
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, archaeology and economics (Henrich, forthcoming; Hoppitt and Laland, 2013; Richerson and Boyd, 2005; Shennan, 2003). Here, we apply these theoretical developments to chimpanzees by reviewing the now large body of evidence on chimpanzee social learning, culture and traditions. Along the way, we provide comparative evidence for humans to assess the similarities and differences between these two 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 flexibly to argue for the presence or absence of qualitatively-distinct, human psychological capacities, abilities or motivations in chimpanzees, with often little or no emphasis on quantifying these differences or exploring the implications of such quantitative differences 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, 1991a; 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 learn *as a consequence* of each other) and (2) on the importance of interaction and sociality. This means that “culture” is now anchored in brains, and traceable to individual cognitive abilities or learning strategies (Henrich and McElreath, 2007; Laland, 2004; Tomasello, 1999b). But, this also means that culture is not reducible to these abilities, since culture is what arises from a combination of learning and social 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. Isolated individuals can learn, but they can’t have culture.

Spreading out from this conceptualization of culture, several 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; 1973) 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 mutually influence 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 and processes (Boyd et al., 2011; Mesoudi, 2011; Whiten, 2012). This research has:

- 1) Tested various hypotheses regarding ‘what’, ‘when’ and ‘from whom’ people will apply their adaptive social learning abilities (e.g., Chudek et al., 2013; Morgan et al., 2012; Muthukrishna et al., forthcoming; Rendell et al., 2011; Wood et al., 2013) as well as ‘when’ and ‘to whom’ they will transmit (teach) cultural information (Kline, 2015; Kline et al., 2013).
- 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).
- 4) 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).
- 5) 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 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 comparative focus is on chimpanzees, we will at times bring in evidence from other primates as well as other species.

DO CHIMPANZEES LEARN SOCIALLY?

Culture-gene coevolutionary 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 discuss later, human attention and social learning abilities appear functionally honed to adaptively extract information from the minds and behaviors of other members of our groups; this information ranges 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, forthcoming; 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 stimuli (Benedetti et al., 2013; Craig, 1986; Craig and Prkachin, 1978; Henrich, forthcoming).

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 different from humans in crucial ways. The most decisive evidence on this question comes from several laboratory studies. Typically, these studies take the following form: a trained demonstrator (a human or chimpanzee¹) shows an observer 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 an 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., 2008a; Horner and Whiten, 2005a; Horner and Whiten, 2005b; Kendal et al., 2015; Tennie et al., 2010b), though the degree of matching is often not substantial and sometimes it is indistinguishable from 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., 2008a; Hopper et al., 2007; Whiten et al., 2005), even though the social learning here may be underpinned by a range of psychological mechanisms that cannot be pinpointed by the experimental methods deployed (Tennie et al., 2009; Tennie et al., 2010a). Nevertheless, from the point of view of existing evolutionary models, what matters most is transmission fidelity (Henrich, 2004b; Lewis and Laland, 2012), and not the specific psychological details; thus, we focus on transmission fidelity.

One large study allows us to directly assess transmission fidelities across a battery of eight two-target tasks deployed within one single study among human toddlers (age 2 years), chimpanzees, gorillas, orangutans and bonobos using conspecific demonstrators (Tennie et al., 2010b). Three different conditions in this study tested for different social learning mechanisms: (1) Full Demonstration, where a conspecific demonstrated the target methods, (2) Intention, where a conspecific demonstrated failed attempts, and (3) Endstate, where subjects observed only the physical endstates of the apparatuses. The tasks were presented in two sets, each with four tasks. Due to limited sample size (n=36), the apes were tested repeatedly while the children were tested in one trial per condition.

Across all five apes species, only the toddlers showed some evidence for copying across all three conditions. The other great apes only ever showed some evidence for copying in the Full Demonstration condition. However, even in the Full Demonstration condition, only the toddlers revealed any evidence of copying in the first trial data. For the other apes, only when all their trials were analyzed together did they reveal any evidence for copying as well, though this only occurred in one set of tasks. In sum, the non-human ape species showed rather weak and inflexible copying abilities compared to children, who copied reliably and robustly. So, regardless of the psychological mechanisms, chimpanzees and other apes reveal only very low transmission fidelities relative to humans (except sometimes in particularly simple tasks (Kendal et al., 2015)). Notably, older children and adults show even higher transmission fidelities than toddlers (McGuigan et al., 2011), rendering the discrepancy even more extreme. We explain the implications of such results below.

While such laboratory studies have proven invaluable for assessing chimpanzee social learning, there are important concerns regarding how transferable such laboratory findings are to the field; in other words, how ecologically valid are these findings? Chimpanzees in typical laboratory studies may be showing more or less social learning than they would in the wild. It may be tempting to simply choose the best performers, but really the question is which population is the most ecologically valid, and only these should be used to (a) explain wild behavior patterns and (b) directly inform evolutionary scenarios—though understanding latent capacities—unexpressed in the wild—may still be important. High performing populations may show a *potential*, but it is questionable if these are ever expressed in wild populations. For example, chimpanzees trained in sign language may use a gestural sign for the colour blue, but this never happens in the wild.

