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Cultural Evolution in Chimpanzees and Humans

JOSEPH HENRICH *and* CLAUDIO TENNIE

Over the last few decades, researchers from diverse disciplines have developed cultural evolutionary and gene-culture coevolutionary theory (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland et al. 2011). Applied to humans, this approach has yielded new insights into our species' evolution, behavior, and cognition, and broadened into research programs in biology, anthropology, psychology, archaeology, and economics (Shennan 2003; Richerson and Boyd 2005; Hoppitt and Laland 2013; Henrich 2016). 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 their shared phylogenetic heritage, and to isolate the selective forces that have distinguished these lineages over the last six to nine million years.

Our review begins with a brief introduction to gene-culture coevolutionary theory, though specific elements of the theory will be rolled out as we go along. 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, often with 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 social learning created a second system of inheritance that evolves and interacts with genetic inheritance in a coevolutionary duet (Campbell 1965; Pulliam and Dunford 1980; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Durham 1991). "Culture" in this view is the emergent product of individuals of various generations or ages interacting with 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 *as a consequence* of each other) and (2) the importance of interaction and sociality. This means that "culture" is now anchored in brains, and traceable to individual cognitive abilities or learning strategies (Tomasello 1999b; Laland 2004; Henrich and McElreath 2007). 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. Cavalli-Sforza and Feldman (1973, 1981) showed how such *population processes* can be formally modeled 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 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.[1] This insight opened the door for full-blown models of culture-gene co-evolution, in which culture and genes mutually influence each other (Aoki 1986; Laland 1994; Laland et al. 1995a, 1995b; Feldman and Laland 1996; Henrich and Boyd 1998; 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; Henrich 2016). This research has:

1. Tested various hypotheses regarding "what," "when," and "from whom" people will apply their adaptive social learning abilities (e.g., Rendell et al. 2011; Morgan et al. 2012; Chudek et al. 2013; Wood et al. 2013; Muthukrishna et al. 2016), as well as "when" and "to whom" they will transmit (teach) cultural information (Kline et al. 2013; Kline 2015).

2. Shown how social learning mechanisms can respond to local ecological variation to generate adaptive population patterns of cultural variation (Henrich and Henrich 2010; Henrich 2016).

3. Established empirical relationships that link the size and interconnectedness of human societies to the complexity of their tool kits and technologies (e.g., Henrich 2004b; Kline and Boyd 2010; Derex et al. 2013; Muthukrishna et al. 2014).

4. Linked the spread of specific genes in response to specific cultural practices (e.g., Holden and Mace 1997; Dediu and Ladd 2007; Chiao and Blizinsky 2010; 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 (Lipo et al. 2006; Tehrani et al. 2010; Walker et al. 2010).

This blossoming now permits us to readily view chimpanzees and other primates through the same evolutionary lens (van Schaik and Burkart 2011; Whiten 2011). 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 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; Tomasello 1999b; Csibra and Gergely 2006). 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 (Corriveau and Harris 2009a, 2009b; Harris and Corriveau 2011; Chudek et al. 2012, 2013; Herrmann et al. 2013). Across diverse societies, children, adolescents, and young adults socially learn vast repertoires of practices and bodies of know-how that are crucial for survival, such as how to find food, detoxify plants, build shelters, organize social groups, track animals, and make fire (Boyd et al. 2011; Henrich and Broesch 2011; Kline et al. 2013; Henrich 2016). Social learning is so powerful in humans that we readily copy actions, motivations, and beliefs that contradict our innate intuitions, tastes, and direct experiences (Rozin and Schiller 1980; Rozin et al. 1981; Billing and Sherman 1998; Henrich 2009a). Social learning even influences our opioid and cannabinoid systems to alter how much pain we experience for the same stimuli (Craig and Prkachin 1978; Craig 1986; Benedetti et al. 2013; Henrich 2016).

