
CULTURAL EVOLUTION IN CHIMPANZEES AND HUMANS

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Over the last few decades researchers from diverse disciplines have developed cultural evolutionary and gene-culture coevolutionary theory (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Laland et al. 2011). Applied to humans, this approach has yielded a range of new insights into our species' evolution, behavior and psychology, and broadened into research programs in biology, anthropology, psychology and economics (Chudek and Henrich 2010; Richerson and Boyd 2005). Here, we apply these theoretical developments to chimpanzees by reviewing the now large body of evidence on chimpanzees' social learning, culture and traditions. Along the way, we provide comparative evidence for humans to assess the similarities and differences between the species. By asking theoretically-driven questions about the nature of culture in each species, we aim to assess both their shared phylogenetic heritage, and to begin to isolate those selective forces that have distinguished these lineages over the last five to six million years.

Our review begins with a brief introduction to culture-gene coevolutionary theory, though specific elements of the theory will be rolled out as we go along, in the relevant sections. We emphasize that our goal here is to apply theoretically-derived insights to the available evidence from chimpanzees, and not to provide a general review of all work on this topic (for this see Whiten 2011). The literature on chimpanzee culture is, perhaps unavoidably, loaded with ad-hoc and often vague concepts that are frequently used to declare the dichotomous presence or absence of purportedly human traits in chimpanzees, with often little or no emphasis on quantifying the differences or exploring their implications for cultural evolution and gene-culture interactions. By sticking close to the theory, we hope to avoid these traps.

THEORIZING CULTURE

Dual inheritance or gene-culture coevolutionary theory arose from the recognition that humans, unlike most other species, are heavily reliant on learning from others, and that this social learning could create a second system of inheritance that could evolve and interact with genetic inheritance in a kind of coevolutionary duet (Boyd and Richerson 1985; Campbell 1965; Cavalli-Sforza and Feldman 1981; Durham 1991; Lumsden and Wilson 1981; Pulliam and Dunford 1980). "Culture" in this view is the emergent product of individuals of various generations or ages interacting and

learning from each other over the course of their lives. This conceptualization focuses our attention on (1) the abilities of individuals to learn from each other (or, at least as a consequence of each other) and (2) on the importance of interaction and sociality. This means that “culture” is now anchored in individuals, and traceable to individual cognitive abilities or learning strategies (Henrich and McElreath 2007; Tomasello 1999b). But, this also means that culture is not reducible to these abilities, since culture is what arises from both social learning and interaction. At any given time, it is the statistical distribution of ideas, beliefs, values or practices stored in the minds of individuals in a population. Lone individuals cannot learn from anyone else, and thus cannot have cultural practices.

From here, several additional possibilities open up. First, culture can evolve over time, as individuals learn from each other and across generations. Putting this insight to work, Cavalli-Sforza and Feldman (1981) showed how such *population processes* can be formally modelled using mathematical tools drawn from population genetics and epidemiology. This permits researchers to connect individual-level psychological or cognitive abilities through social interaction and social structure or organization to ask what the outcome is for cultural evolution—the change in the distribution of practices over time. Second, there is no reason to take these social learning abilities as given. Instead, Boyd and Richerson (1985) began approaching them as genetic adaptations that have evolved to allow individuals to more effectively extract useful information from patterns of behavior exhibited by those around them. This insight opened the door for full-blown models of culture-gene coevolution, in which culture and genes were mutually influencing each other (Aoki 1986; Feldman and Laland 1996; Henrich and Boyd 1998; Laland 1994; Laland et al. 1995a; Laland et al. 1995b; McElreath et al. 2003).

Since the turn of the century, this approach has been fruitfully applied to humans to understand individual-level psychological abilities and population-level patterns, structures or processes (Boyd et al. 2011; Whiten 2012). This research has (1) tested various hypotheses regarding ‘when’ and ‘from whom’ people will apply their adaptive social learning abilities (e.g., Chudek et al. 2013; Morgan et al. 2012; Rendell et al. 2011) as well as ‘when’ and ‘to whom’ they will transmit (teach) cultural information (Kline et al. 2013; Kline under review), (2) shown how social learning mechanisms can respond to local ecological variation to generate adaptive population patterns of cultural variation (Henrich and Henrich 2010), (3) established empirical relationships that link the size and interconnectedness of human societies to the complexity of their toolkits and technologies (e.g., Collard et al. 2013; Henrich 2004b; Kline and Boyd 2010; Muthukrishna et al. 2014), (3) linked the spread of specific genes in response to specific cultural practices (e.g., Chiao and Blizinsky 2010; Dediu and Ladd 2007; Holden and Mace 1997; Laland et al. 2010; Richerson et al. 2010), and (4) explored the degree to which culture, like genes, is a process of descent with modification that builds tree-like patterns of descent (Collard et al. 2006; Lipo et al. 2006; Tehrani et al. 2010). This blossoming of research now permits us to readily view chimpanzees and other primates through this same evolutionary lens (van Schaik and Burkart 2011a; Whiten 2011) that has been so fruitfully applied to humans. Though our focus is on chimpanzees, we will at times bring in evidence from other primates and other species.

DO CHIMPANZEES LEARN SOCIALLY?

This body of theory tells us where to start. Culture and cultural evolution are consequences of social learning (Boyd and Richerson 1995; Hoppitt and Laland 2013). If a species does not engage in social learning, in some form or fashion, it cannot have culture and will not experience cultural evolution. An immense amount of evidence shows that humans are automatic, unconscious and

frequent social learners (Bandura 1977; Csibra and Gergely 2006; Tomasello 1999b). As we will discuss later, our attention and social learning abilities appear functionally honed to adaptively extract information from the minds and behaviors of other members of our groups, ranging from the meaning of words and the proper use of artifacts to the existence of invisible agents like germs or angels (Chudek et al. 2013; Chudek et al. 2012; Corriveau and Harris 2009a; b; Harris and Corriveau 2011; Herrmann et al. 2013). Across diverse societies, children, adolescents and young adults socially learn vast repertoires of practices and bodies of know-how that are crucial for survival, such as how to find food, detoxify plants, build shelters, organize social groups, track animals and make fire (Boyd et al. 2011; Henrich and Broesch 2011; Kline et al. 2013). Social learning is so powerful in humans that we readily copy actions, motivations and beliefs that contradict our innate intuitions, tastes and direct experiences (Billing and Sherman 1998; Henrich 2009a; Rozin et al. 1981; Rozin and Schiller 1980). Social learning even influences our opioid and cannabinoid systems to alter how much pain we experience for the same pain-inducing stimuli (Benedetti et al. 2013; Craig 1986; Craig and Prkachin 1978).

So, do chimpanzees socially learn? Yes, though as we will see in later sections the character, frequency and life history of their social learning is rather different from humans in crucial ways. The most decisive evidence on this question comes from several, simple laboratory studies. Typically, these studies take the following form: a trained demonstrator (a human or chimpanzee¹) shows an observing chimpanzee how to open a baited puzzle box in one of two ways (the “two-target method”). Half of the observers see one way to open the box, and the other half see the alternative method. For example, half the observers might see the demonstrator push a bolt to open a door while the other half see the bolt pulled out. If observers tend to match the method of their demonstrators, then some form of social learning is taking place. Typically, observer chimpanzees indeed match demonstrations to some detectable degree (Hopper et al. 2008b; Horner and Whiten 2005; Tennie et al. 2010b; Whiten et al. 1996b), though the degree of matching is not great and sometimes it is zero (Tennie et al. 2006). Such results are often interpreted as revealing human-like social learning (e.g., Bonnie et al. 2007; Hopper et al. 2008b; Hopper et al. 2007; Whiten et al. 2005), even though social learning may be underpinned by a range of psychological mechanisms that cannot be pinpointed by the experimental methods deployed (Tennie et al. 2009a; Tennie et al. 2010a). However, from the point of view of existing evolutionary models, what matters (among other things) is transmission fidelity (Henrich 2004b; Lewis and Laland 2012), and not the specific psychological details. From this point of view, no matter what the mechanisms are, the results generally show rather low fidelity transmission for chimpanzees. We explain the implications of this below.

While laboratory studies have proven invaluable for assessing chimpanzee social learning, there are important concerns regarding how transferable such laboratory findings are to the field. The issue is: are the chimpanzees in typical laboratory studies showing more or less social learning than they would in the wild? To get at this, laboratory chimpanzees can be divided up into three categories (Furlong et al. 2008): (1) apes who have received extensive human interaction, training and enculturation (from here on, *enculturated* chimpanzees), (2) those living in social groups of other chimpanzees under non-deprived conditions but without having received intensive human interaction (hereafter, *semi-enculturated*), and (3) those who have experienced prolonged socially and physically deprived conditions (e.g., isolation; hereafter *deprived*). In terms of social learning,

¹ For chimpanzee participants, the species of demonstrator does not seem to have a significant impact on the outcome (Boesch 2007; Dean et al. 2012; Marshall-Pescini and Whiten 2008). For humans, the impact of other-species demonstrators has not been explored, though efforts to co-rear humans and chimpanzees suggest that infants and young children will readily copy older, more physically-skilled, apes (Kellogg and Kellogg 1933).

and related abilities such as pointing (Leavens et al. 2010), enculturated chimpanzees are generally superior (Bjorklund et al. 2002; Tomasello et al. 1993), followed by semi-enculturated ones (Furlong et al. 2008), and finally the deprived apes (Menzel Jr et al. 1970).

Consequently, though far from ideal, we feel that semi-enculturated apes probably provide the best available population from which to draw conclusions about wild populations. Clearly, deprived apes are not acceptable. Similarly, enculturated apes are unlikely to be the best model for wild apes, since extensive and intimate contact with humans (not occurring in the wild) seems to alter cognitive skills and motivations in significant ways. This leaves the semi-enculturated populations, who live in social groups, are well-fed (better fed than wild apes) and experience (somewhat) enriched physical environments.² Note that the social learning studies reported above involved semi-enculturated apes.

If anything, the available evidence, weak as it is, suggests that the greater human contact experienced among captive chimpanzees might improve—not inhibit—the development of learning skills and related abilities. Consider three relevant bits of evidence. First, in a field experiment, Gruber et. al (2011; 2009) show that wild chimpanzees who lacked a stick-based fluid-dip technique in their behavioral repertoire could not readily solve an artificial honey-dip problem. Compared to semi-enculturated chimpanzees this appears odd since subjects in the laboratory can figure out similar tasks (Call and Tennie 2009; Yamamoto et al. 2013) despite being less hungry. Second, captive chimpanzees are also developmentally *faster* in learning these tasks: in the laboratory, three infant chimpanzees learned to honey dip earlier in development than their wild counterparts on the same task (Hirata and Celli 2003). The authors suggest that the enriched environment in the laboratory accelerated their cognitive development. Such “captivity effects” may be due to greater motivations and fewer distractions; a result perhaps of more free time and energy than in the wild. In addition, it may be further influenced by increased contact with humans and among conspecifics (Haslam 2013). Third, enculturated chimpanzees, but not semi-enculturated apes, will drop unnecessary steps in a manner consistent with more sophisticated and human-like forms of social learning.³ But, whatever the exact causes (a ripe research topic on its own), there is little reason to suspect that semi-enculturated apes will show inferior learning abilities compared to their wild counterparts.

These lines of evidence leave little doubt that chimpanzees have at least some forms of social learning. Next, we consider whether chimpanzee social learning has been shaped by natural selection, as it appears to have been in humans (Henrich and Gil-White 2001a; Henrich and

² Not everyone agrees. Boesch (2012) argues that human training and high exposure are substitutes for the rich environments found in the wild. Perhaps. But, why then is finger pointing quite common in enculturated chimpanzees but extremely rare in wild chimpanzees (Leavens et al. 2010)?

³ Human children sometimes choose to imitate in a manner that suggest they are inferring the goals or strategies of their models, and then selectively copying only parts of demonstrations based on those inferred goals or strategies (though see recent critique: Beisert et al. 2012; called “rational imitation”: Gergely et al. 2002). In a single study, Buttelmann et. al. (2007) show that *enculturated* chimpanzees possess some ability to engage in this more sophisticated form of social learning. A later study (Buttelmann et al. 2008) tested semi-enculturated apes, including bonobos, orangutans, chimpanzees and gorillas. Of their three studies, only the third was capable of showing a more sophisticated form of “rational” social learning. In this study, none of the semi-enculturated apes reveal tendencies toward “rational” social learning. The other two studies tested either for the rational choice of one tool over another (“rational tool choice”; Study 3) or for the rational choice of a tool over no tool (“rational tool use”). Studies 1 and 2 only found “extremely weak” evidence for rational tool use, and this mostly in orangutans, not in chimpanzees. Overall, limited as this data is, it suggests that wild chimpanzees are unlikely to engage in the even more sophisticated “rational imitation” that has been observed in human infants.