To get at the population with the highest ecological validity, captive great apes can be heuristically divided up into four categories: (1) those that have received extensive human training and enculturation (hereafter *highly enculturated*; e.g. Kanzi, the bonobo), (2) apes who have received extensive human interaction, training and some enculturation, such as some of the apes housed in Zoos (from here on, *semi-enculturated* chimpanzees; e.g. human reared chimpanzees who then continue to live among conspecifics), (3) apes living in conspecific groups under non-deprived conditions—but without having received intensive human interaction (hereafter, *enriched captive* apes; e.g., many zoos and sanctuaries), and (4) those who have been traumatized and/or have experienced prolonged socially and physically deprived conditions (e.g., isolation; hereafter *deprived*; some Hollywood/Circus trained apes or those isolated in medical laboratories). Again, we should note base our choice of study population on performance, but note that a choice is necessary, since these populations can differ in their levels of skills. For example, in terms of social learning, and related abilities such as pointing (Leavens et al., 2010), highly enculturated chimpanzees are generally superior (Bjorklund et al., 2002; Tomasello et al., 1993; van Schaik and Burkart, 2011b), followed by semi-enculturated ones (Furlong et al., 2008), then enriched captives and finally the deprived apes (Menzel Jr et al., 1970).

Consequently, though far from ideal, we feel that enriched captive apes probably provide the best available population from which to draw the most valid conclusions about wild populations.² Clearly, deprived apes are not acceptable—though short-term deprivations during certain developmental periods may not create enduring cognitive or motivational problems (Ferdowsian et al., 2011 though see; Wobber and Hare, 2011). Similarly, highly-and semi-enculturated apes are unlikely to be the best model for wild apes, since extensive and intimate contact with humans does not occur in the wild: and this does seem to alter cognitive skills and motivations in significant ways. This leaves as the currently most ecologically valid choice the enriched captive populations, who live in social groups, are well-fed (better than wild apes) and experience (somewhat) enriched

physical environments (note that wild chimpanzees live also in a range of environments). Note that the social learning studies above all involved enriched captive apes.³

These lines of evidence leave little doubt that chimpanzees have at least some forms of social learning. Psychologists, aiming to distinguish qualitatively different types of social learning in humans and other species, have worked extensively to distinguish cognitive mechanisms such as imitation from others such as emulation and local enhancement. Cultural evolutionary theory, however, suggests that while these psychological categories provide useful proximate distinctions, our focus here should remain on thinking quantitatively (not qualitatively) about the frequency, fidelity and durability of social learning. This is especially important since high fidelity transmission might be achieved by using a combination of different psychological mechanisms, such as by copying some motor patterns (imitation), inferring some goals (goal emulation) and noting some mechanical affordances—often helped by various sorts of socially-enhanced individual learning. Showing that some chimpanzees can sometimes imitate, for example, doesn't tell us if this imitation is likely to give rise to *any* cultural diffusion or evolution. If not enough chimpanzees can copy and spread the behavior further, and/or if the imitation is too crude or rare, there will not be any resulting cultural evolution. A little imitation is the same as no imitation in many situations. However, this does not mean that other types of social learning could not provide the basis for some cultural evolution (unless of course, the trait in question is purely action based and imitation fueled). Thus, we refer readers interested in various psychological categories of social learning mechanisms to the many excellent reviews (see reviews in Hoppitt and Laland, 2013; Tennie et al., 2009; Whiten, 2011; Zentall, 2006).

Next, we consider whether chimpanzee social learning has been shaped by natural selection, as it appears to have been in humans, to expand and hone the behavioral repertoires of individuals by facilitating 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 (asocial) 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 (Heyes, 2012; Reader and Laland, 2002), so it is possible that selection for one delivers some amount of the other “for free” as a byproduct of selection for asocial learning abilities.

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).

Testing this copy-when-uncertain bias, Kendal and her collaborators (2015) studied the open diffusion of the practice of sliding a door to the right or left to access a grape (i.e. using a very simple two target task). They found that the more experience an individual had with sliding the door, the less they relied on the observations of others in deciding which way to slide the door. The idea is that if you aren't sure which way the door might slide, you might as well try sliding it in the direction you've previously observed, either most recently or most frequently.

Beyond this, we know of no other tests of these predictions in chimpanzees, though 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). In our view, however, a combination of methodological problems and conceptual ambiguities 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, these individuals may drop their new techniques, and instead revert back (‘conform’, is the claim) to the technique they first learned. For example, 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 reversions in 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, forthcoming), normative conformity does exist in humans and is not ruled out in these experimental designs.⁴

In one well-designed study focused on these issues, Van Leeuwen et al. (2013) directly tested the strength of chimpanzee conservativeness. In contrast to most such research, chimpanzees in this study first individually learned their own ways to solve the task (the tasks were either to place one of two tokens into the same container or the same token into one of two containers – upon which food rewards were handed out). The main question was whether chimpanzees would ever abandon their first-learned behavior in favor of another one shown by the majority of subjects in their social group, which would have been evidence for informational conformity. Chimpanzees did not show any conformity in this study. Instead, they stuck to their initially learned asocial solution. This occurred despite the fact that chimpanzees who performed the minority strategy paid greater attention to what majority chimpanzees were doing. Thus, conservatism appears to be a potent tendency in chimpanzees.