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 studies of captive chimpanzees. Typically, these studies take the following form: a trained demonstrator (a human or chimpanzee[2]) 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, ob-

server chimpanzees do indeed match these demonstrations to some detectable degree (Horner and Whiten 2005; Hopper et al. 2008; Kendal et al. 2015; Tennie et al. 2010b), though the degree of matching is often not substantial and sometimes is indistinguishable from zero (Tennie et al. 2006). Such results are often interpreted as revealing human-like social learning (e.g., Whiten et al. 2005; Bonnie et al. 2007; Hopper et al. 2007, 2008), even though the learning may involve a range of psychological mechanisms that cannot be pinpointed by the experimental methods deployed (Tennie et al. 2009, 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 a single study involving human toddlers (aged two years), chimpanzees, gorillas, orangutans, and bonobos using conspecific (same species) 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 species, only the toddlers showed evidence for copying across all conditions. The other great apes showed evidence for copying only 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 of their trials were analyzed together—in this one condition—did they reveal any evidence for copying at all, though this only occurred in one set of tasks. In sum, the nonhuman ape species showed rather weak and inflexible copying abilities compared to children, who copied reliably and robustly across contexts and informational conditions. 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 consider the implications of such results below.

While captive studies have proven invaluable for assessing chimpanzee social learning, there are important concerns regarding how transferable such findings are to the field. In other words, how ecologically valid are these findings? Chimpanzees in typical captive 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 only the most ecologically valid populations should be used (1) to explain wild behavior patterns and (2) to directly inform evolutionary scenarios, though understanding latent capacities, unexpressed in the wild, may still be important. High-performing populations may show *potentials* that are never expressed in wild populations. For example, chimpanzees trained in sign language may use a gestural sign for the color blue, but this never happens in the wild (Terrace 1979).

To assess ecological validity, captive apes can be heuristically divided 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 (hereafter *semi-enculturated* chimpanzees; e.g., human-reared chimpanzees who then continue to live among conspecifics); (3) apes living in conspecific groups under nondeprived 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 not 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 in related abilities such as pointing (Leavens et al. 2010), highly enculturated chimpanzees are generally superior (Tomasello et al. 1993; Bjorklund et al. 2002; van Schaik and Burkart 2011), followed by semi-enculturated ones (Furlong et al. 2008), then enriched captives, and finally the deprived apes (Menzel et al. 1970).

Consequently, though far from ideal, we believe that enriched captive apes provide the best available population from which to draw the most valid conclusions about wild populations (apart from studying wild populations directly, of course).[3] 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. Enriched captive populations live in social groups, are well fed (better than wild apes), and experience (somewhat) enriched physical environments (wild chimpanzees also live in a range of environments). Note that the social learning studies above all involved enriched captive apes.

There is 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 whether 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 Zentall 2006; Tennie et al. 2009; Whiten 2011; Hoppitt and Laland 2013).

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 plausible that chimpanzees possess some degree of social learning as a by-product of having brains

selected for individual (asocial) learning—that is, for the ability to figure things out on their own. Individual and social learning involve many of the same cognitive skills and neurological resources (Reader and Laland 2002; Heyes 2012), so it is possible that selection for one delivers some amount of the other.

Do Chimpanzees Show the Predicted Social Learning Mechanisms or Biases?

Theorists have explored how natural selection might have shaped the cognition of learners 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, 1995; Henrich and Boyd 1998; Laland 2004; Wakano et al. 2004; Nakahashi et al. 2012; Aoki and Feldman 2014). 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; Muthukrishna et al. 2016) and in non-primate taxa such as rats and fish (Kendal et al. 2005; Galef et al. 2008; Galef 2009b; 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., a 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" are common (Whiten et al. 2005; Whiten and van Schaik 2007; Hopper et al. 2011a, 2011b; van de Waal et al. 2013). 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 ("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*.[4] Conservatism is a tendency to "stick with" or revert 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, conservatism, or even normative conformity. Since most studies show that chimpanzees are conservative (though see Manrique et al. 2013; Yamamoto et al. 2013), this is a likely alternative explanation (Whiten 1998). While we think—on theoretical grounds—that normative conformity is unlikely to be found in chimpanzees (Henrich 2016), it is not ruled out in these experimental designs (see van Leeuwen and Haun 2013).[5]

In one well-designed study focused on these issues, van Leeuwen et al. (2013) tested the strength of chimpanzee conservatism. In contrast to most such research, chimpanzees in this study first individually learned their own ways to solve a task (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 such conformity. 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-payoff factors. In another condition, chimpanzees did abandon their first-learned strategy in favor of the demonstrated alternative. This was not due to conformity, however, but because the new method yielded a fivefold increase in food rewards.

