity, trust, and the sense of control - A cross-societal study. *Rationality and Society* 11(1): 27-46.
- Heath, C., Bell, C. & Sternberg, E. (2001) Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology* 81(6): 1028-1041.
- Henrich, J. (2004) Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization* 53: 3-35.
- Henrich, J. (2006) Cooperation, Punishment, and the Evolution of Human Institutions. *Science* 312: 60-61.
- Henrich, J. (2008) A cultural species. In: *Explaining Culture Scientifically*, ed. M. Brown, University of Washington Press.
- Henrich, J. (2009a) The evolution of costly displays, cooperation and religion: credibility enhancing displays and their implications for cultural evolution. *Evolution and Human Behavior* 30(4): 244-260.
- Henrich, J. (2009b) The evolution of costly displays, cooperation, and religion: credibility enhancing displays and their implications for cultural evolution. *Evolution and Human Behavior* 30: 244-260.

- Henrich, J., Bowles, S., Smith, E. A., Young, H. P., Boyd, R., Sigmund, K., Richerson, P. J. & Hopfensitz, A. (2003) The Cultural and Genetic Evolution of Human Cooperation. In: *Genetic and Cultural Evolution of Cooperation*, ed. P. Hammerstein, MIT Press.
- Henrich, J. & Boyd, R. (1998) The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior* 19: 215-242.
- Henrich, J. & Boyd, R. (2001) Why People Punish Defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology* 208: 79-89.
- Henrich, J. & Boyd, R. (2002) On Modeling Cultural Evolution: Why replicators are not necessary for cultural evolution. *Journal of Cognition and Culture* 2(2): 87-112.
- Henrich, J. & Boyd, R. (2008) Division of Labor, Economic Specialization, and the Evolution of Social Stratification. *Current Anthropology* 49(4): 715-724.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R., Alvard, M., Barr, A., Ensminger, J., Henrich, N. S., Hill, K., Gil-White, F., Gurven, M., Marlowe, F. W., Patton, J. Q. & Tracer, D. (2005) "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences* 28(6): 795-855.
- Henrich, J., Ensminger, J., McElreath, R., Barr, A., Barrett, C., Bolyanatz, A., Cardenas, J. C., Gurven, M., Gwako, E., Henrich, N., Lesorogol, C., Marlowe, F., Tracer, D. P. & Ziker, J. (2010) Market, religion, community size and the evolution of fairness and punishment. *Science* 327: 1480-1484.
- Henrich, J. & Gil-White, F. (2001) The Evolution of Prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22(3): 165-196.
- Henrich, J. & McElreath, R. (2003) The Evolution of Cultural Evolution. *Evolutionary Anthropology* 12(3): 123-135.
- Henrich, J. & McElreath, R. (2007) Dual Inheritance Theory: The Evolution of Human Cultural Capacities and Cultural Evolution. In: *Oxford Handbook of Evolutionary Psychology*, eds. R. Dunbar & L. Barrett, Oxford University Press.
- Henrich, N. & Henrich, J. (2007) *Why Humans Cooperate: A Cultural and Evolutionary Explanation* Oxford University Press.
- Herrmann, B., Thöni, C. & Gächter, S. (2008) Antisocial punishment across societies. *Science* 319: 1362-1367.
- Heyman, J. & Ariely, D. (2004) Effort for payment - A tale of two markets. *Psychological Science* 15(11): 787-793.
- Hill, K. R., Walker, R., Bozicevic, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A. M., Marlowe, F. W., Wiessner, P. & Wood, B. (n.d.) Unique ancestral human social structure indicated by coresidence patterns in hunter-gatherer societies.
- Hruschka, D. & Henrich, J. (2006) Friendship, Cliquishness, and the Emergence of Cooperation. *Journal of Theoretical Biology* 239(1): 1-15.
- Jaswal, V. K. (2004) Don't Believe Everything You Hear: Preschoolers' Sensitivity to Speaker Intent in Category Induction. *Child Development* 75(6): 1871-1885.
- Jensen, K., Call, J. & Tomasello, M. (2007) Chimpanzees are rational maximizers in an ultimatum game. *Science* 318(5847): 107-109.
- Jensen, K., Hare, B., Call, J. & Tomasello, M. (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B-Biological Sciences* 273(1589): 1013-1021.
- Johnson, D., Stopka, P. & Knights, S. (2003) The puzzle of human cooperation. *Nature* 421: 911-912.
- Joshi, N. V. (1987) Evolution of cooperation by reciprocity within structured demes. *Journal of Genetics* 66(1): 69-84.
- Keeley, L. (1997) *War Before Civilization*, Oxford University Press.