Nevertheless, this conservatism can be overridden by social factors. In another condition, chimpanzees did abandon their first learned strategy in favour of the demonstrated alternative, but again this was not due to conformity. Instead, the chimpanzees abandoned their learned strategy because in this condition, the new method yielded a five-fold increase in food rewards. Thus, the chimpanzees were able to override their conservative nature to increase their payoffs; i.e., when you see a method that delivers much more, switch.

OBLIQUE TRANSMISSION USING AGE, SUCCESS, KNOWLEDGE 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 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 (or perceived knowledge), 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 individuals 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 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; Wood et al., 2013), as well as providing some evidence in other non-primate species (Galef, 2009a; Laland et al., 2011; Rendell et al., 2011).

Building on these insights, researchers have also proposed that learners should take into account the costs of accessing their preferred models (those who they deem skilled, successful and prestigious). Placing this 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 to update their cultural traits from their preferred models (Henrich, 2004b; Henrich and Broesch, 2011; Kline et al., 2013). 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. Accessing these preferred models will require learners to pay costs in the form of spending time with these individuals, and in paying them deference in the form of gifts and services in exchange for access and potentially instruction (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; 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 older and more experience practitioners, 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 that this extra attention results in social learning because, otherwise, such attention could be merely part of a scrounging strategy—scroungers should likewise attend the most skilled because it's often more productive to scrounge from them (Stammbach, 1988).

In one study, observational data indicate not only the transmission of a specific part of a behavior (in this case: the length of their termite dips), but also a sex-bias in transmission, 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 (females stay home), 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.

In the lab, two experiments aim to address the possibility of adaptive biases in captive chimpanzees. Both studies reveal some selective tendencies in either social learning or attention, though it's less clear as to whether these each confirm apriori predictions drawn directly from theory. In the more recent paper (mentioned above), Kendal et. al. studied the diffusion of door-sliding practices (left vs. right) as chimpanzees repeatedly operated a slide-box to access grapes. In some groups, all individuals were initially naïve to the apparatus while in other groups one middle-ranking female was trained to operate it by always going to one side. The data show three patterns (1) low and middle ranking individuals tended to *copy* their side choices more than dominant individuals, (2) dominant individuals were *watched* more by inexperienced lower rankers, and (3) trained females were *watched* more by inexperienced individuals of the same or lower rank. Notably, the data do not show that dominant individuals or the trained females were *copied* more, only watched more. The authors argue that the variation in the choice data was insufficient to reveal any biased copying, but that the visual attention biases were likely 'for learning' (as opposed to, say, 'for scrounging') because this attention was limited to inexperienced individuals. But, as we noted above, attention differences have failed to translate into actual learning in another recent study (Van Leeuwen et al., 2013).

Theoretically, we don't see how the patterns of 'copy when not dominant' and 'watch the dominant' arise from the logic of natural selection applied to social learning, and aren't aware of these as existing predictions. There also seem to be alternative explanations for the selectivity observed. Dominants, for reasons related to status competition, may tend to garner attention when they are engaged in novel activities. Similarly, lower ranking individuals may be more affected by social learning in novel tasks because they are looking around more, monitoring more dominant others for threats. So, these patterns might represent non-adaptive biases that arise as a byproduct of status-competition.

In the other study, Horner et. al. (2010) show that chimpanzees possess some ability to distinguish among potential models during social learning. Each of two social groups was exposed to two different potential female models from their own group, one 'experienced model' and one 'inexperienced model'. 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 participants, 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

We think both studies are interesting and should spur further research. Drawing them together, the most support seems to be for some tendency to copy experienced or knowledgeable mid-ranking females. Perhaps these individuals are successful enough to be worth attending to but not so high ranking that watching them is dangerous or uncomfortable. However, an additional problem is that these demonstrators were all carefully selected by the researchers for training. Horner et. al. specifically used previously successful transmitters, and Kendall et. al. selected their models because they were “comfortable being briefly separated from their group for training” (extroverted) and “fast learners” (ideal individuals to scrounge from). Thus, more research will be needed to figure out why mid and low ranked chimpanzees tended to watch or copy these particular individuals.

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. All else being equal, variant A will eventually spread to fixation. Largely consistent with predictions derived from several formal models, research shows that humans use conformist transmission under some conditions (Efferson et al., 2008b; Morgan and Laland, 2012; Morgan et al., 2012; Muthukrishna et al., forthcoming). 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 or majority in chimpanzees or any other primates (van Leeuwen and Haun, 2013).⁶ To the contrary, neither Kendal et. al. (2015) nor van Leeuwen et al. (2013) found support for conformist transmission in their diffusion experiments.