McElreath 2007), to expand and hone the behavioral repertoires of individuals by fostering the acquisition of adaptive practices from others. Alternatively, it is not implausible that chimpanzees possess some degree of social learning as a byproduct of having brains selected for individual learning, for the ability to figure things out on their own. Individual and social learning involve many of the same cognitive skills and neurological resources (Reader and Laland 2002), so it is possible that selection for one delivers some amount of the other “for free”.

DO CHIMPANZEES SHOW THE PREDICTED SOCIAL LEARNING MECHANISMS OR BIASES?

Theorists have explored how natural selection might have shaped the cognition of learners so as to allow them to most effectively extract information from both the environment and their social milieu. Here we review the evidence for these hypotheses in chimpanzees, and provide a comparative perspective with humans.

UNCERTAINTY AND CONFORMITY

Much theoretical work has focused on how learners should respond to uncertainty or task difficulty (Boyd and Richerson 1988; Boyd and Richerson 1995; Henrich and Boyd 1998; Laland 2004; Wakano et al. 2004). Under many conditions, learners should respond to greater uncertainty or task difficulty (including poorer individual information or ambiguous environmental cues) by increasing their reliance on social learning—thus prioritizing social information over their own perceptions and inferences. Psychologists have termed this response *informational conformity*. The predicted shifts have been observed in humans (Baron et al. 1996; Efferson et al. 2008b; McElreath et al. 2008; Morgan et al. 2012) and in non-primate taxa such as rats and fish (Galef 2009a; Galef et al. 2008; Kendal et al. 2005; Laland et al. 2011).

To date, we know of no tests of these predictions in chimpanzees, and only suggestive evidence of informational conformity (a reliance on social over individual information). While claims of “conformity” in chimpanzees and other primates are common (Hopper et al. 2011a; Hopper et al. 2011b; van de Waal et al. 2013; Whiten et al. 2005; Whiten and van Schaik 2007a), a combination of methodological problems and conceptual ambiguity deflate such interpretations (Galef and Whiskin 2008; van Leeuwen and Haun 2013). For example, evidence for conformity has been claimed from “reversion designs” in which individuals first acquire and master one technique, as it spreads to become common in their group. Then, later, if some individuals perform a different technique, they may drop it and revert back (‘conform’) to the technique they first learned. In the diffusion experiments described above, after the initial spread of either the ‘poke’ or ‘lift’ techniques in different groups, researchers have argued that the fact that some individuals subsequently tried a different technique but then switched back to their initial technique is evidence of “conformity” (Whiten et al. 2005).

Conceptually, these studies fail to distinguish *informational conformity* from either *conservatism* or *normative conformity*. Conservatism is a tendency to ‘stick with’ or revert back to old habits—previously acquired and more deeply ingrained practices or preferences. Normative conformity is a tendency to ‘go along with the group’ to avoid appearing deviant, which could result in sanctions or ostracism (it is not a form of social learning in the sense currently used by theorists). The observations of reversion by chimpanzees could be informational conformity, or they could be conservatism, or even normative conformity. Since most studies show that chimpanzees are

conservative (reverting back to or sticking with old habits even in the absence of any social input, though see Manrique et al. 2013), this is a likely alternative explanation (Whiten 1998). And, while we think—on theoretical grounds—that normative conformity is unlikely to be found in chimpanzees (Henrich and Henrich 2007), normative conformity does exist in humans and is not ruled out in these experimental designs.⁴

OBLIQUE TRANSMISSION USING AGE, SUCCESS AND PRESTIGE BIASES

A great deal of theoretical work has examined the conditions under which natural selection will favor social learners who strategically target their social learning attention and efforts at those individuals most likely to possess fitness-enhancing behaviors, beliefs, motivations or practices (Boyd and Richerson 1985; Henrich and Gil-White 2001b; Laland 2004; McElreath et al. 2003; McElreath and Strimling 2008; Rendell et al. 2010). Theorists have argued that learners should use ‘model-based’ cues like skill, competence, success, age, experience, prestige and self-similarity cues, like sex or ethnicity (based on cues related to language or dialect). Combinations of these cues help learners rapidly triangulate in on those most likely to have adaptive information, which could be useful to the learner in the roles they will assume, and problems they will encounter, later in life. An immense amount of empirical work, much of it within the last 15 years, has substantiated these predictions in human adults, children and even infants (Buttelmann et al. 2012; Chudek et al. 2013; Chudek et al. 2012; Corriveau and Harris 2009a; b; Corriveau et al. 2013; Corriveau et al. 2009; Efferson et al. 2008a; Jaswal and Neely 2006; Koenig and Harris 2005; McElreath et al. 2008; Morgan et al. 2012; Rendell et al. 2011), as well as in other non-primate species (Galef 2009a; Laland et al. 2011; Rendell et al. 2011).

Building on these insights, some researchers have proposed that learners should take into account the costs of accessing their preferred models (those who they deem skilled, successful and prestigious). Placing these within a life history framework suggests that infants and children will first learn all they can from their parents, siblings and other easily-accessible models, and then subsequently, pay access costs and update their cultural traits from their preferred models under some conditions (Henrich 2004b; Henrich and Broesch 2011). The idea here is that children have easy access to their family and household members, who themselves have kinship incentives for transmitting useful cultural information to the learner. However, potentially more valuable models, with greater skill, success and prestige, will often be available outside the household. But, accessing these people will require learners to pay costs in the form of locating and spending time with these models, and in paying them deference in the form of gifts and services in exchange for access and help (Henrich and Gil-White 2001a). This can be characterized as a switch from primarily vertical cultural transmission to various forms of biased oblique transmission over the life course. Broadly, field work in small-scale human societies provides evidence consistent with these predictions (Henrich and Broesch 2011; Hewlett et al. 2011; Kline et al. 2013; Tehrani and Collard 2009).

Chimpanzees also show some of these patterns, although the evidence is limited. Among wild populations, detailed observational studies focused on three different practices—termite fishing, ant-dipping, and nut-cracking—do indicate a clear shift from primarily watching the mother to increasingly watching others engaged in the practice. This is the expected vertical to oblique shift in attention. Moreover, the data make it clear that chimpanzee learners are preferentially attending to

⁴ Drawing terminology from psychology, dual inheritance theorist have long made and explored the distinction between informational and normative conformity (Boyd and Richerson 1985: 224; Chudek and Henrich 2010; Henrich and Boyd 2001: 81; Henrich and McElreath 2007; Henrich and Henrich 2007: 22-27), though see Claidiere and Whiten (2012) for a claim to the contrary.

older and more experience practioners, and largely ignoring their younger and less experienced conspecifics (Biro et al. 2003; Humle et al. 2009; Lonsdorf 2013; Melber et al. 2007). This is consistent with some form of age, experience or skill bias in attention. Though, of course, attention is merely a necessary precursor to social learning (Corp and Byrne 2002). It needs to be shown in addition that, what, and how something is learned in the process, as otherwise attempts at scrounging could explain such patterns—scroungers watch to most skilled because it's easy to scrounge from them (Stammach 1988).

In one study, observational data indicates not only a clear indication of a specific transmission of part of the behavior (in this case: the length of the stick tool), but also a sex-bias, with female offspring preferentially learning from their mothers, relative to males from their mothers (Lonsdorf et al. 2004). To our knowledge, other studies have not revealed similar patterns among chimpanzees (Lonsdorf 2013). However, sex-biased attention and social learning, oriented specifically toward females, suggests that natural selection may adjust sex-biases in attention to adapt to different forms of social organization. For example, since vervet monkeys are female philopatric, we would expect females to be the most locally knowledgeable—and, in accordance with this hypothesis, females are indeed the most attentively observed by others (Renevey et al. 2013; van de Waal et al. 2010), including by males.

Only one published laboratory experiment aims to address the possibility of adaptive biases in chimpanzees. Horner et. al.'s (2010) experiment reveals that chimpanzees possess some ability to distinguish among potential models during social learning, which is consistent with the field evidence. Each of two social groups was exposed to two different potential models from their own group, one 'experienced model' and one 'inexperienced model'. Both were female. The 'experienced model' was roughly two decades older and more dominant than the 'inexperienced model', who was just barely out of her juvenile period. Moreover, the 'experienced models' had previously introduced successful innovations in a series of other experiments, so the experimenters knew she was a good transmitter. Of the 22 chimpanzees exposed to these two models, 14 decided to participate (which meant effectively copying one of the two models). Of these 14, eight revealed no significant preference for either model. The remaining six tended to copy the 'experienced model' by making deposits in the same location.⁵

One puzzling feature of Horner et. al.'s results is that the observing chimpanzees show no significant difference (reported as "NS" for non-significant by the authors) in their patterns of attention toward the 'experienced models'. Ideally, there would be a correlation between attention to a model and the copying of that model. The lack of such a relationship contradicts both a prediction of the model being tested (Henrich and Gil-White 2001a), and the empirical patterns observed in humans (Cheng et al. 2013; Cheng et al. 2010; Foulsham et al. 2010), capuchins (Ottoni et al. 2005) and macaques (Stammach 1988). Both capuchins and macaques, for example, may simply track the most successful producers in order to better scrounge food (see Corp and Byrne 2002).

⁵ The labels 'experienced' and 'inexperienced' are ours. The authors of this study interpret their findings as showing the effects of 'prestige' cues on social learning, testing the Dominance-Prestige Theory (Henrich and Gil-White 2001a). Unfortunately, this experiment cannot test this idea since their potential models are distinguished by many cues, including age, experience, competence, dominance and past success. By contrast, young children track others' visual attention (a carefully manipulated 'prestige cue') and preferentially attend to and learn from those who are watched more by others (Chudek et al. 2012). Similarly, adults copy those who have been imitated more in the past by others (Atkisson et al. 2012), independent of other factors.

2.2.1. MAJORITY AND CONFORMIST TRANSMISSION BIASES

Theorists have examined the conditions under which learners should rely on conformist transmission over other strategies for social and individual learning (Boyd and Richerson 1985; Kendal et al. 2009; Nakahashi et al. 2012; Perreault et al. 2012). Conformist transmission is the tendency to disproportionately ‘copy the plurality’. For example, suppose there are three behavioural variants, A, B, and C, at frequencies of 40%, 30% and 30%, respectively, in a population. If the new generation of learners just pick a model at random, the next generation would—on average—have the same frequencies of A, B and C. However, if individuals are using conformist transmission, the frequencies shift to favor the plurality, changing to, say, 60%, 20% and 20%, respectively, in the next generation. *Ceteris paribus*, variant A will eventually spread to fixation. In humans, research has only just begun, though some empirical work does indicate that humans use conformist transmission, at least under some conditions (Coultas 2004; Efferson et al. 2008b; Morgan and Laland 2012; Morgan et al. 2012). Conformist transmission has been shown, perhaps most decisively, in fish (Pike and Laland 2010).

Despite suggestions to the contrary, no study has isolated conformist transmission by showing the requisite disproportionate tendency to copy the plurality in chimpanzees or any other primates (van Leeuwen and Haun 2013).⁶ However, Haun and colleagues (2012) used a carefully designed experiment that controlled for both the frequency of times learners observed a depositing location (for dropping an object into an apparatus) and the number of different models observed using the depositing location. Their evidence shows that chimpanzees—but not orangutans—use the commonness of a location among potential models as a learning cue. However, these authors lacked the statistical power to distinguish a merely linear tendency to copy the majority from the non-linear effects of conformist transmission.

TEACHING IN CHIMPANZEES

Now, we shift our focus away from the learner, towards the model, who can facilitate or foster more effective acquisition in learners. From an evolutionary perspective, however, teaching involves paying at least small costs to help another individual—so it is a type of altruism. Evolutionary models suggest that teaching and social learning can coevolve, though because of the costs to self and benefits to others, the conditions favoring teaching are narrower than those favoring social learning (Castro and Toro 2002; Fogarty et al. 2011). Because of the altruistic nature of teaching, we would primarily expect it to emerge between parents and their offspring.

Teaching is any costly behavior by the model that facilitates learning in conspecific (Caro and Hauser 1992). Teachers may (1) structure the environment for their students to enhance their chances of individually figuring things out (e.g., by leaving the right tools around), (2) approve or disapprove of their pupil’s activities, which guides learners via re-enforcement, (3) actively drawing the learners’ attention to key elements of a demonstration with cues like pointing or eye contact (‘pedagogical cues’, see Csibra and Gergely 2006; 2009), (4) mold the learners’ hands or position their feet, (5) slow down demonstrations or exaggerate key aspects in order to make it easier for the learner to take in, and (5) scaffolding the learner by providing challenges just above

⁶ Whiten et al. (2005) imply they found conformist transmission by using the term “conformity bias”, and citing Richerson and Boyd (2005) who only discuss conformist transmission biases.

their current skill level (Boesch 2012; Hoppitt et al. 2008). This behavioral definition permits us to cast a wide net and to compare teaching in humans with other species.⁷

Characterizing teaching in humans turns out to be tricky, since most work on teaching comes from developmental psychologists who study mostly children in Western societies (e.g., Csibra and Gergely 2009; Tomasello 1999a). By comparison to many other societies, middle and upper class westerners place immense emphasis on active and often verbal forms of teaching. Western parents likely engage in more hand molding and provide explicit verbal feedback and justifications compared to parents in many small-scale societies. Overall, in the smallest-scale human societies including foragers, teaching exists – but is much less common and largely passive (Fiske 1998; Gaskins and Paradise 2010; Hewlett et al. 2011; Lancy 1996; 2009; Strauss and Ziv 2012). As usual, many have missed the boat by focusing on ‘presence’ vs. ‘absence’ debates, which so frequently come down to arguments about definitions. Recent detailed and quantitative studies of Fijian villages show patterns of teaching unlike Westerners, but largely consistent with the predictions from evolutionary models and reasoning. Thus, the right puzzle may be why westerners, so called WEIRD people (Henrich et al. 2010), teach as much as they do and in the ways they do.⁸

As expected from theory, teaching is much rarer than social learning in nature. However, several studies have established clear evidence of teaching (Hoppitt et al. 2008; Thornton and Raihani 2008). For example, tutor meerkats provide live – but previously disarmed – scorpions to inexperienced meerkats, and who in turn learn to handle scorpions earlier than untutored meerkats (Thornton and McAuliffe 2006).