- Kelly, R. C. (1985) *The Nuer Conquest*, University of Michigan Press.
- Kendal, J., Feldman, M. W. & Aoki, K. (2006) Cultural coevolution of norm adoption and enforcement when punishers are rewarded or non-punishers are punished. *Theoretical Population Biology* 70(1): 10-25.
- Kinzler, K. D., Dupoux, E. & Spelke, E. S. (2007) The native language of social cognition. *Proceedings of the National Academy of Sciences of the United States of America* 104(30): 12577-12580.
- Knauft, B. M. (1985) *Good Company and Violence: Sorcery and Social Action in a Lowland New Guinea Society*.
- Kohler, T. A., VanBuskirk, S. & Ruscavage-Barz, S. (2004) Vessels and villages: evidence for conformist transmission in early village aggregations on the Pajarito Plateau, New Mexico. *Journal of Anthropological Archaeology* 23(1): 100-118.
- Lachmann, M. & Bergstrom, C. T. (2004) The disadvantage of combinatorial communication. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271(1555): 2337-2343.
- Laland, K., Odling-Smee, J. & Myles, S. (2010) How culture shaped the human genome: Bringing genetics and the human sciences together. *Nature Reviews Genetics* 11(2): 137-148.
- Langergraber, K. E., Mitani, J. C. & Vigilant, L. (2007) The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences* 104(19): 7786-7790.
- Lehmann, L. & Feldman, M. W. (2008) The co-evolution of culturally inherited altruistic helping and cultural transmission under random group formation. *Theoretical Population Biology* 73(4): 506-516.
- Lehmann, L., Feldman, M. W. & Foster, K. R. (2008) Cultural transmission can inhibit the evolution of altruistic helping. *American Naturalist* 172(1): 12-24.
- Lehmann, L., Rousset, F., Roze, D. & Keller, L. (2007) Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. *American Naturalist* 170(1): 21-36.
- Leimar, O. & Hammerstein, P. (2001) Evolution of cooperation through indirect reciprocity. *Proceedings: Biological Sciences* 268(1468): 745-753.
- Levitt, S. D. & Dubner, S. J. (2009) *Super freakonomics : global cooling, patriotic prostitutes and why suicide bombers should buy life insurance*, HarperCollins.
- Mackie, G. (1996) Ending Footbinding and Infibulation: A Convention Account. *American Sociological Review* 61(6): 999-1017.
- Marlowe, F. W. (2003) The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research* 37(3): 282-306.
- Marlowe, F. W. (2004) Marital residence among foragers. *Current Anthropology* 45(2): 277-284.
- McElreath, R. & Boyd, R. (2007) *Mathematical Models of Social Evolution: A Guide for the Perplexed*, Univ of Chicago Press.
- McElreath, R., Boyd, R. & Richerson, P. J. (2003) Shared Norms and the Evolution of Ethnic Markers. *Current Anthropology* 44(1): 122-129.
- McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. & Paciotti, B. (2005) Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior* 26(6): 483-508.
- McElreath, R. & Strimling, P. (2008) When Natural Selection Favors Imitation of Parents. *Current Anthropology* 49(2): 307-316.
- Mesoudi, A. (2008) An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer-scrounger dynamics, and informational access costs. *Evolution and Human Behavior* 29(5): 350-363.
- Mesoudi, A., Whiten, A. & Dunbar, R. (2006) A bias for social information in human cultural transmission. *British Journal of Psychology* 97: 405-423.

- Mischel, W. & Liebert, R. M. (1966) Effects of discrepancies between observed and imposed reward criteria on their acquisition and transmission. *Journal of Personality and Social Psychology* 3: 45-53.
- Nakahashi, W. (2007) The evolution of conformist transmission in social learning when the environment changes periodically. *Theoretical Population Biology* 72(1): 52-66.
- Newton-Fisher, N. (1999) Infant killers of Budongo. *Folia Primatologica* 70(3): 167-169.
- Nowak, M. A., Page, K. M. & Sigmund, K. (2000) Fairness versus reason in the Ultimatum Game. *Science* 289(5485): 1773-1775.
- Nurmsoo, E. & Robinson, E. J. (2009) Identifying unreliable informants: do children excuse past inaccuracy? *Developmental Science* 12(1): 41-47.
- O'Gorman, R., Wilson, D. S. & Miller, R. R. (2008) An evolved cognitive bias for social norms. *Evolution and Human Behavior* 29(2): 71-78.
- Ohtsuki, H. & Iwasa, Y. (2004) How should we define goodness?--reputation dynamics in indirect reciprocity. *Journal of Theoretical Biology* 231(1): 107-120.