However, while no conformist transmission has emerged, chimpanzees may sometimes still use the frequency with which a trait is used by different individuals as a cue about whether to adopt it. Revealing what they termed “majoritarian bias,” Haun and colleagues (2012) used a carefully designed experiment that controlled for both the frequency of times learners observed the use of a particular location for deposit (for dropping an object into an apparatus) and the number of different models observed using each location. Their evidence shows that chimpanzees—but not orangutans—use the prevalence of a particular location among their models as a learning cue.

TEACHING IN CHIMPANZEES

Now, we shift our focus away from the learner towards the model, who can facilitate the acquisition of useful practices by the learner. From an evolutionary perspective, however, teaching involves paying at least small costs to help another individual or individuals—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 conspecifics (Caro and Hauser, 1992). Various, teachers may (1) structure the environment to enhance the learners' 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 draw 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 demonstrations down or exaggerate key aspects in order to make it easier for the learner to take in, and (5) scaffold the learner by providing challenges just above 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 as a species turns out to be tricky, since most work on teaching comes from developmental psychologists who primarily study 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 and other teachers 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). Moreover, some of the teaching observed by ethnographers in small-scale societies may have been culturally introduced by so called WEIRD societies (Henrich et al., 2010). In our view, many in this debate about teaching across human societies may have missed key questions by focusing on 'presence' vs. 'absence' debates, which so frequently come down to arguments about definitions. By contrast, recent quantitative studies in Fijian villages show patterns of teaching quite unlike those common among Westerners, but largely consistent with the predictions from evolutionary reasoning (Kline, 2015). Thus, the real puzzle for evolutionary researchers may be why WEIRD people teach as much as they do and in the ways they do.⁸

In nature, as expected from theory, teaching is much rarer than social learning. However, several studies have revealed solid 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 set of skills is an ideal place to look for teaching, since, as we argue below, social learning likely plays at least a facilitating role in their acquisition in the wild (Tennie et al. 2009). Researchers have studied how chimpanzees between the ages of about 1 and 6 years of age 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 (also see Moore and Tennie, 2015).

The one potential 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 (Humble 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 herself, as mothers are less mobile and 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 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, to 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 but so few non-humans advanced. 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; Watts et al., 2015).

These cultural patterns are often adaptive, and systematically associated with ecological variables for several reasons (Billing and Sherman, 1998; 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; Richerson et al., forthcoming).

To illustrate this, consider 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; Henrich, forthcoming). However, cultural evolution only assembles the relevant know-how when the environmental conditions favor the practice. Thus, we should expect cultural evolution to create 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 empirical evidence supports the existence and persistence of neutral or maladaptive cultural variation among groups (Boyd and Richerson, 1985; Durham, 1991b; 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 (1) probes (e.g., sticks) to obtain ants, termites or honey (or to clear the nose), (2) leaves as sponges, wipes or brushes, (3) stones as hammers or anvils for nuts, and (4) sticks as levers to open and access the nests of birds or insects. Some categories include several variants. For example, nut hammering accounts for five variants, with some variants merely swapping the materials used for the hammers and anvils (stone vs. wood). Each of 69 variants 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., 2009) 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 this effort, but the 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 (Byrne, 2007; Laland and Janik, 2006). Second, in removing the 'rarities' the authors suggest that social learning will cause traits to be common in groups—implying 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. Notably, these first

two limitations suggest that the number of cultural traits may in fact be underestimated by Whiten et. al. However, third, the ecological forces that shape individual learning or other non-cultural ontogenetic responses may arise from non-obvious or even subtle ecological differences (e.g., differences in the number of available nuts to crack), so their approach only mitigates this issue. Indeed, a recent review concluded that ecological opportunities were one of the main drivers of these tool use patterns in chimpanzees, as well as in orangutans and capuchin monkeys (Koops et al., 2014). And, fourth, these nine groups span a vast territory and can be classified into three subspecies, with much internal genetic structure. Thus, genes are a potentially important competing explanation for this behavioral variation. These last two limitations imply a tendency towards overestimating the number of cultural traits.

Expanding on this last point about genetic 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 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.

In this study, the correlation between the geographical distance between communities and the genetic distance (mtDNA) is 0.96. Some argue that this means that genes and culture are merely moving together as populations spread out in space, a common pattern when human populations expand via migration. So, perhaps the correlations between genes and behavior revealed by Langergraber et. al. are merely non-causal associations created by a spreading population. To the contrary, this view misses two key differences between humans and chimpanzees: (1) all human migrations that have been studied in this fashion are relatively recent and therefore shallow compared to the spread of chimpanzees across Africa (and the emergence of different subspecies), and (2) the fidelity of human cultural transmission is substantially higher than chimpanzees (and both are much lower in fidelity than genetic transmission). This implies, given the time depths involved in the spread of chimpanzee populations, there should be no remaining correlation between behavioral dissimilarity and geographic distance due to shared cultural inheritance. Given enough time, cultural drift, losses, inventions and transmission noise will eventually wipe out the correlation between geography and culture created by migration. In humans, the correlations between culture and genes observed only exists because the temporal depth of human expansions are recent and the fidelities of cultural transmission are high. Of course, a firmer answer to this question awaits proper modelling.¹⁰