In chimpanzees, three long-term and detailed studies have focused on understanding the factors that influence the acquisition of the skills for termite fishing, ant-dipping and nut-cracking. In both termite fishing and ant-dipping, chimpanzees make a probing tool out of immediately available materials and then dip the tool into the habitat of the insects. To open nuts, chimpanzees use stone or wooden ‘hammers’ to smash the nut shells on ‘anvils’. This trio of skills is an ideal place to look for teaching, since, as we argue below, social learning likely plays a facilitating role in their acquisition in the wild. Researchers have studied how chimpanzees between the ages of about 1 and 6 years acquire these skills. As part of this, they observed, coded and analyzed the behaviors of both mothers and other nearby adults and juveniles for any hint of teaching (Biro et al. 2003; Humle et al. 2009; Inoue-nakamura and Matsuzawa 1997; Lonsdorf 2005; 2006; 2013; Lonsdorf et al. 2004).

The results are consistent across different researchers and different field sites. Adults, particularly mothers, are highly tolerant of the activities of young chimpanzees (< 5 years), permitting them to play with tools and ‘steal’ or ‘scrounge’ the harvest, but they do not actively facilitate learning. Mothers generally reacted neutrally to their infant’s efforts, providing no feedback of any kind, and never molded learners’ hands, pointed, made eye-contact or provided other pedagogical cues. Eye-contact was rarely made at all, as mothers were focused on their own foraging activities. Mothers never handed their offspring a tool or some of the harvest.⁹ In short, no teaching was found.

⁷ We avoid mentalistic approaches to teaching to permit comparisons across species (Kline under review).

⁸ Arguably, from the perspective of small-scale societies, westerners have to teach so much because they begin transmitting before learners are ready—in terms of maturation—to learn things on their own.

⁹ These otherwise consistent patterns, showing no teaching, contradict earlier work on nut-cracking at Tai forest (Boesch 1991; Boesch 2012). Aside from two anecdotes (see Maestripieri 1995 for a critique), much of the seeming discrepancy comes from whether the young chimpanzees were ‘stealing’ hammers and nuts from their mother, with her tolerating it, or whether she was actively ‘giving’ the hammers and nuts. What all three

The one exception to this occurs in dipping for army ants. This foraging task can be done at more dangerous nests or at less dangerous trails. Mothers with infant learners showed a bias to ant-dip at the less productive trails (paying a cost), thereby providing a safer environment for their offspring to learn in (Humle et al. 2009). Of course, an important question is whether this is merely a byproduct of mother's concerns about her offspring getting attacked by army ants (or even about protecting herself, as mothers are less mobile and even handicapped by her offspring), or if it was selected (by mothers or natural selection) because it facilitates social learning.

In the laboratory, there has been one detailed comparative study of teaching in human children (below 5 years of age), chimpanzees and capuchins. Dean et al. (2012) presented participants with a three step task in which solving each step successively supplied the learner with a reward and opened the opportunity to complete the next step and obtain an even larger reward. While teaching in the children was common and increased with task difficulty (as predicted by theory), neither monkeys nor chimpanzees engaged in any teaching. In the children, teaching correlated with greater success on the task, and may help explain why so many children reached the final stage while so few non-humans did. We will return to the presence and importance of teaching in humans when we discuss cumulative cultural evolution.

POPULATION-LEVEL PATTERNS OF BEHAVIOR

Cultural evolutionary models show that social learning abilities can, under some conditions, give rise to stable behavioral variation between groups. Practices, beliefs and ideas—cultural variants—clearly spread via cultural transmission among humans within groups and from group to group (Bell et al. 2009; Henrich 2001; Rogers 1995). Alternatively, sometimes groups expand, fission, and spread geographically, taking their cultural variants with them. Both kinds of processes can create spatially structured networks of cultural similarity, and in some cases tree-like patterns of descent with modification (Shennan 2009; Tehrani and Collard 2009).

These cultural patterns are often adaptive, and systematically associated with ecological variables for several reasons (Billing and Sherman 1998; Edgerton 1971; Henrich and Henrich 2010; Hruschka and Henrich 2013; Jordan and Shennan 2003; Shennan 2003). First, as discussed above, human social learning has likely been honed by natural selection to use a wide range of adaptive cues, like success, age and prestige, to more effectively target attention and learning. This means that cultural evolution will respond to local environments and spread locally adaptive practices through populations. Second, since natural selection also influences cultural inheritance, those with locally less well-adapted repertoires will tend to be less available to transmit their cultural variants (Richerson and Boyd 2005). Third, human groups compete and those with better-adapted cultural repertoires, including norms and forms of social organization, spread at the expense of those with less-well adapted cultural packages (Currie and Mace 2009; Diamond 1997; Henrich 2004a).

Consider, for example, that the practice of constructing and inhabiting snow houses—as seen among Inuit foragers—is closely correlated with climatic temperature or latitude. The practice itself requires substantial culturally learned know-how, and cannot be figured out by, for example, lost Arctic explorers even when their survival depends on it (Boyd et al. 2011). However, cultural evolution only assembles the relevant know-how when the environmental conditions favor the

of the other research team coded as 'stealing' and 'scrounging' appears to have been coded as mother 'giving' by Boesch (Lonsdorf 2013).

practice. Thus, we should expect cultural evolution creates correlations between ecology and behavior.

Of course, evolutionary approaches to cultural transmission also predict, at least under some conditions, that cultural transmission can spread and stabilize neutral or even maladaptive variants. This can occur through a variety of mechanisms that need not concern us here, but whatever the mechanism, much evidence supports the existence and persistence of neutral or maladaptive cultural variation among groups (Boyd and Richerson 1985; Edgerton 1992; Henrich and Henrich 2010).

In light of the available theory, the evidence from humans, and the presence of some degree of social learning in chimpanzees, we can ask two questions:

- 1) Does chimpanzee social learning contribute to the spread of certain behaviors that remain locally stable and vary among groups?
- 2) Are these patterns of variation broadly adaptive, showing predictable and patterned ecological variation?

Field evidence gleaned from nine different chimpanzee populations scattered across tropical Africa does indeed reveal substantial *behavioral* variation across populations (Whiten et al. 1999; 2001). This research team isolated and categorized 69 different behavioral variants across their sites. These variants included using probes (e.g., sticks) to obtain ants, termites or honey (or to clear the nose), leaves as sponges, wipes or brushes, stones as hammers or anvils for nuts, and sticks as levers to open and access nests of birds or insects. Some categories include several variants. For example, some version of nut hammering created five of the 69 variants, with some variant swapping the materials used for the hammer and anvils (stone vs. wood). Each variant was classified according to its local frequency as (1) 'customary' (most adults do it, or most of some subclass do it (e.g., all females)), (2) 'habitual' (commonly observed but not customary), (3) 'present', (4) 'absent' or (5) 'status not established'.

The tricky part turns out to be showing that this substantial and important *behavioral* variation is in fact *cultural* variation, as opposed to (1) genetic variation (Galef 2009b; Laland et al. 2009; Langergraber et al. 2011b; Tennie et al. 2009b) or (2) locally adaptive responses to ecological variation that depend only on individual learning or other ontogenetic responses to environmental cues (Galef 1992; Laland et al. 2009; Tomasello 1994). Of course, the authors recognized all these issues and did try to handle them. To argue for cultural variation, they removed variants that were (1) universal, (2) very rare, or (3) could be readily explained by ecological variables, to arrive at a list of 39 putatively cultural variants. This catalogue of behaviours is indeed impressive, and analyses of it has led researchers to argue that chimpanzee cultures are special (Whiten and van Schaik 2007b) and even more sophisticated than that of crows (McGrew 2013).

We are sympathetic to the effort, but this approach has some interpretative limitations. First, cultural evolution is adaptive, at least in humans, so removing things that are universal or explained by ecology potentially removes important cultural variants (Laland and Janik 2006). Second, the ecological forces that shape individual learning or other non-cultural ontogenetic responses may arise from non-obvious or even subtle ecological differences, so the approach only mitigates this issue. Third, in removing the 'rarities' the authors suggest that social learning will cause traits to be common in groups—so rare traits are not socially learned. Theoretically, this is just not true. How common a cultural trait becomes within a group depends on many factors, including on how hard it is to learn, how easy it is to forget, how adaptively important it is, how the social network of the group interconnects, and what other variants it might be competing with. Fourth, these nine groups

span a vast territory and can be classified into three subspecies, with much internal genetic structure. Thus, genes are a competing explanation for the behavioral variation.

Subsequent analyses of these putatively cultural variants has further informed the issue. To begin, it turns out to be difficult to exclude genetic variation as a potential cause of much of the behavioral variation. Langergraber et al. (2011a) assembled mitochondrial DNA on the nine populations and correlated measures of both cultural and genetic dissimilarity for all possible pairs of groups. The correlations range from 0.36 to 0.52. This suggests that genes are difficult to exclude. However, when the data are analyzed at the level of particular variants, the authors are able to establish that genetic variation is unlikely to explain 5 of the behavioral variants and possibly as many as 20 of the variants. Of course, it is still possible that most or all of these variants are cultural, we just cannot tell for many or even most of the traits.¹⁰

Consequently, we prefer regional or local studies of specific variants over continental-level analyses because they reduce or eliminate concerns with genetic variation, narrow the potential sources of ecologically-induced variation, and provide direct observation of the potential learning processes involved for different aspects of behavior. Here, we focus again on three practices: (1) termite fishing, (2) ant dipping and (3) nut cracking. At the local and regional level, all three (a) appear adaptively responsive to ecological or environmental changes, including seasonal variation, (b) are learned by young chimpanzees in a manner that is likely facilitated by mothers engaging in the skills (and others to a much lesser degree), and yet (c) show some patterned variation among communities that cannot be readily traced to obvious ecological differences.

Termite fishing is a good place to start since it was one of the five behavioral variants that Langergraber et al. (2011a) evaluated as unlikely to be due to genetic differences among chimpanzee groups, and is widespread across Africa (Whiten et al. 1999), but not found in some populations where termite mounds do exist. In termite fishing, individuals fashion simple tools out of vegetation in the immediate vicinity of the mounds, and insert these tools to extract the termites. Within chimpanzee groups the frequency of termite fishing varies seasonally with rainfall and temperature, and constitutes an important food source in some populations (Bogart and Pruett 2009), particularly among populations living in Savanna-woodlands (Bogart and Pruett 2011). Meanwhile, in locales with more limited opportunities for exploiting termites, relative to other resources, the practice is non-existent (Koops et al. 2013; Sanz and Morgan 2013). Overall, termite fishing is responsive to ecology and environment.

It is clear that termite fishing involves substantial individual learning, through practice and trial and error. The key question is how this individual learning is enhanced by social factors. Detailed studies of the acquisition of termite fishing skills in East Africa have helped illuminate the learning process. As mentioned above, Lonsdorf (2006) studied termite fishing by following 11 infants

¹⁰ Lycett et al. (2010; 2011) have analyzed Whiten et al.'s 39 traits using the tools of cladistic analysis, which were developed to infer genetic phylogenies from extant variation. They argue that their analysis reveals a 'phylogenetic' (actually, phylocultural) signal, which they use to construct a phylocultural tree for chimpanzees. Reviewing our concerns with this approach is beyond the scope of this paper, but suffice it to say that, combining what we know about the low fidelity of chimpanzee cultural transmission and the high rates of both loss and reinvention in chimpanzees with the deep time scales involved with the expansion of chimpanzees across Africa, we find it unlikely that the signal revealed by Lycett et al. represents a cultural descent with modification at the group level from an ancestral population of chimpanzees. To be clear, this is not to argue the observed differences are not cultural. Theoretically, from a cultural evolutionary perspective, it is perfectly plausible that these variants are all 100% cultural, yet virtually no cultural signal remains, given the time scales involved. Social learning need not produce either group-level heritability or tree-like patterns of descent. For more on the debate see (Langergraber et al. 2011a; Langergraber and Vigilant 2011).