- Panchanathan, K. & Boyd, R. (2004) Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* 432: 499-502.
- Pillutla, M. M. & Chen, X. P. (1999) Social Norms and Cooperation in Social Dilemmas: The Effects of Context and Feedback. *Organizational Behavior and Human Decision Processes* 78(2): 81-103.
- Price, M., Tooby, J. & Cosmides, L. (2002) Punitive sentiment as an anti-free rider psychological device. *Evolution and Human Behavior* 23: 203-231.
- Rakoczy, H., Wameken, F. & Tomasello, M. (2008) The sources of normativity: Young children's awareness of the normative structure of games. *Developmental Psychology* 44(3): 875-881.
- Richerson, P. & Boyd, R. (1998) The Evolution of Ultrasociality. In: *Indoctrinability, Ideology and Warfare*, eds. I. Eibl-Eibesfeldt & F. K. Salter, Berghahn Books.
- Richerson, P. J., Boyd, R. & Bettinger, R. L. (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *American Antiquity* 66(3): 387-411.
- Rilling, J. K., Sanfey, A. G., Nystrom, L. E., Cohen, J. D., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S. & Kilts, C. D. (2004) Imaging the social brain with fMRI and interactive games. *International Journal of Neuropsychopharmacology* 7: S477-S478.
- Ross, L. & Ward, A. (1996) Naive Realism: Implications for Social Conflict and Misunderstanding. In: *Values and Knowledge*, eds. T. Brown, E. Reed & E. Turiel, Lawrence Erlbaum Associates.
- Rushton, J. P. (1975) Generosity in children: Immediate and long term effects of modeling, preaching, and moral judgement. *Journal of Personality and Social Psychology* 31: 459-466.
- Rushton, J. P. & Campbell, A. C. (1977) Modeling, vicarious reinforcement and extraversion on blood donating in adults. Immediate and long-term effects. *European Journal of Social Psychology*.
- Sahlins, M. (1961) The Segmentary Lineage: An Organization of Predatory Expansion. *American Anthropologist* 63(2): 322-345.
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E. & Cohen, J. D. (2003) The Neural Basis of Economic Decision-Making in the Ultimatum Game. *Science* 300: 1755-1758.
- Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaró, J. & Shapiro, S. J. (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437: 1357-1359.
- Soltis, J., Boyd, R. & Richerson, P. J. (1995) Can group-functional behaviors evolve by cultural group selection? An empirical test. *Current Anthropology* 36(3): 473-494.
- Spencer, C. & Redmond, E. (2001) Multilevel Selection and Political Evolution in the Valley of Oaxaca. *Journal of Anthropological Archaeology* 20: 195-229.
- Sutter, M. & Kocher, M. (2007) Age and the development of trust and reciprocity. *Games and Economic Behavior* 59: 364-382.

- Tabibnia, G., Satpute, A. B. & Lieberman, M. D. (2008) The sunny side of fairness - Preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychological Science* 19(4): 339-347.
- Taylor, C. & Nowak, M. (2007) Transforming the dilemma. *Evolution; international journal of organic evolution* 61(10): 2281.
- Tooby, J. & Cosmides, L. (1992) The psychological foundations of culture. In: *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, eds. J. Barkow, L. Cosmides & J. Tooby, Oxford University Press.
- Trivers, R. (2004) BEHAVIORAL EVOLUTION: Mutual Benefits at All Levels of Life. *Science* 304(5673): 964-965.
- Trivers, R. L. (1971) The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology* 46: 34-57.
- Tversky, A., Kahneman, D. & Slovic, P. (2005) Judgment under uncertainty: Heuristics and biases. *Social Cognition: Key Readings*: 167.
- Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. (2001) Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America* 98(23): 12890-12895.
- Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., Schapiro, S. J. & Povinelli, D. J. (2008) Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour* 75: 1757-1770.
- Wakano, J. Y. & Aoki, K. (2007) Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theoretical Population Biology* 72(4): 504-512.
- Watts, D., Muller, M., Amsler, S., Mbabazi, G. & Mitani, J. (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American journal of primatology* 68(2): 161.
- West, S., Griffin, A. & Gardner, A. (2007) Evolutionary explanations for cooperation. *Current Biology* 17(16): R661-R672.
- Wilson, M., Wallauer, W. & Pusey, A. (2004) New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology* 25(3): 523-549.
- Young, D. & Bettinger, R. L. (1992) The Numic Spread: A computer simulation. *American Antiquity* 57(1): 85-99.
- Young, H. P. (1998) *Individual strategy and social structure : an evolutionary theory of institutions*, Princeton University Press.