In light of this evolutionary logic, we are concerned about recent efforts to apply phylogenetic techniques to broad patterns of chimpanzee behavioral variation. 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' signal, which they use to construct a phylocultural tree for chimpanzees. 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 cultural descent with modification at the group level from an ancestral population of chimpanzees. To illustrate this, consider that the deepest human cultural phylogeny, which was constructed based on "ultraconserved words," goes back only 15,000 years (Pagel et al., 2013). By contrast, the trans-

African geographic spread that eventually led chimpanzees to subspeciate occurred over a million years ago and then again about 500,000 years ago (Bjork et al., 2011). So, cultural signals in humans don't last more than 15,000 years but chimpanzee cultural signals endure for half a million years? To be clear, this is not to argue that the observed differences are not cultural. Theoretically, it is perfectly plausible that these variants are all 100% cultural, yet virtually no phylocultural signal remains, given the time scales involved. Social learning need not produce either group-level heritability or tree-like patterns of descent.

Because of these issues, 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 (see Byrne, 2007). 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 found around 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 Pruettz, 2009), particularly among populations living in Savanna-woodlands (Bogart and Pruettz, 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 (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, that is, at a time 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).

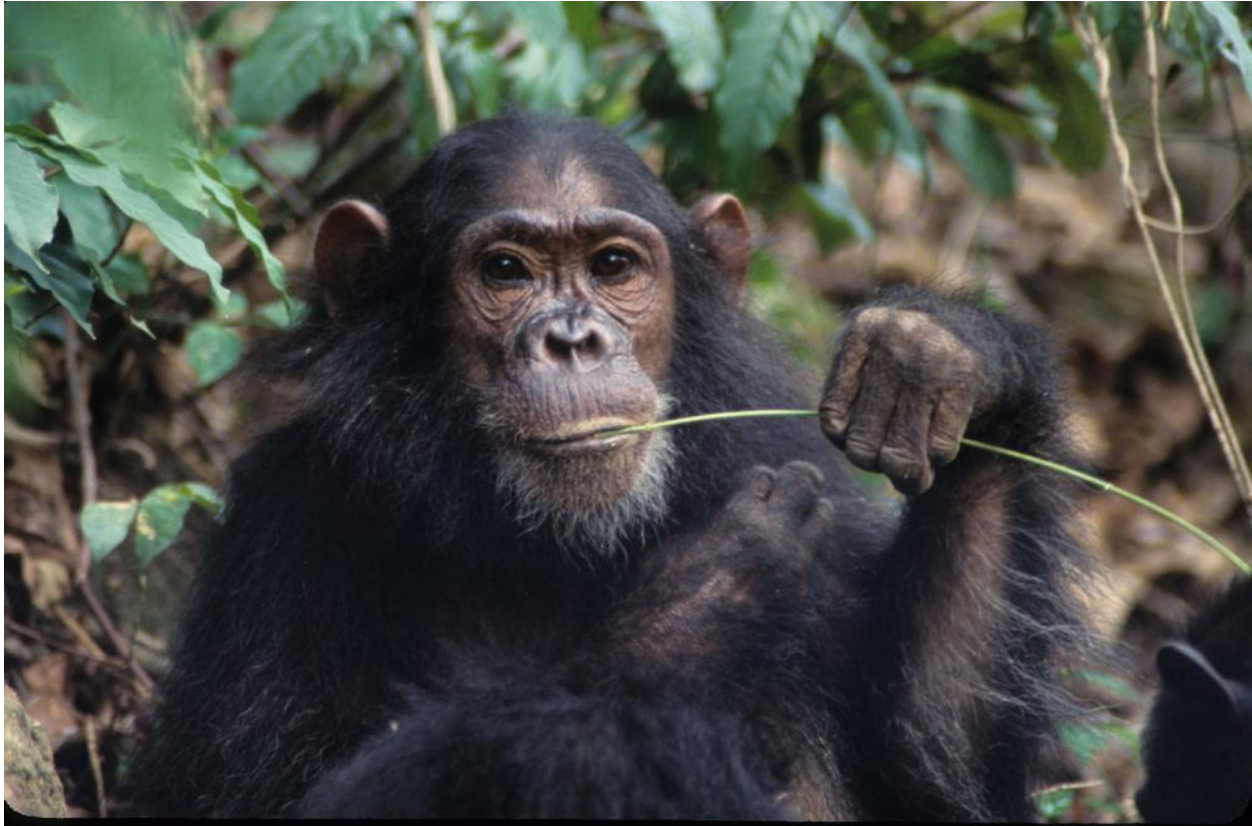


FIGURE 1: TERMITE FISHING BY AN EIGHT YEAR OLD FEMALE (“GAIA”) IN THE KASEKELA COMMUNITY IN GOMBE NATIONAL PARK, TANZANIA (2001). THANKS TO IAN GILBY FOR THE IMAGE.