(unweaned, typically less than age 5) and juveniles, along with their five mothers, for 65 hours. The rate at which these young wild chimpanzees increased their fishing skills depended on what the mother did, for how long, and with whom. Being exposed to a small group of fishers helped early on, when learners were mostly watching. Then, later, being alone with mother helped more, perhaps by reducing competition for access to the mound and tools. The correlation between the proficiency of the mother and her older offspring (over age 6) was 0.63. Though this correlation may be due, entirely or in part, to genetic similarities between mothers and their offspring, this seems less likely since mother-offspring correlations on other such tasks are generally small or zero. This is consistent with other work suggesting that the complexity of termite fishing rods depends on direct experience and learning opportunities (Sanz and Morgan 2011).

All of this is consistent with at least “exposure” (Thorndike 1911) individual learning, meaning the youngsters were aided in learning to fish because hanging around their mother provided access to termite mounds, tools and opportunities to practice. However, as noted above, a comparison of male and female learners revealed that females watched their mothers (and other females) more, achieved proficiency faster than their brothers, and ended up more skilled. Instead of watching, the males engaged in more individual experimentation (play). Moreover, these analysis reveal that daughters tended to match their mother’s dipping strategy (in terms of stick length alone – not necessarily a sign of high-fidelity copying (Moore 2013)), while their sons did not (Lonsdorf 2005; Lonsdorf et al. 2004). In a manner consistent with theoretical expectations discussed above, this suggests that more may be afoot than mere exposure.

The practice of ant-dipping shows patterns that parallel termite fishing. Like termite fishing, ant-dipping is widespread across Africa, often seasonal, and responsive to ecological variation (Mobius et al. 2008; Schöning et al. 2008). But, nevertheless, patterns of variation remain that are not readily accounted for as direct adaptive responses to ecological variation, unmediated by social interaction. In a study similar to that just described, Humle et. al. (2009) studied ant-dipping among 13 mother-offspring pairs at Bossou in East Africa. Young chimpanzees tended to watch mothers’ dipping, and then increasingly engaged in dipping as they got older. The time spent ant-dipping by juveniles (weaned offspring) correlated highly with the time spent dipping by their mothers. Dipping proficiency, as measured by failed dips (or errors), increased with age (error rates declined). And, juveniles with mothers who dipped a lot made fewer errors. Dipping proficiency, as measured by dip duration, was correlated 0.87 between mothers and their juvenile offspring. Mother provides access to ants and tools as well as time and tolerance. This permits their offspring to learn through direct experience. The more time mother provides, the better both she and her offspring get. To go beyond this, Humle et. al. did look for mother-offspring correlations between their (1) dipper stick lengths and (2) techniques used, but did not find any—unlike in the termite fishing studies above.

Nut-cracking, the use of wooden or stone ‘hammers’ to crack nuts of various kinds, was once thought to be found exclusively among West African chimpanzees (see below on recent findings), which highlighted the possibility of genetic influences (Langergraber et al. 2011b). Many other wild chimpanzees, inhabiting environments with the requisite nuts, stones and wood, do not crack nuts. Nut-cracking—including the choices of particular nut species and the tool materials used—also appears to be influenced by ecological factors in adaptive ways (Biro et al. 2003; Yamakoshi 1998), but not solely determined by ecological factors. For example, Luncz et al. (2012) studied the nut cracking behavior of three neighboring communities of chimpanzees in the Tai National Park, Côte d’Ivoire. Though they found little or no differences in ecology between these three communities, this team did observe some differences in the nut cracking behavior between the three groups. These differences were relatively subtle, being related to the selection of hammer material and size,

rather than to the technique of nut cracking itself. Such differences are unlikely to be related to genetic variation among these neighbors, since they can be assumed to interbreed.

As with both ant-dipping and termite fishing, observational studies reveal it is the exposure to, and possibly the observation of, nutcrackers, their tools, and the fruit of their labors that stimulates the trial and error process necessary for chimpanzees to acquire nut-cracking skills. This work also identified a sensitive window for the acquisition of nut-cracking, between about age 3 and 5 (Biro et al. 2003; Inoue-nakamura and Matsuzawa 1997; Marshall-Pescini and Whiten 2008), though if the ability to crack one kind of nut is acquired during the window, this ability can be extended to different kinds of nuts later in life. As noted, younger individuals tend to watch older nutcrackers (especially the mother), though they do not copy the mother's specific use of her right or left hand for bringing down the hammer.

So far, we have reviewed laboratory evidence showing the existence of experimentally-induced "traditions" and field evidence of patterns of behavioral differences among chimpanzee populations. This evidence seems sufficient to establish that social learning can facilitate the spread of novel practices. And, without it, novel inventions disappear. But, what the laboratory studies of chimpanzees also show is that the fidelity of their social learning is not sufficient to explain the sustained persistence of arbitrarily different or maladaptive practices (Claidière and Sperber 2009). Most of the patterns we have reviewed are consistent with social learning facilitating the spread of practices, but with individual learning in response to the economics of the local ecology maintaining the practices, and accounting for why ecology seems so important to the distribution of practices.

CHIMPANZEES AND CUMULATIVE CULTURAL EVOLUTION

The survival of human groups, including hunter-gatherers, depends critically on socially-learned skills, know-how, motivations, tastes and practices. Stripped of this culturally acquired information, humans cannot survive as foragers. This fact has been repeatedly demonstrated as lost or stranded European explorers struggled to survive in "hostile" environments where local populations of hunter-gatherers had been living for centuries or millennia (Boyd et al. 2011; Henrich and McElreath 2003). Thus, the massive ecological success and global expansion of our species into an immense diversity of environments, from the frozen Arctic to the arid deserts of Australia, was made possible by the ability of human populations to gradually, over generations, accrete large bodies of skills and know-how that no individual could ever figure out in one lifetime. Tomasello refers to this process as the "ratchet effect", capturing the idea that each generation can 'ratchet up' from where the last generation left off (Tomasello 1999b).

This addiction to cultural information in our species has led culture-gene coevolutionary theorists to propose that many aspects of human psychology, anatomy, and physiology are products of an ongoing interaction between culture and genes (Laland et al. 2010; Richerson et al. 2010). We are a 'cultural species' (Tomasello 1999b), meaning cultural evolution has driven much of our genetic evolution. For example, the know-how and skills surrounding cooking and fire-making are clearly culturally-transmitted, at least in part. Yet, the length of our colons and the size of our stomachs, teeth and gape only make sense in a species that has genetically adapted to eating cooked food (Henrich and McElreath 2007; Wrangham and Carmody 2010). More broadly, researchers have suggested that this process of cumulative cultural evolution created the genetic selection pressures for our long distance running abilities (e.g., foot anatomy), folkbiological and artifact cognition, 'over-imitative' tendencies, status psychology (prestige) and verbal mimicry, among other aspects of our species (Boyd et al. 2011).

Thus, applying this theoretical work, we next ask how much cumulative cultural evolution exists in chimpanzees. Then, since our answer is that little or no cumulative cultural evolution has emerged, we ask: why so little?

Cumulative cultural evolution creates practices, bodies of manufacturing know-how and whole behavioral repertoires that no single individual could invent in their lifetime (Boyd and Richerson 1996; Tennie et al. 2009b; Tomasello 1999a). The question is then, how much of chimpanzee repertoires could a group of naïve chimpanzees reinvent, without any social input, in their lifetimes? The question is not, can everyone re-invent everything, but can anyone in the group re-invent it?

In the field, the existence of variation in tool-using skills, as discussed with nut-cracking, termite fishing and ant-dipping, among populations would seem to suggest this may be the case. However, since these practices have already been shown to be susceptible to ecological pressures, including variation in the relative frequency of certain resources (not just the existence of the resource), it is hard to exclude subtle influences rooted in the economics of various resource distributions and the availability of learning opportunities (Sanz and Morgan 2013). Moreover, few of these variations among local communities have been shown to be stable for long periods. In some cases, we may be looking at ephemeral fluctuations as practices are lost and reinvented over years or decades.

In the laboratory, this issue has been recently put to the test by giving naïve chimpanzees opportunities to independently invent practices that have been observed in the field. So-called leaf swallowing behavior, a proposed tool against internal parasites, develops in full in naïve chimpanzees (Huffman et al. 2010; Huffman and Hirata 2004; Menzel et al. 2013). Similarly, food washing and food mining behavior – i.e. the “classic” cases of primate culture also spontaneously re-emerge in naïve chimpanzees (Allritz et al. 2013). The same is true for other behaviours and/or for other primates. For example, mountain gorilla nettle feeding behavior—a complex non-tool-use behavior—re-appeared in naïve captive gorillas (Tennie et al. 2008); see also (Masi 2011) and (Byrne et al. 2011). Leaf swallowing also occurs in naïve bonobos (Menzel et al. 2013). Food washing and food mining behavior re-emerges in naïve orangutans (Allritz et al. 2013).

However, laboratory tests in naïve individuals still remain outstanding for most cases of purported wild chimpanzee “cultural” traits (e.g., for ant-dipping). In the case of termite fishing, Lonsdorf and colleagues actually ran a laboratory test in naïve semi-enculturated chimpanzees – who became very proficient at this behaviour. Even though this study presented the task to the whole group, rather than individually, it nevertheless showed that at the very least one of the chimpanzees developed the technique spontaneously, i.e. without the need to observe others engage in it. In other cases, like nut-cracking, previous research did not take seriously the possibility that subjects would develop the target behavior on their own, and thus baseline conditions, in which naïve individuals require time to develop the behavior on their own, have been largely neglected.

Recent field evidence converges with laboratory work, indicating that chimpanzee behavioral traits can be readily invented. Nut-cracking, once thought to be locally restricted, has now also been found in chimpanzees living 1700km to the East of its originally described occurrence (Morgan and Abwe 2006). The most interesting “two-handed” ant-dipping techniques (in the current context) likewise appear in several populations (Bossou, Guinea and Gombe, Tanzania), thousands of kilometers apart (see e.g., Yamakoshi and Myowa-Yamakoshi 2004). Finally, termite fishing also occurs in widely disconnected populations of chimpanzees, such as in both Fongoli, Senegal as well as in Gombe, Tanzania, again, thousands of kilometers apart (see e.g., Bogart and Pruettz 2011).

To be clear, we are not arguing that social learning plays no role in these practices. In fact, to the contrary, it likely plays a big role in widely spreading behaviors that are only occasionally re-invented by some individuals (Tennie et al. 2009a), e.g., nut-cracking can spread once one individual invents it (Marshall-Pescini and Whiten 2008). Deploying social learning in these cases is adaptive, since these skills are easier to learn using a combination of individual and social learning. For example, after observing subjects who showed leaf swallowing behavior, others who beforehand resisted reinvention expressed the same behavior themselves (Huffman et al. 2010; Huffman and Hirata 2004; Menzel et al. 2013). Nevertheless, the fact that the behavior appears in some naïve individuals, without any social input, means that it is not so complicated or non-intuitive that no single individual can reinvent it in their lifetime. It is not cumulative culture¹¹.

Currently, the best candidate for a cumulative cultural evolutionary product is a particular ant-dipping rod used in the Goulougo Triangle, in the Republic of Congo (Sanz et al. 2009; Sanz and Morgan 2011). Using camera-traps, Sanz et al. found that chimpanzees in one particular location use several tools in succession to access army ants, with the last one being a stick whose tip has been 'brushed' using the chimpanzees' teeth. The brushed tip is more efficient in gathering the target prey than a non-brushed tip. While generally similar behavior has been inferred elsewhere (Boesch 2012), Sanz et al. argue that theirs is a cumulative cultural case because the videos show that the chimpanzees brush the tip of the stick even before this tool is used.¹² We concur that, currently, this type of brush tool is the best potential example for cumulative culture in chimpanzees.

Finally, recent analyses by Kamilar and Atkinson (2013) of Whiten et. al.'s 39 traits, while not showing evidence of cumulative cultural evolution, do reveal a kind of nested structuring of traits, which the authors argue presents an expected precursor to cumulative cultural evolution. We agree that this could be consistent with a reliance on social learning, but the same patterns could arise from purely individual learning if learning one trait tends to bias the acquisition of other traits. Since, as we have seen, Whiten et. al.'s 39 traits includes several versions of different variants (5 forms of nut cracking, 6 types of dipping, and 3 types of food pounding) it is not hard to see why this might be. In fact, the tendency of the different researchers to split or lump variants into sub-varieties may actually account for much of the apparent nested structure.

Research has just begun on this, so it remains to be seen if any of the practices of wild chimpanzees can resist reinvention in the laboratory, or elsewhere. So far, albeit with only a handful of cases, laboratory apes have readily reinvented all behaviors seen in the field. However, whatever the final score turns out to be on cumulative cultural evolution in chimpanzees, the important theoretical point already seems clear: chimpanzees have relatively little cumulative cultural evolution compared to humans. Thus, at this point, there is no reason to suspect that they have gone down the same (or even a somewhat similar) culture-gene coevolutionary pathway as humans.