All of this is consistent with at least “exposure” learning (Thorndike, 1911), meaning the youngsters were aided in learning to fish because hanging around their mother provided access to termite mounds, tools and opportunities to practice (aka local enhancement). 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 the 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). 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. Mom 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.

Trying 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 study above. This may not be altogether surprising, given that in an earlier study, Humle and Matsuzawa (2002) had already described that differences in ant characteristics (species and current behavior and location of the ants) were the major drivers of dipper stick length and perhaps also – in turn – of dipping technique (Humle et al., 2009).

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 recent findings below), 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 ecology. 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, they 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 are known to interbreed.



FIGURE 2: NUT CRACKING BY AN ADULT MALE (“JEJE”) AT BOSSOU, GUINEA, WEST AFRICA (2012). THANKS TO KATHELIJNE KOOPS FOR THE IMAGE.

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 years (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 hammering.

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 chimpanzee social learning is not sufficient to explain the sustained persistence of arbitrarily different, maladaptive or otherwise costly practices (Claidière and Sperber, 2009) as it does in humans. 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 (Koops et al., 2014).

CHIMPANZEES AND CUMULATIVE CULTURAL EVOLUTION

The survival of humans, 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, forthcoming). 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’ in know-how from where the last generation left off (Tomasello, 1999b)—though unfortunately the ratchet metaphor occludes the fact that groups can lose cultural traits, practices and know-how in a variety of ways.

Our species’ addiction to cultural information 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 (Henrich, forthcoming; Laland et al., 2010; Richerson et al., 2010). We are a ‘cultural species’, meaning that 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, forthcoming; 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 (Henrich, forthcoming).

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 (Tennie et al., 2009; Tomasello, 1999a). The question is then, how much of chimpanzee repertoires could a group of naïve chimpanzees reinvent, without any social input? 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 that practices aren’t easily reinvented. 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 repeatedly 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 (a research

line promoted by Tennie et al. 2009). 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 (Masi, 2011; Tennie et al., 2008); but see also (Byrne et al., 2011). Similarly, ‘leaf swallowing’ also occurs in naïve bonobos (Menzel et al., 2013), and both food washing and food mining behaviors re-emerges in naïve orangutans (Allritz et al., 2013).

However, laboratory tests in naïve individuals still remain outstanding for most cases of purported cultural traits in wild chimpanzees (e.g., for ant-dipping). In the case of termite fishing, Lonsdorf and colleagues (2009) ran a laboratory test in both naïve enriched captive chimpanzees and gorillas. Both species became proficient at the task, with many chimpanzees and some gorillas engaging with the task and succeeding on Day 1 (on-average chimpanzees learned more quickly than gorillas). Even though this study presented the task to the whole group, rather than individually, it nevertheless shows that at the very least one of the apes in each species developed the technique spontaneously, i.e. without the need to observe others engage in it. For other chimpanzee behavioral traits, such as nut-cracking, research has often not taken seriously the possibility that subjects would develop the target behavior on their own, and thus baseline conditions in which naïve individuals are given time to learning individually, have been largely neglected (Hayashi et al., 2005; Sumita et al., 1985). For example, in a paper on the emergence of stone tools, Hayashi et al. (2005) did not include any asocial baseline, instead providing demonstrations even before the first trial.¹¹ Indeed, given that capuchin monkeys develop nut-cracking *without* social cues (Visalberghi, 1987), it would be surprising if chimpanzees could not figure it out by themselves.

Recent field evidence converges with this 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). Similarly, the most interesting “two-handed” ant-dipping techniques 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 Pruett, 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 spreading behaviors that are only occasionally re-invented by some individuals (Tennie et al., 2009), 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. Thus, it is not cumulative culture.¹²

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 at gathering the target prey than a non-brushed tip. While broadly similar behaviors have 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.¹³ We concur that, currently, this type of brush tool is the best candidate example for cumulative culture in chimpanzees, though we would not be surprised if it, too, would reappear in naïve subjects when tested.

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. For example, work by Gruber et. al. (2011; 2009) shows that prior knowledge of how to “fluid-dip” increases an ape’s chances of individually figuring out how to “honey-dip” in a somewhat novel context. Lastly, we also worry that the tendency of different researchers to either split or lump variants into sub-varieties may actually account for part of the apparent nested structure.

Research on whether naïve chimpanzees can individually reinvent the various practices found among wild chimpanzees has just begun, so it remains to be seen which practices (if any) prove too difficult. So far, albeit with only a handful of cases, laboratory apes have readily reinvented all behaviors seen in the field. Moreover, bonobos and gorillas even invent traits that their wild brethren don’t perform. 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 (or no) 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.

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.¹⁴

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 as well as other apes. Chimpanzees are excellent individual learners and keen explorers—the latter more in captivity, though see Forss et al. (2015). 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, 2005b; Nagell et al., 1993). Moreover, field studies have repeatedly observed that while wild chimpanzees often invent novel behaviors, these novelties are not picked up by others, and eventually peter out (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).

The *fidelity* of 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 (see above), and, rare in this field of research, there is even some kind of agreement on this point across several researchers (Tennie et al., 2009; 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., 1996). 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 poor at actively transmitting them (teaching). 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 (Bandura, 1977). Consistent with this, recent neuroimaging studies found major deficits in brain structures enabling detailed action copying 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 persistent and potent feature of human social learning (Herrmann et al., 2013; Lyons et al., 2007; Nielsen and Tomaselli, 2010). By contrast, chimpanzees readily drop any unnecessary steps once they perceive that specific steps are superfluous (Horner and Whiten, 2005b). Overall, most analyses of chimpanzee data strive to detect a transmission fidelity above zero. But, only in a few cases involving trivially easy tasks does the data support a fidelity comparable to humans (Hopper et al., 2008b).

Cultural evolutionary models also show how *sociality* influences the emergence and rate of cumulative cultural evolution (Henrich, forthcoming: Chapter 12). 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 and other apes 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 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; Hill et al., 2014; Wiessner, 2002).

Second, from a life history perspective, the intersection of broadening opportunities for social learning and developmental timing of learning windows may be crucial. 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 narrow 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 short time when young chimpanzees are developmentally ready and able to learn these (and presumably other) skills *and* able to access a broad range of models. Note that, as in humans, we don't expect these windows to entirely shut, but merely to narrow: some flexibility is retained into adulthood in, for example, what type of hammer (wood or stone) to use for cracking nuts (Luncz and Boesch, 2014).

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 remain highly plastic (Henrich, 2008, forthcoming), 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 importance of group size in the creation of large behavioral repertoires, including tools, may explain why bonobos and gorillas don't show the repertoires seen in chimpanzees and orangutans (Tennie et al., 2009) despite showing substantial individual-level cognitive abilities in the laboratory. Realize first that, limited as they are, current analyses of the available data from both chimpanzees and orangutans reveal that larger or more socially connected populations have more extensive behavioral repertoires (Lind and Lindenfors, 2010; van Schaik et al., 2003), though in chimpanzees it's the number of females that matters. Gorillas tend to live in small groups with only one male and his mates, and the particulars of their social life also seem less suited for social transmission than those of chimpanzees (Lonsdorf et al., 2009). Meanwhile, though bonobos live in larger groups (mean size 23), their average group size is half that of chimpanzees (mean size 46).¹⁵ By expanding the size of the cultural repertoires of chimpanzees, group size differences may have generated more tools and techniques, thereby precipitating a genetic response that led to greater object-focused *individual learning* and exploration in chimpanzees (Koops et al., 2015).

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., 2009). 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; 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-driven genetic evolution.

JUMP-STARTING CUMULATIVE CULTURAL EVOLUTION

Cultural evolutionary theorists have identified what they call the “start-up problem”, which aims to explain why something as seemingly valuable to survival and reproduction as cumulative cultural evolution is so rare in nature (Boyd and Richerson, 1996). The core of the idea is that cumulative cultural evolution drove human brain expansion, selecting for bigger brains and longer juvenile periods to facilitate acquiring, storing, and organizing vast amounts of cultural know-how (Boyd et al., 2011; Henrich, forthcoming). The more cultural know-how accumulates in the form of adaptive practices, the stronger the selective pressures are for brains capable of acquiring all that know-how from the minds of others. To see the challenge in starting this process, first realize that big, powerful (and energetically expensive) brains capable of sophisticated high-fidelity social learning can only pay for themselves if there are lots of valuable practices, related to tool-making and food processing for example, already out there in the minds of others, waiting to be learned. Once there is a lot of complex cultural information in the world, natural selection has no choice but to favor brains that are better at acquiring, organizing and storing this information. However, in the beginning, before cumulative cultural evolution got going, there wouldn't have been very much out there, in terms of valuable practices, in the minds and behavior of others. And, what was there, could be figured out on one's own using individual learning (Tennie et al. 2009). Now, one might think that a little culture can accumulate, and natural selection will incrementally favor bigger brains that are better at cultural learning. However, the problem is that natural selection faces a choice between investing either in brains that are better at individual learning OR social learning—either you are spending your time engaged in trial and error experimentation or you are watching and hanging around others. Earlier on, individual learning will often be favored by natural selection because not only does improved individual learning increase one's chances of figuring stuff out on one's own, but it also improves some simple forms of social learning (e.g., if you hang around nut-crackers, you tend to be around nuts and anvils more, so improved individual learning focused on objects increases your chances of figuring out how those nuts and anvils go together). However,

when natural selection invests in individual learning, it prevents cumulative cultural evolution from getting going.