¹¹ Tennie et al. (2009) labeled such behaviors "latent solutions".

¹² Since some reports only relied on the tool descriptions without having actually seen the behavior being performed (Boesch et al. 2009), there is a possibility that in other places brush/fray tools are also produced prior to usage. Indeed Boesch (2012, page 132) claims that most other tool modifications in Tai chimpanzees are made prior to use. Thus, modifications prior to use may actually be common in chimpanzees.

FACTORS INFLUENCING CUMULATIVE CULTURAL EVOLUTION, OR LACK THEREOF

What might account for the relative lack of cumulative cultural evolution in chimpanzees?

Theoretical work has isolated four areas that influence the emergence and rate of cumulative cultural evolution: (1) individual inventiveness, trial and error exploration or general cognitive abilities, (2) high transmission fidelity via social learning due to cognitive abilities or motivations, (3) sociality (including teaching), network size and social structures, and (4) a life history with extended periods of brain plasticity and learning. We briefly discuss each of these in turn.

Cognitive abilities for, or motivations to, individually figure out novel practices foster greater cumulative cultural evolution (Henrich 2004b; 2009b; Kobayashi and Aoki 2012; van Schaik and Pradhan 2003). Of all four factors that influence cumulative cultural evolution, we suspect that this one creates the least hindrance for chimpanzees. Chimpanzees are excellent individual learners and keen explorers (the latter more in captivity, though). Laboratory studies show that their cognitive skills related to number, space and quantities are equivalent to human toddlers (Herrmann et al. 2007), and their working memories are competitive with undergraduates (Inoue and Matsuzawa 2007; Silberberg and Kearns 2009). Chimpanzees can even outcompete children in figuring out the most efficient way to accomplish a task, in part because children slavishly rely on imitation (Horner and Whiten 2005; Nagell et al. 1993). Moreover, field studies have repeatedly noted that wild chimpanzee often invent novel behaviors. But, these novelties are not picked up by others, and eventually vanish (Biro et al. 2003; Nishida et al. 2009; O'Malley et al. 2012). This is not to say that chimpanzees' cognitive skills and motivations are sufficient for human-like cumulative cultural evolution, but merely that it is not a show stopper for getting the process started. This is underlined by theoretical work showing that individual smarts are often relatively less important for generating cumulative cultural evolution than sociality and transmission fidelity (Henrich 2009b; Lewis and Laland 2012; Pradhan et al. 2012).

Social learning is a different story. While arguments about the details, categories and classifications of various forms of chimpanzee social learning are not settled, a vast body of experimental work shows that chimpanzee social learning is generally of lower fidelity than human social learning – and, rare among this field of research, there is even some kind of agreement on this point across several researchers (Tennie et al. 2009a; Whiten et al. 2009). However, theoretical work shows that transmission fidelity is crucial for cumulative cultural evolution (Henrich 2004b; 2009b; Kobayashi and Aoki 2012; Lewis and Laland 2012; Pradhan et al. 2012). In many direct comparisons of humans and chimpanzees, the children are near ceiling and the apes near floor in performance – at least with regard to action copying (Call et al. 2005; Herrmann et al. 2007; Nagell et al. 1993; Tennie et al. 2010b; Whiten et al. 1996a). Thus, compared with humans, chimpanzees are worse at copying motor patterns (Tennie et al. 2012; Tomasello and Call 1997) but also at inferring underlying goals, strategies and motivations (Dean et al. 2012; Tennie et al. 2010a) and especially when it comes to “sharing” them socially (Call 2009). Chimpanzees copy less frequently and usually require clear incentives to do any copying—and even then, their copying is very restricted (Tennie et al. 2012). Meanwhile, children are “imitation machines” (Tomasello 1999a), copying automatically, unconsciously and persistently. Consistent with this, recent neuroimaging studies found major deficits in brain structures enabling detailed action copying imitation in chimpanzees relative to humans (Hecht et al. 2012). These deficits can result in an effective blocking of certain types of cultural evolution, namely those that depend on the transmission of action styles (e.g., dance, sign language).

Another relevant element may be the degree to which learners rely on their own intuitions and experience over information gleaned from social learning—the *informational conformity* mentioned earlier. In humans, various forms of “over-imitation”, which involves copying apparently unnecessary steps, are a persistence and potent feature of learning (Lyons et al. 2007; Nielsen and Tomaselli 2010). By contrast, chimpanzees readily drop any unnecessary step once they perceive that specific steps are superfluous (Horner and Whiten 2005). Overall, most analyses of chimpanzee data strive to detect a transmission fidelity is above zero. But, only in a few trivial cases does the data support a fidelity comparable to humans (Hopper et al. 2008a).

Cultural evolutionary models also show how sociality influences the emergence and rate of cumulative cultural evolution. In short, the larger and more interconnected populations are, the more likely the emergence of cumulative cultural evolution is, and the faster the rate if it does emerge. In humans, these predictions have been tested using a combination of laboratory experiments (Muthukrishna et al. 2014), field studies (Collard et al. 2013; Kline and Boyd 2010), and ethno-historical cases (Boyd et al. 2011; Henrich 2004b). Strikingly, when populations suddenly shrink or get disconnected from larger social networks, they begin to lose complex technologies over generations. Overall, growing up in a larger, more interconnected network, gives people access to more models to select among and learn from.

From this perspective, chimpanzees have several strikes against them. First, the fission-fusion social structure of chimpanzees and their overall group size means that young chimpanzees have access to only a very limited range of potential models. For the most part, they can access only their mothers, and essentially never get to access individuals from other residential groups. To help them acquire nut-cracking skills, for example, the percentage of the time that infants have access to models beyond the mother increases from 0% at 6 months of age to a mere 10% at age 3.5 years. When given the opportunity, young chimpanzees do attend to others, besides their mother, but they just do not get many opportunities (Lonsdorf 2013). By contrast, human foragers live enmeshed in vast social webs that network together hundreds or thousands of people across many residential groups (Apicella et al. 2012; Henrich and Broesch 2011; Hill et al. 2011; Wiessner 2002).

Second, the intersection of broadening opportunities for social learning and developmental timing of learning windows may be crucial here. Infant chimpanzees wean at about age 4-5 years, after which time they begin interacting in a wider social circle (though, still, sticking relatively close to their mother for several more years). But, the developmental window on learning to nut-crack, ant-dip, and termite fish seems to close around age 5-6 (Biro et al. 2003; Inoue-nakamura and Matsuzawa 1997; Lonsdorf 2013; Marshall-Pescini and Whiten 2008). This means that there may only be a narrow slit when young chimpanzees are developmentally ready and able to learn these (and presumably other) skills and able to access a broad range of models.

This suggests that part of the secret of human cumulative cultural evolution may lie in creating a situation in which learners can access a broad range of models while their brains are still highly plastic (Henrich 2008), and the developmental window for many skills remains open. This implies a different form of social organization and a different life history, one that adds middle childhood and adolescence (Bogin 2009). Moreover, humans retain much greater brain plasticity into adulthood compared to chimpanzees (Miller et al. 2012), and they have longer lives, which give them more time to meet and learn from a broader range of individuals. This has an effect similar to increasing group size or social interconnectedness.

The prosociality of potential models is the final important element – for example, teaching is a form of altruism, and greatly facilitates the evolution of culture (Dean et al. 2012; Tennie et al. 2009a). There is now a substantial literature comparing the sociality of chimpanzees to humans, including

both children and adults. No matter how you look at the comparative data, humans are much more prosocial across a wide range of circumstances than chimpanzees. As with imitation studies, the issue is never whether chimpanzees are as prosocial as humans (or more prosocial), but only whether non-zero levels of prosociality can be detected, and what lengths researchers go to in order to pry any prosociality out of these apes (Brosnan et al. 2009; Henrich 2004c; Henrich and Silk 2013; House et al. 2012; House et al. 2013; Jensen et al. 2007a; b; Jensen et al. 2006; Silk et al. 2005; Silk and House 2011; Vonk et al. 2008; Warneken et al. 2006; Warneken and Tomasello 2006).

Experimental work described above highlights how important sociality is for cumulative cultural evolution. Dean et al. (2012) not only shows that children teach and act prosocially towards each other and chimpanzees do not, they also show that the success of children in acquiring the multi-step procedure was associated with their willingness to actively assist and reward each other. The lack of any chimpanzee teaching, assisting or rewarding in this experiment is consistent with most field observations.

Of course, the culture-gene coevolutionary approach predicts that forms of social organization, life history and prosociality (including teaching) may be as much a consequence of cumulative cultural evolution as its cause (Burkart et al. 2009; Chudek and Henrich 2010; Henrich 2008; van Schaik and Burkart 2011b; van Schaik et al. 2012). However, any ape species that for unrelated reasons had a form of social organization, prosocial motivations or life history more conducive to cumulative cultural evolution, would have had an advantage in crossing the threshold into a regime of culture-gene coevolution.

INFERENCE TO A COMMON ANCESTOR

Cultural evolutionary theory predicts that the selection pressures for more sophisticated forms of social learning will increase as environmental variability increases. As environmental variability shifts from time scales of hundreds of thousands or millions of years to that of millennia and centuries, greater social learning will be favored (Boyd and Richerson 1985). The available data from lake and ice cores suggests that after about 3 million years ago, paleo-climates began increasing in variability, plausibly on the time scales favoring social learning (Richerson et al. 2005). High levels of variability continued until about 10,000 years ago. This combination of theory and evidence suggests that *after* humans and chimpanzee split from our last common ancestor, climatic changes may have increased selection pressures for social learning in both primate lineages, as well as in other taxa.

This view is consistent with the argument that selection for social learning or behavioral flexibility drove the expansion of brains in several taxa, including some in primates and birds (Reader et al. 2011; Reader and Laland 2002). Various measures of brain size are correlated with both social learning and innovation, and brains appear to have expanded across many taxa over several million years. Indeed, culture-gene coevolutionary simulations can reproduce the extant empirical relations observed across species, between group size and brain size, between brain size and juvenile length, and between social learning, innovation and brain size (Muthukrishna and Henrich 2013).

The upshot of this is that chimpanzees likely set an upper boundary for the social learning abilities, traditions and cultural evolved patterns that we might expect in our last common ancestor.

REFERENCES

- Allritz M, Tennie C, and Call J. 2013. Food washing and placer mining in captive great apes. *Primates*:1-10.
- Aoki K. 1986. A Stochastic-Model of Gene Culture Coevolution Suggested by the Culture Historical Hypothesis for the Evolution of Adult Lactose Absorption in Humans. *P Natl Acad Sci USA* 83(9):2929-2933.
- Apicella CL, Marlowe FW, Fowler JH, and Christakis NA. 2012. Social networks and cooperation in hunter-gatherers. *Nature* 481(7382):497-U109.
- Atkisson C, O'Brien MJ, and Mesoudi A. 2012. Adult Learners in a Novel Environment Use Prestige-Biased Social Learning. *Evol Psychol-US* 10(3):519-537.
- Bandura A. 1977. *Social learning theory*. Englewood Cliffs, N.J: Prentice Hall.
- Baron R, Vandello J, and Brunsman B. 1996. The forgotten variable in conformity research: impact of task importance on social influence. *Journal of Personality & Social Psychology* 71(5):915-927.
- Beisert M, Zmyj N, Liepelt R, Jung F, Prinz W, and Daum MM. 2012. Rethinking 'Rational Imitation' in 14-Month-Old Infants: A Perceptual Distraction Approach. *PLoS ONE* 7(3):e32563.
- Bell AV, Richerson PJ, and McElreath R. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *P Natl Acad Sci USA* 106(42):17671-17674.
- Benedetti F, Thoen W, Blanchard C, Vighetti S, and Arduino C. 2013. Pain as a reward: Changing the meaning of pain from negative to positive co-activates opioid and cannabinoid systems. *Pain* 154(3):361-367.
- Billing J, and Sherman PW. 1998. Antimicrobial functions of spices: Why some like it hot. *Q Rev Biol* 73(1):3-49.
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, and Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition* 6(4):213-223.
- Bjorklund DF, Yunger JL, Bering JM, and Ragan P. 2002. The Generalization of Deferred Imitation in Enculturated Chimpanzees (*Pan troglodytes*). *Animal Cognition* 5(1):49-58.
- Boesch C. 1991. Teaching Among Wild Chimpanzees. *Animal Behaviour* 41(3):530-532.
- Boesch C. 2007. What Makes Us Human (*Homo sapiens*)? The Challenge of Cognitive Cross-Species Comparison. *Journal of Comparative Psychology* 121(3):227-240.
- Boesch C. 2012. *Wild cultures: a comparison between chimpanzee and human cultures*. New York: Cambridge University Press.
- Boesch C, Head J, and Robbins MM. 2009. Complex Tool Sets for Honey Extraction Among Chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* 56(6):560-569.
- Bogart SL, and Pruettz JD. 2009. Savanna chimpanzee (*Pan troglodytes verus*) feeding ecology at Fongoli, Senegal. *Am J Phys Anthropol*:95-95.
- Bogart SL, and Pruettz JD. 2011. Insectivory of Savanna Chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *Am J Phys Anthropol* 145(1):11-20.
- Bogin B. 2009. Childhood, adolescence, grandmotherhood and the non-symmetrical, variant nature of human life history. *Am J Phys Anthropol*:95-95.
- Bonnie KE, Horner V, Whiten A, and de Waal FBM. 2007. Spread of arbitrary conventions among chimpanzees: a controlled experiment. *P R Soc B* 274(1608):367-372.
- Boyd R, and Richerson PJ. 1985. *Culture and the Evolutionary Process*. Chicago, IL: University of Chicago Press. 331 p.
- Boyd R, and Richerson PJ. 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall TR, and Galef BG, editors. *Social Learning: Psychological and Biological Perspectives*. Hillsdale, NJ: Lawrence Erlbaum Associates. p 29-48.

- Boyd R, and Richerson PJ. 1995. Why Does Culture Increase Human Adaptability. *Ethol Sociobiol* 16(2):125-143.
- Boyd R, and Richerson PJ. 1996. Why Culture is Common, but Cultural Evolution is Rare *Proceedings of the British Academy* 88:77-93.
- Boyd R, Richerson PJ, and Henrich J. 2011. The cultural niche: Why social learning is essential for human adaptation. *P Natl Acad Sci USA* 108:10918-10925.
- Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, and Schapiro SJ. 2009. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Anim Cogn* 12(4):587-597.
- Burkart JM, Hrdy SB, and Van Schaik CP. 2009. Cooperative Breeding and Human Cognitive Evolution. *Evol Anthropol* 18(5):175-186.
- Buttelmann D, Carpenter M, Call J, and Tomasello M. 2007. Enculturated chimpanzees imitate rationally. *Developmental Science* 10(4):F31-F38.
- Buttelmann D, Carpenter M, Call J, and Tomasello M. 2008. Rational Tool Use and Tool Choice in Human Infants and Great Apes. *Child Development* 79(3):609-626.
- Buttelmann D, Zmyj N, Daum MM, and Carpenter M. 2012. Selective Imitation of In-Group Over Out-Group Members in 14-Month-Old Infants. *Child Dev*.
- Byrne RW, Hobaiter C, and Klailova M. 2011. Local Traditions in Gorilla Manual Skill: Evidence for Observational Learning of Behavioral Organization. *Animal Cognition* 14(5):683-693.
- Call J. 2009. Contrasting the Social Cognition of Humans and Nonhuman Apes: The Shared Intentionality Hypothesis. *Topics in Cognitive Science* 1(2):368-379.
- Call J, Carpenter M, and Tomasello M. 2005. Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition* 8(3):151-163.
- Call J, and Tennie C. 2009. Animal Culture: Chimpanzee Table Manners? *Current biology : CB* 19(21):R981-R983.
- Campbell DT. 1965. Variation and selective retention in socio-cultural evolution. In: Barringer HR, Glanksten GI, and Mack RW, editors. *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory*. 1965 ed. Cambridge, Massachusetts: Schenkman Publishing Company. p 19-49.
- Caro TM, and Hauser MD. 1992. Is There Teaching in Nonhuman Animals? *Quarterly Review of Biology* 67(2):151-174.
- Castro L, and Toro MA. 2002. Cultural Transmission and the Capacity to Approve or Disapprove of Offspring's Behavior. *Journal of Memetics* 6(2).
- Cavalli-Sforza LL, and Feldman M. 1981. *Cultural Transmission and Evolution*. Princeton: Princeton University Press.
- Cheng J, Tracy J, Foulsham T, and Kingstone A. 2013. Dual Paths to Power: Evidence that Dominance and Prestige are Distinct yet Viable Avenue to Social Status. *J Pers Soc Psychol* 104:103-125.
- Cheng JT, Tracy JL, and Henrich J. 2010. Pride, Personality, and the Evolutionary Foundations of Human Social Status. *Evol Hum Behav* 31(5):334-347.
- Chiao JY, and Blizinsky KD. 2010. Culture-gene coevolution of individualism-collectivism and the serotonin transporter gene. *Proceedings of the Royal Society B: Biological Sciences* 277(1681):529-537.
- Chudek M, Brosseau P, Birch S, and Henrich J. 2013. Culture-gene coevolutionary theory and children's selective social learning. In: Banaji M, and Gelman S, editors. *The Development of Social Cognition*. New York: Oxford.
- Chudek M, Heller S, Birch S, and Henrich J. 2012. Prestige-biased cultural learning: bystander's differential attention to potential models influences children's learning. *Evol Hum Behav* 33(1):46-56.

- Chudek M, and Henrich J. 2010. Culture-Gene Coevolution, Norm-Psychology, and the Emergence of Human Prosociality. *Trends Cogn Sci* 15(5):218-226.
- Claidière N, and Sperber D. 2009. Imitation Explains the Propagation, Not the Stability of Animal Culture. *Proceedings of the Royal Society of London B Biological Sciences* 277(1681):651-659.
- Claidière N, and Whiten A. 2012. Integrating the Study of Conformity and Culture in Humans and Nonhuman Animals. *Psychol Bull* 138(1):126-145.
- Collard M, Ruttle A, Buchanan B, and O'Brien MJ. 2013. Population Size and Cultural Evolution in Nonindustrial Food-Producing Societies. *PLoS ONE* 8(9):e72628.
- Collard M, Shennan SJ, and Tehrani JJ. 2006. Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evol Hum Behav* 27:168-184.
- Corp N, and Byrne R. 2002. The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba florida*. *Behaviour* 139(1):137-168.
- Corriveau K, and Harris PL. 2009a. Choosing your informant: weighing familiarity and recent accuracy. *Developmental Sci* 12(3):426-437.
- Corriveau K, and Harris PL. 2009b. Preschoolers continue to trust a more accurate informant 1 week after exposure to accuracy information. *Developmental Sci* 12(1):188-193.
- Corriveau KH, Kinzler KD, and Harris PL. 2013. Accuracy Trumps Accent in Children's Endorsement of Object Labels. *Dev Psychol* 49(3):470-479.
- Corriveau KH, Meints K, and Harris PL. 2009. Early tracking of informant accuracy and inaccuracy. *Brit J Dev Psychol* 27:331-342.
- Coultas J. 2004. When in Rome... An Evolutionary Perspective on Conformity. *Group Processes & Intergroup Relations* 7(4):317-331.
- Craig KD. 1986. Social Modeling Influences: Pain in Context. In: Sternbach RA, editor. *The Psychology of Pain*. New York: Raven Press.
- Craig KD, and Prkachin KM. 1978. Social Modeling Influences on Sensory Decision-Theory and Psychophysiological Indexes of Pain. *J Pers Soc Psychol* 36(8):805-815.
- Csibra G, and Gergely G. 2006. Social Learning and Social Cognition: The Case of Pedagogy. In: Johnson MH, and Munakata Y, editors. *Processes of Change in Brain and Cognitive Development Attention and Performance, XXI*. Oxford: Oxford University Press. p 249-274.
- Csibra G, and Gergely G. 2009. Natural Pedagogy. *Trends in Cognitive Sciences* 13(4):148-153.
- Currie TE, and Mace R. 2009. Political complexity predicts the spread of ethnolinguistic groups. *Proceedings of the National Academy of Sciences* 106(18):7339-7344.
- Dean LG, Kendal RL, Schapiro SJ, Thierry B, and Laland KN. 2012. Identification of the Social and Cognitive Processes Underlying Human Cumulative Culture. *Science* 335(6072):1114-1118.
- Dediu D, and Ladd DR. 2007. Linguistic tone is related to the population frequency of the adaptive haplogroups of two brain size genes, ASPM and Microcephalin. *P Natl Acad Sci USA* 104(26):10944-10949.
- Diamond JM. 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. New York: W.W. Norton & Co.
- Durham W. 1991. *Coevolution: Genes culture and human diversity*. Stanford, CA: Stanford University Press.
- Edgerton RB. 1971. *The individual in cultural adaptation: a study of four east african Peoples*. Berkeley: University of California Press.
- Edgerton RB. 1992. *Sick societies : challenging the myth of primitive harmony*. New York: Free Press.
- Efferson C, Lalive R, and Fehr E. 2008a. The coevolution of cultural groups and ingroup favoritism. *Science* 321(5897):1844-1849.
- Efferson C, Lalive R, Richerson PJ, McElreath R, and Lubell M. 2008b. Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evol Hum Behav* 29(1):56-64.

- Feldman MW, and Laland KN. 1996. Gene-culture coevolutionary theory. *Trends Ecol Evol* 11(11):453-457.
- Fiske AP. 1998. Learning A Culture The Way Informants Do: Observing, Imitating, and Participating.
- Fogarty L, Strimling P, and Laland KN. 2011. The Evolution of Teaching. *Evolution* 65(10):2760-2770.
- Foulsham T, Cheng J, Tracy J, Henrich J, and Kingstone A. 2010. Gaze Allocation in a Dynamic Social Situation of Social Status and Speaking. *Cognition* 117:319-331.
- Furlong EE, Boose KJ, and Boysen ST. 2008. Raking It In: The Impact of Enculturation on Chimpanzee Tool Use. *Animal Cognition* 11(1):83-97.
- Galef BG. 2009a. Strategies for Social Learning: Testing Predictions from Formal Theory. *Advances in the Study of Behavior* 39:117-151.
- Galef BG, Dudley KE, and Whiskin EE. 2008. Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Anim Behav* 75:631-637.
- Galef BG, Jr. 1992. The Question of Animal Culture. *Human Nature* 3(2):157-178.
- Galef BG, Jr. 2009b. Culture in Animals? In: Laland KN, and Galef BG, Jr., editors. *The Question of Animal Culture*. Cambridge, MA: Harvard University Press. p 222-246.
- Galef BG, and Whiskin EE. 2008. 'Conformity' in Norway rats? *Anim Behav* 75:2035-2039.
- Gaskins S, and Paradise R. 2010. Learning Through Observation in Daily Life. In: Lancy DF, Bock J, and Gaskins S, editors. *The Anthropology of Learning in Childhood: Rowman & Littlefield Publishing Group, Inc.* p 85-117.
- Gergely G, Bekkering H, and Kiraly I. 2002. Developmental psychology: Rational imitation in preverbal infants. *Nature* 415(6873):755-755.
- Gruber T, Muller MN, Reynolds V, Wrangham R, and Zuberbuhler K. 2011. Community-specific evaluation of tool affordances in wild chimpanzees. *Sci Rep-Uk* 1.
- Gruber T, Muller MN, Strimling P, Wrangham R, and Zuberbuhler K. 2009. Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task. *Current Biology* 19(21):1806-1810.
- Harris PL, and Corriveau KH. 2011. Young children's selective trust in informants. *Philos T R Soc B* 366(1567):1179-1187.
- Haslam M. 2013. 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1630).
- Haun Daniel BM, Rekers Y, and Tomasello M. 2012. Majority-Biased Transmission in Chimpanzees and Human Children, but Not Orangutans. *Current Biology* 22(8):727-731.
- Hecht EE, Gutman DA, Preuss TM, Sanchez MM, Parr LA, and Rilling JK. 2012. Process Versus Product in Social Learning: Comparative Diffusion Tensor Imaging of Neural Systems for Action Execution-Observation Matching in Macaques, Chimpanzees, and Humans. *Cerebral Cortex(Online First)*.
- Henrich J. 2001. Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change and much of sociocultural evolution. *American Anthropologist* 103:992-1013.
- Henrich J. 2004a. Cultural group selection, coevolutionary processes and large-scale cooperation. *J Econ Behav Organ* 53:3-35.
- Henrich J. 2004b. Demography and Cultural Evolution: Why adaptive cultural processes produced maladaptive losses in Tasmania. *Am Antiquity* 69(2):197-214.
- Henrich J. 2004c. Inequity Aversion in Capuchins? *Nature*.
- Henrich J. 2008. A cultural species. In: Brown M, editor. *Explaining Culture Scientifically*. Seattle: University of Washington Press. p 184-210.
- Henrich J. 2009a. The evolution of costly displays, cooperation, and religion: credibility enhancing displays and their implications for cultural evolution. *Evol Hum Behav* 30:244-260.