To bypass the start-up problem, Henrich (forthcoming) has recently suggested that human ancestors may have experienced ecological conditions favorable to creating cumulative cultural evolution without an initial change in social learning abilities. In the late Pliocene, fluctuating environmental conditions could have favored greater social learning (also predicted by theory (Richerson and Boyd, 2000)) and a much larger predator guild in Africa would have forced terrestrial primates into larger social groups. As just noted, much theory suggests that larger and more interconnected groups will experience greater cultural accumulations, as will groups more reliant on social learning. These two factors would have enlarged the sizes of learned repertoires of these primates, potentially shifting the balance of costs and benefits in favor of investing specifically in social learning abilities over individual learning. Henrich also argues that larger groups, induced by territoriality and predation, would have favored greater pair-bonding (as it may in chimpanzees, Langergraber et al., 2009), which could have expanded the circle of identifiable kin and the potential for alloparenting. Greater alloparenting by fathers, aunts and grandmothers would have permitted longer juvenile periods and more opportunities for teaching—which would have further fueled cumulative cultural evolution.

Early cultural evolution wouldn't have involved the continuous improvements in technical know-how and skills that many paleoanthropologists seem to expect (Henrich, forthcoming). Instead, it would have had many fits and starts, with some groups occasionally surging ahead and other groups losing tools and know-how. This is because both the size of toolkits and their complexity is heavily influenced by the size and sociality of groups. Environmental shocks, climatic fluctuations and migrations would have consistently set groups back in cultural complexity. In light of such theoretical insights, Henrich argues that the oldest tool assemblages (3.2 to 1.8 mya) were likely not static, but instead stood on the precipice of cumulative cultural evolution, and reveal a diversity consistent with repeated gains and losses. After about 2 million years ago, a pattern of cumulative cultural evolution does begin to emerge, at least in some populations. By 750,000 years ago, based on findings at Geshen Benot Ya'aqov, Henrich argues that some populations were clearly reliant on the products of cumulative cultural evolution.

INFERENCE TO A COMMON ANCESTOR

What can we say about cultural evolution in our common ancestor with chimpanzees? Cultural evolutionary theory predicts that the selection pressures for more sophisticated forms of social learning will increase as environmental variability increases (Boyd and Richerson, 1985). Empirically, 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 period, and between social learning, innovation and brain size (Muthukrishna and Henrich, n.d.).

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.

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¹ For chimpanzee observers, the species of the 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 (Henrich and McElreath, 2003; Kellogg and Kellogg, 1933).

² Not everyone agrees: Boesch (2012) argues that human training and high human exposure are substitutes for the rich environments found in the wild. Perhaps. But there is no data to support this. In contrast, there are clear differences between these two populations. For example, finger pointing is quite common in enculturated chimpanzees but extremely rare in wild chimpanzees (Leavens et al., 2010).

³ Of course, as we noted, potential insights can be gleaned from studies of all of these categories of captive apes. Overall, by contrast with enriched captive apes, deprived subjects often do not perform well. However, the available evidence, weak as it is, suggests that semi- and highly-enculturated apes may often outperform enriched captive chimpanzees in the development of learning skills, and their attendant abilities and motivations. Consider three relevant bits of evidence. First, in a field experiment, Gruber et. al (2011; 2009) show that wild chimpanzees who didn't routinely use dip-sticks to obtain fluids, like water, could not readily solve an artificial honey-dip problem, where one needed to dip a branch into a hole to obtain honey. Compared to semi-enculturated chimpanzees this is surprising since enriched captive subjects in the laboratory can readily figure out similar tasks (Call and Tennie, 2009; Yamamoto et al., 2013) despite being less hungry. Second, enriched 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). Third, semi-enculturated chimpanzees, but not their captive brethren, might drop unnecessary steps in a manner consistent with more sophisticated and human-like forms of social learning. Such "captivity effects" may be due to (1) an enriched cognitive environment with fewer distractions (Hirata and Celli, 2003), (2) better nutrition leading to faster development (Hamada et al., 1996; Pusey et al., 2005) and/or (3) increased contact with humans and among conspecifics (Haslam, 2013). But, whatever the exact causes for higher performances in these populations (a ripe research topic), there is little reason to suspect that enrich captive apes will show inferior learning abilities compared to their wild counterparts.

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 an incorrect contrary claim.

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. What the authors do show that chimpanzees will continue selectively copying those they have selectively copied in the past. 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.

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.

⁷ We avoid mentalistic approaches to teaching in order to facilitate comparisons across species (Kline, 2015).

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

¹⁰ For more on the debate see (Langergraber et al., 2011a; Langergraber and Vigilant, 2011).

¹¹ In an earlier study (Sumita et al., 1985), five chimpanzees were tested, but four of the five subjects only ever received a single baseline session (of about one hour each).

¹² Tennie et al. (2009) labeled such behaviors “latent solutions”.

¹³ 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: 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.

¹⁴ Some argue that language increases the fidelity of cultural transmission. While this is certainly true for some domains of culture, languages are themselves clearly the product of cumulative cultural evolution. So, pointing to languages is like pointing to writing or literacy. Language was first a consequence of cumulative cultural evolution before it improved fidelity and fostered further cumulative cultural evolution (Henrich, forthcoming: Chapter 13).

¹⁵ These average were generated using the data in Wilson et. al. (2014).