- Henrich J. 2009b. The Evolution of Innovation-Enhancing Institutions. In: Shennan SJ, and O'Brien MJ, editors. *Innovation in Cultural Systems: Contributions in Evolution Anthropology*. Cambridge: MIT.
- Henrich J, and Boyd R. 1998. The evolution of conformist transmission and the emergence of between-group differences. *Evol Hum Behav* 19:215-242.
- Henrich J, and 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.
- Henrich J, and Broesch J. 2011. On the Nature of Cultural Transmission Networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1139-1148.
- Henrich J, and Gil-White F. 2001a. The Evolution of Prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol Hum Behav* 22(3):165-196.
- Henrich J, and Gil-White FJ. 2001b. The evolution of prestige - Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol Hum Behav* 22(3):165-196.
- Henrich J, Heine SJ, and Norenzayan A. 2010. The Weirdest People in the World? *Behavior and Brain Sciences* 33(2/3):1-23.
- Henrich J, and Henrich N. 2010. The Evolution of Cultural Adaptations: Fijian taboos during pregnancy and lactation protect against marine toxins. *P R Soc B* 366:1139-1148.
- Henrich J, and McElreath R. 2003. The Evolution of Cultural Evolution. *Evol Anthropol* 12(3):123-135.
- Henrich J, and McElreath R. 2007. Dual Inheritance Theory: The Evolution of Human Cultural Capacities and Cultural Evolution. In: Dunbar R, and Barrett L, editors. *Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press. p 555-570.
- Henrich J, and Silk JB. 2013. Interpretative Problems with Chimpanzee Ultimatum Games. SSRN.
- Henrich N, and Henrich J. 2007. *Why Humans Cooperate: A Cultural and Evolutionary Explanation* Oxford: Oxford University Press.
- Herrmann E, Call J, Hernández-Lloreda MV, Hare B, and Tomasello M. 2007. Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. *Science* 317(5843):1360-1366.
- Herrmann PA, Legare CH, Harris PL, and Whitehouse H. 2013. Stick to the script: The effect of witnessing multiple actors on children's imitation. *Cognition* 129(3):536-543.
- Hewlett BS, Fouts HN, Boyette AH, and Hewlett BL. 2011. Social Learning Among Congo Basin Hunter-Gatherers. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 366(1567):1168-1178.
- Hill KR, Walker RS, Božičević M, Eder J, Headland T, Hewlett B, Hurtado AM, Marlowe F, Wiessner P, and Wood B. 2011. Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. *Science* 331(6022):1286-1289.
- Hirata S, and Celli ML. 2003. Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Anim Cogn* 6(4):235-244.
- Holden C, and Mace R. 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Hum Biol* 69(5):605-628.
- Hopper LM, Lambeth SP, Schapiro SJ, and Brosnan SF. 2011a. Chimpanzees' (Pan Troglodytes) Learning Indicates Both Conformity and Conservatism. *Am J Primatol* 73:75-75.
- Hopper LM, Lambeth SP, Schapiro SJ, and Whiten A. 2008a. Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society B: Biological Sciences* 275(1636):835-840.

- Hopper LM, Lambeth SP, Schapiro SJ, and Whiten A. 2008b. Observational Learning in Chimpanzees and Children Studied Through 'Ghost' Conditions. *Proceedings of the Royal Society of London B Biological Sciences* 275(1636):835-840.
- Hopper LM, Schapiro SJ, Lambeth SP, and Brosnan SF. 2011b. Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Anim Behav* 81(6):1195-1202.
- Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, and Whiten A. 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim Behav* 73:1021-1032.
- Hoppitt W, and Laland KN. 2013. Social learning : an introduction to mechanisms, methods, and models. pages cm p.
- Hoppitt WJE, Brown GR, Kendal R, Rendell L, Thornton A, Webster MM, and Laland KN. 2008. Lessons from Animal Teaching. *Trends in Ecology & Evolution* 23(9):486-493.
- Horner V, Proctor D, Bonnie KE, Whiten A, and de Waal FBM. 2010. Prestige Affects Cultural Learning in Chimpanzees. *PLoS ONE* 5(5):e10625.
- Horner V, and Whiten A. 2005. Causal Knowledge and Imitation/Emulation Switching in Chimpanzees (*Pan troglodytes*) and Children (*Homo sapiens*). *Animal Cognition* 8(3):164-181.
- House BR, Henrich J, Brosnan SF, and Silk JB. 2012. The ontogeny of human prosociality: behavioral experiments with children aged 3 to 8. *Evol Hum Behav* 33(4):291-308.
- House BR, Silk JB, Henrich J, Barrett HC, Scelza BA, Boyette AH, Hewlett BS, McElreath R, and Laurence S. 2013. Ontogeny of prosocial behavior across diverse societies. *P Natl Acad Sci USA* 110(36):14586-14591.
- Hruschka DJ, and Henrich J. 2013. Institutions, Parasites and the Persistence of In-group Preferences. *Plos One* 8(5).
- Huffman M, Spiezio C, Sgaravatti A, and Leca J-B. 2010. Leaf Swallowing Behavior in Chimpanzees (*Pan troglodytes*): Biased Learning and the Emergence of Group Level Cultural Differences. *Animal Cognition* 13(6):871-880.
- Huffman MA, and Hirata S. 2004. An Experimental Study of Leaf Swallowing in Captive Chimpanzees: Insights Into the Origin of a Self-Medicative Behavior and the Role of Social Learning. *Primates* 45(2):113-118.
- Humle T, Snowdon CT, and Matsuzawa T. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim Cogn* 12:S37-S48.
- Inoue-nakamura N, and Matsuzawa T. 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J Comp Psychol* 111(2):159-173.
- Inoue S, and Matsuzawa T. 2007. Working memory of numerals in chimpanzees. *Current biology : CB* 17(23):R1004-R1005.
- Jaswal VK, and Neely LA. 2006. Adults don't always know best: Preschoolers use past reliability over age when learning new words. *Psychol Sci* 17(9):757-758.
- Jensen K, Call J, and Tomasello M. 2007a. Chimpanzees are rational maximizers in an ultimatum game. *Science* 318(5847):107-109.
- Jensen K, Call J, and Tomasello M. 2007b. Chimpanzees are vengeful but not spiteful. *P Natl Acad Sci USA* 104(32):13046-13050.
- Jensen K, Hare B, Call J, and Tomasello M. 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *P R Soc B* 273(1589):1013-1021.
- Jordan P, and Shennan S. 2003. Cultural transmission, language, and basketry traditions amongst the California Indians. *J Anthropol Archaeol* 22(1):42-74.
- Kamilar JM, and Atkinson QD. 2013. Cultural assemblages show nested structure in humans and chimpanzees but not orangutans. *Proceedings of the National Academy of Sciences*.

- Kellogg W, and Kellogg L. 1933. *The ape and the child: a study of environmental influence upon early behavior*. New York: McGraw-Hill.
- Kendal J, Giraldeau LA, and Laland K. 2009. The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *J Theor Biol* 260(2):210-219.
- Kendal RL, Coolen I, van Bergen Y, and Laland KN. 2005. Trade-Offs in the Adaptive Use of Social and Asocial Learning. In: Peter J. B. Slater CTSTJRHJB, and Marc N, editors. *Advances in the Study of Behavior: Academic Press*. p 333-379.
- Kline M, Boyd R, and Henrich J. 2013. Teaching and the Life History of Cultural Transmission in Fijian Villages. *Human Nature* 24(4):351-374.
- Kline MA. under review. How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals.
- Kline MA, and Boyd R. 2010. Population size predicts technological complexity in Oceania. *P R Soc B* 277(1693):2559-2564.
- Kobayashi Y, and Aoki K. 2012. Innovativeness, population size and cumulative cultural evolution. *Theor Popul Biol* 82(1):38-47.
- Koenig MA, and Harris PL. 2005. Preschoolers mistrust ignorant and inaccurate speakers. *Child Dev* 76(6):1261-1277.
- Koops K, McGrew WC, and Matsuzawa T. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Anim Behav* 85(1):175-185.
- Laland K. 1994. Sexual selection with a culturally-transmitted mating preference. *Theor Popul Biol* 45:1-15.
- Laland KN. 2004. Social learning strategies. *Learn Behav* 32(1):4-14.
- Laland KN, Atton N, and Webster MM. 2011. From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philos T R Soc B* 366(1567):958-968.
- Laland KN, and Janik VM. 2006. The animal cultures debate. *Trends Ecol Evol* 21(10):542-547.
- Laland KN, Kendal JR, and Kendal RL. 2009. Animal Culture: Problems and Solutions. In: Laland KN, and Galef BG, Jr., editors. *The Question of Animal Culture*. Cambridge, MA: Harvard University Press. p 174-197.
- Laland KN, Kumm J, and Feldman MW. 1995a. Gene-Culture Coevolutionary Theory - a Test-Case. *Curr Anthropol* 36(1):131-156.
- Laland KN, Kumm J, Vanhorn JD, and Feldman MW. 1995b. A Gene-Culture Model of Human Handedness. *Behav Genet* 25(5):433-445.
- Laland KN, Odling-Smee J, and Myles S. 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nat Rev Genet* 11(2):137-148.
- Lancy D. 1996. *Playing on Mother Ground: Cultural Routines for Children's Development*. London: The Guilford Press.
- Lancy D. 2009. *The Anthropology of Childhood: Cherubs, Chattel and Changlings*. Cambridge: Cambridge University Press. 488 p.
- Langergraber KE, Boesch C, Inoue E, Inoue-Murayama M, Mitani JC, Nishida T, Pusey A, Reynolds V, Schubert G, Wrangham RW et al. . 2011a. Genetic and 'cultural' similarity in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 278(1704):408-416.
- Langergraber KE, Boesch C, Inoue E, Inoue-Murayama M, Mitani JC, Nishida T, Pusey A, Reynolds V, Schubert G, Wrangham RW et al. . 2011b. Genetic and 'Cultural' Similarity in Wild Chimpanzees. *Proceedings of the Royal Society of London B Biological Sciences* 278(1704):408-416.
- Langergraber KE, and Vigilant L. 2011. Genetic differences cannot be excluded from generating behavioural differences among chimpanzee groups. *P R Soc B* 278(1715):2094-2095.
- Leavens DA, Bard KA, and Hopkins WD. 2010. BIZARRE chimpanzees do not represent "the chimpanzee". *Behav Brain Sci* 33(2-3):100-+.

- Lewis HM, and Laland KN. 2012. Transmission fidelity is the key to the build-up of cumulative culture. *Philos T R Soc B* 367(1599):2171-2180.
- Lipo CP, O'Brien MJ, Collard M, and Shennan S, editors. 2006. *Mapping our Ancestors*. Piscataway: Aldine Transactions.
- Lonsdorf EV. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Anim Behav* 70:673-683.
- Lonsdorf EV. 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Anim Cogn* 9(1):36-46.
- Lonsdorf EV. 2013. The Role of Mothers in the Development of Complex Skills in Chimpanzees. In: Clancy KBH, Hinde K, and Rutherford JN, editors. *Building Babies: Primate Development in Proximate and Ultimate Perspective*. New York: Springer.
- Lonsdorf EV, Eberly LE, and Pusey AE. 2004. Sex differences in learning in chimpanzees. *Nature* 428(6984):715-716.
- Lumsden C, and Wilson EO. 1981. *Genes, mind, and culture: the coevolutionary process*. Cambridge, Mass: Harvard University Press.
- Luncz LV, Mundry R, and Boesch C. 2012. Evidence for Cultural Differences between Neighboring Chimpanzee Communities. *Current Biology* 22(10):922-926.
- Lycett SJ, Collard M, and McGrew WC. 2010. Are Behavioral Differences Among Wild Chimpanzee Communities Genetic Or Cultural? An Assessment Using Tool-Use Data and Phylogenetic Methods. *Am J Phys Anthropol* 142(3):461-467.
- Lycett SJ, Collard M, and McGrew WC. 2011. Correlations between genetic and behavioural dissimilarities in wild chimpanzees (*Pan troglodytes*) do not undermine the case for culture. *Proceedings of the Royal Society B: Biological Sciences* 278(1715):2091-2093.
- Lyons DE, Young AG, and Keil FC. 2007. The Hidden Structure of Overimitation. *Proceedings of the National Academy of Sciences of the United States of America* 104(50):19751-19756.
- Maestriperi D. 1995. First Steps in the Macaque World: Do Rhesus Mothers Encourage Their Infants' Independent Locomotion? *Animal Behaviour* 49(6):1541-1549.
- Manrique HM, Völter CJ, and Call J. 2013. Repeated innovation in great apes. *Animal Behaviour* 85(1):195-202.
- Marshall-Pescini S, and Whiten A. 2008. Social learning of nut-cracking behavior in east African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *J Comp Psychol* 122(2):186-194.
- Masi S. 2011. Differences in Gorilla Nettle-Feeding Between Captivity and the Wild: Local Traditions, Species Typical Behaviors or Merely the Result of Nutritional Deficiencies? *Animal Cognition* 14(6):921-925.
- McElreath R, Bell AV, Efferson C, Lubell M, Richerson PJ, and Waring T. 2008. Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philos T R Soc B* 363(1509):3515-3528.
- McElreath R, Boyd R, and Richerson PJ. 2003. Shared norms and the evolution of ethnic markers. *Curr Anthropol* 44(1):122-129.
- McElreath R, and Strimling P. 2008. When Natural Selection Favors Imitation of Parents. *Curr Anthropol* 49(2):307-316.
- McGrew WC. 2013. Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1630).
- Melber TN, Lonsdorf EV, and Ross SR. 2007. Social learning of tool-use skills in captive chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 69:100-101.
- Menzel C, Fowler A, Tennie C, and Josep C. 2013. Leaf Surface Roughness Elicits Leaf Swallowing Behavior in Captive Chimpanzees (*Pan troglodytes*) and Bonobos (*P. paniscus*), but not in

- Gorillas (*Gorilla gorilla*) or Orangutans (*Pongo abelii*). *International Journal of Primatology* 34(3):533-553.
- Menzel Jr EW, Davenport RK, and Rogers CM. 1970. The Development of Tool Using in Wild-Born and Restriction-Reared Chimpanzees. *Folia Primatologica* 12(4):273-283.
- Miller DJ, Duka T, Stimpson CD, Schapiro SJ, Baze WB, McArthur MJ, Fobbs AJ, Sousa AMM, Sestan N, Wildman DE et al. . 2012. Prolonged myelination in human neocortical evolution. *P Natl Acad Sci USA* 109(41):16480-16485.
- Mobius Y, Boesch C, Koops K, Matsuzawa T, and Humle T. 2008. Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Anim Behav* 76:37-45.
- Moore R. 2013. Social learning and teaching in chimpanzees. *Biology & Philosophy* 28(6):879-901.
- Morgan BJ, and Abwe EE. 2006. Chimpanzees use stone hammers in Cameroon. *Current biology : CB* 16(16):R632-R633.
- Morgan TJH, and Laland K. 2012. The biological bases of conformity. *Frontiers in Neuroscience* 6(87):1-7.
- Morgan TJH, Rendell LE, Ehn M, Hoppitt W, and Laland KN. 2012. The evolutionary basis of human social learning. *P R Soc B* 279(1729):653-662.
- Muthukrishna M, Shulman BW, Vasilescu V, and Henrich J. 2014. Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences* 281(1774).
- Nagell K, Olguin RS, and Tomasello M. 1993. Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology* 107(2):174-186.
- Nakahashi W, Wakano JY, and Henrich J. 2012. Adaptive Social Learning Strategies in Temporally and Spatially Varying Environments How Temporal vs. Spatial Variation, Number of Cultural Traits, and Costs of Learning Influence the Evolution of Conformist-Biased Transmission, Payoff-Biased Transmission, and Individual Learning. *Hum Nature-Int Bios* 23(4):386-418.
- Nielsen M, and Tomaselli K. 2010. Overimitation in Kalahari Bushman Children and the Origins of Human Cultural Cognition. *Psychological Science* 21(5):729-736.
- Nishida T, Matsusaka T, and McGrew WC. 2009. Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates* 50(1):23-36.
- O'Malley RC, Wallauer W, Murray CM, and Goodall J. 2012. The Appearance and Spread of Ant Fishing among the Kasekela Chimpanzees of Gombe A Possible Case of Intercommunity Cultural Transmission. *Curr Anthropol* 53(5):650-663.
- Ottoni EB, de Resende BD, and Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Anim Cogn* 8(4):215-219.
- Perreault C, Moya C, and Boyd R. 2012. A Bayesian approach to the evolution of social learning. *Evol Hum Behav* 33(5):449-459.
- Pike TW, and Laland KN. 2010. Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol Letters* 6(4):466-468.
- Pradhan GR, Tennie C, and van Schaik CP. 2012. Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution* 63(1):180-190.
- Pulliam HR, and Dunford C. 1980. Programmed to Learn: An Essay on the Evolution of Culture. New York: Columbia University Press.
- Reader SM, Hager Y, and Laland KN. 2011. The evolution of primate general and cultural intelligence. *Philos T R Soc B* 366(1567):1017-1027.
- Reader SM, and Laland KN. 2002. Social intelligence, innovation, and enhanced brain size in primates. *P Natl Acad Sci USA* 99(7):4436-4441.

- Rendell L, Boyd R, Cownden D, Enquist M, Eriksson K, Feldman MW, Fogarty L, Ghirlanda S, Lillicrap T, and Laland KN. 2010. Why Copy Others? Insights from the Social Learning Strategies Tournament. *Science* 328(5975):208-213.
- Rendell L, Fogarty L, Hoppitt WJE, Morgan TJH, Webster MM, and Laland KN. 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* 15(2):68-76.
- Renevey N, Bshary R, and van de Waal E. 2013. Philopatric vervet monkey females are the focus of social attention rather independently of rank. *Behaviour* 150(6):599-615.
- Richerson PJ, Bettinger RL, and Boyd R. 2005. Evolution on a restless planet: Were environmental variability and environmental change major drivers of human evolution? In: Wuketits FM, and Ayala FJ, editors. *Handbook of Evolution: Evolution of Living Systems (including Hominids)*. Weinheim: Wiley-VCH. p 223-242.
- Richerson PJ, and Boyd R. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
- Richerson PJ, Boyd R, and Henrich J. 2010. Gene-Culture Coevolution in the Age of Genomics. *Proceedings of the National Academy of Sciences of the United States of America* 107(Supplement 2):8985-8992.
- Rogers EM. 1995. *Diffusion of innovations*. New York: Free Press.
- Rozin P, Mark M, and Schiller D. 1981. The Role of Desensitization to Capsaicin in Chili Pepper Ingestion and Preference. *Chem Senses* 6(1):23-31.
- Rozin P, and Schiller D. 1980. The nature and acquisition of a preference for chili pepper by humans. *Motivation and Emotion* 4(1):77-101.
- Sanz C, Call J, and Morgan D. 2009. Design Complexity in Termite-Fishing Tools of Chimpanzees (*Pan troglodytes*). *Biology Letters* 5(3):293-296.
- Sanz CM, and Morgan DB. 2011. Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biol Letters* 7(4):634-637.
- Sanz CM, and Morgan DB. 2013. Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1630).
- Schöning C, Humle T, Möbius Y, and McGrew WC. 2008. The nature of culture: Technological variation in chimpanzee predation on army ants revisited. *J Hum Evol* 55(1):48-59.
- Shennan S. 2003. *Genes, Memes, and Human History: Darwinian Archaeology and Cultural Evolution*. London: Thames & Hudson.
- Shennan S. 2009. *Pattern and process in cultural evolution*. Berkeley: University of California Press. vii, 341 p. p.
- Silberberg A, and Kearns D. 2009. Memory for the order of briefly presented numerals in humans as a function of practice. *Animal Cognition* 12(2):405-407.
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaró J, and Shapiro SJ. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437:1357-1359.
- Silk JB, and House BR. 2011. Evolutionary foundations of human prosocial sentiments. *P Natl Acad Sci USA* 108:10910-10917.
- Stammbach E. 1988. Group responses to specially skilled individuals in a *Macacca fascicularis* group. *Behavior* 107:241-266.
- Strauss S, and Ziv M. 2012. Teaching Is a Natural Cognitive Ability for Humans. *Mind, Brain, and Education* 6(4):186-196.
- Tehrani JJ, and Collard M. 2009. On the relationship between interindividual cultural transmission and population-level cultural diversity: a case study of weaving in Iranian tribal populations. *Evol Hum Behav* 30(4):286-300.

- Tehrani JJ, Collard M, and Shennan SJ. 2010. The cophylogeny of populations and cultures: reconstructing the evolution of Iranian tribal craft traditions using trees and jungles. *Philos T R Soc B* 365(1559):3865-3874.
- Tennie C, Call J, and Tomasello M. 2006. Push or Pull: Imitation vs. Emulation in Great Apes and Human Children. *Ethology* 112(12):1159-1169.
- Tennie C, Call J, and Tomasello M. 2009a. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos T R Soc B* 364(1528):2405-2415.
- Tennie C, Call J, and Tomasello M. 2009b. Ratcheting Up the Ratchet: On the Evolution of Cumulative Culture. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 364(1528):2405-2415.
- Tennie C, Call J, and Tomasello M. 2010a. Evidence for Emulation in Chimpanzees in Social Settings Using the Floating Peanut Task. *PLoS ONE* 5(5):e10544.
- Tennie C, Call J, and Tomasello M. 2012. Untrained Chimpanzees (*Pan troglodytes schweinfurthii*) Fail to Imitate Novel Actions. *PLoS ONE* 7(8):e41548.
- Tennie C, Greve K, Gretscher H, and Call J. 2010b. Two-Year-Old Children Copy More Reliably and More Often than Nonhuman Great Apes in Multiple Observational Learning Tasks. *Primates* 51(4):337-351.
- Tennie C, Hedwig D, Call J, and Tomasello M. 2008. An Experimental Study of Nettle Feeding in Captive Gorillas. *American Journal of Primatology* 70(6):584-593.
- Thorndike EL. 1911. *Animal Intelligence*. New York: Macmillan.
- Thornton A, and McAuliffe K. 2006. Teaching in Wild Meerkats. *Science* 313(5784):227-229.
- Thornton A, and Raihani NJ. 2008. The Evolution of Teaching. *Animal Behaviour* 75(6):1823-1836.
- Tomasello M. 1994. The question of chimpanzee culture. In: Wrangham R, McGrew WC, de Waal FBM, and Heltne PG, editors. *Chimpanzee Cultures*. Cambridge, MA: Harvard University Press. p 301-317.
- Tomasello M. 1999a. *The Cultural Origins of Human Cognition*. Cambridge, MA: Harvard University Press. vi, 248 p.
- Tomasello M. 1999b. The Human Adaptation for Culture. *Annun Rev Anthropol* 28:509-529.
- Tomasello M, and Call J. 1997. *Primate Cognition*. New York, NY, USA: Oxford University Press. ix, 517 p.
- Tomasello M, Savage-Rumbaugh S, and Kruger AC. 1993. Imitative Learning of Actions on Objects by Children, Chimpanzees, and Enculturated Chimpanzees. *Child Development* 64(6):1688-1705.
- van de Waal E, Borgeaud C, and Whiten A. 2013. Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science* 340(6131):483-485.
- van de Waal E, Renevey N, Favre CM, and Bshary R. 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *P R Soc B* 277(1691):2105-2111.
- van Leeuwen EJC, and Haun DBM. 2013. Conformity in nonhuman primates: fad or fact? *Evol Hum Behav* 34(1):1-7.
- van Schaik CP, and Burkart JM. 2011a. Social Learning and Evolution: The Cultural Intelligence Hypothesis. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 366(1567):1008-1016.
- van Schaik CP, and Burkart JM. 2011b. Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1567):1008-1016.
- van Schaik CP, Isler K, and Burkart JM. 2012. Explaining brain size variation: from social to cultural brain. *Trends Cogn Sci* 16(5):277-284.
- van Schaik CP, and Pradhan GR. 2003. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *J Hum Evol* 44:645-664.

- Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ, and Povinelli DJ. 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Anim Behav* 75:1757-1770.
- Wakano JY, Aoki K, and Feldman MW. 2004. Evolution of social learning: a mathematical analysis. *Theor Popul Biol* 66(3):249-258.
- Warneken F, Chen F, and Tomasello M. 2006. Cooperative activities in young children and chimpanzees. *Child Dev* 77(3):640-663.
- Warneken F, and Tomasello M. 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311(5765):1301-1303.
- Whiten A. 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 112(3):270-281.
- Whiten A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Philos T R Soc B* 366(1567):997-1007.
- Whiten A. 2012. *Culture evolves*. Oxford ; New York: Oxford University Press. xvi, 454 p p.
- Whiten A, Custance DM, Gomez J-C, Teixidor P, and Bard KA. 1996a. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* Vol 110(1):3-14.
- Whiten A, Custance DM, Gómez J-C, Teixidor P, and Bard KA. 1996b. Imitative Learning of Artificial Fruit Processing in Children (*Homo sapiens*) and Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 110(1):3-14.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, and Boesch C. 1999. Cultures in chimpanzees. *Nature* 399(6737):682-685.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, and Boesch C. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481-1516.
- Whiten A, Horner V, and de Waal FBM. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437(7059):737-740.
- Whiten A, McGuigan N, Marshall-Pescini S, and Hopper LM. 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364(1528):2417-2428.
- Whiten A, and van Schaik CP. 2007a. The evolution of animal 'cultures' and social intelligence. *Philos T R Soc B* 362(1480):603-620.
- Whiten A, and van Schaik CP. 2007b. The Evolution of Animal 'Cultures' and Social Intelligence. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 362(1480):603-620.
- Wiessner P. 2002. Hunting, healing, and hxaro exchange - A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evol Hum Behav* 23(6):407-436.
- Wrangham R, and Carmody R. 2010. Human Adaptation to the Control of Fire. *Evol Anthropol* 19(5):187-199.
- Yamakoshi G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *Am J Phys Anthropol* 106(3):283-295.
- Yamakoshi G, and Myowa-Yamakoshi M. 2004. New observations of ant-dipping techniques in wild chimpanzees at Bossou, Guinea. *Primates* 45(1):25-32.
- Yamamoto S, Humle T, and Tanaka M. 2013. Basis for Cumulative Cultural Evolution in Chimpanzees: Social Learning of a More Efficient Tool-Use Technique. *PLoS ONE* 8(1):e55768.