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 attention toward those individuals most likely to possess fitness-enhancing behaviors, beliefs, motivations, or practices (Boyd and Richerson 1985; McElreath et al. 2003; Laland 2004; McElreath and Strimling 2008; Rendell et al. 2010). Theorists have argued that learners should use "model-based" cues such as 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 identify 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 fifteen years, has substantiated these predictions in adults, children, and even infants (Koenig and Harris 2005; Jaswal and Neely 2006; Efferson et al. 2008a; McElreath et al. 2008; Corriveau and Harris 2009a, 2009b; Corriveau et al. 2009, 2013; Rendell et al. 2011; Buttelmann et al. 2012; Chudek et al. 2012, 2013; Morgan et al. 2012; Wood et al. 2013), as well as providing some evidence in other non-primate species (Galef 2009b; Laland et al. 2011; Rendell et al. 2011).

Building on these insights, researchers have proposed that learners should take into account the costs of accessing their preferred models (those who they deem skilled, successful, and prestigious). Placing this within a life history framework, infants and children are expected to first learn all they

can from their parents, siblings, and other accessible models, and then subsequently pay access costs to update 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 2001). This can be characterized as a switch from primarily vertical cultural transmission to various forms of biased oblique transmission over the life course. Broadly, fieldwork in small-scale human societies provides evidence consistent with these predictions (Tehrani and Collard 2009; Henrich and Broesch 2011; Hewlett et al. 2011; Henrich et al. 2015).

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—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; Melber et al. 2007; Humle et al. 2009; Lonsdorf 2013). This is consistent with some form of age, experience, or skill bias in attention. Attention, however, 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, and is not simply part of a scrounging strategy, in which skilled or experienced individuals are scrutinized because they are more productive targets for scrounging (Stammbach 1988; Henrich and Gil-White 2001).

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, 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. In accordance with this hypothesis, females are indeed the most attentively observed by others (van de Waal et al. 2010; Renevey et al. 2013), including males.

Two experiments address the possibility of adaptive biases in captive chimpanzees. Both reveal some selective tendencies in either social learning or attention, but it is not clear as to whether these confirm a priori theoretical predictions. In the more recent paper (mentioned above), Kendal et al. (2015) studied the diffusion of door-sliding practices (left versus right) as chimpanzees repeatedly operated a slide-box to access grapes. In some groups, all individuals were initially naïve to the apparatus, while in others 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 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 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. Alternative explanations are available for the selectivity observed. Dominants, for reasons related to status competition, may tend to garner attention when they are engaged in novel activities. And lower-ranking individuals may look around more, monitoring more dominant individuals for threats. Consequently, these patterns might represent non-adaptive biases arising from 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 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 model had previously introduced successful innovations in a series of other experiments, so the experimenters knew she was a good transmitter. Of the twenty-two chimpanzees exposed to these two models, fourteen decided to participate (which meant effectively copying one of the two models). Of these fourteen 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.[6]

We think both studies are interesting and should spur further research. Together they support some tendency to copy experienced or knowledgeable mid-ranking females. Perhaps these individuals are successful enough to be worth attending to, but not so dominant that watching them is dangerous or uncomfortable. It is problematic, however, that demonstrators were all carefully selected by the researchers for training. Horner et al. 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-ranking chimpanzees tended to watch or copy these individuals.

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 behavioral variants, A, B, and C, at frequencies of 40 percent, 30 percent, and 30 percent, respectively, in a population. If the new generation of learners picks 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 will shift to favor the plurality, changing to, say, 60 percent, 20 percent, and 20 percent, in the next generation. All else being equal, variant A will eventually spread to fixation. Largely consistent with predictions derived from 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. 2016). Other than in primates,

conformist transmission has been shown, perhaps most decisively, in fish (Pike and Laland 2010).[7]

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; Acerbi et al. 2016).[8] 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 conformist transmission has not emerged, chimpanzees may sometimes still use the frequency with which a trait is demonstrated 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 suggests that chimpanzees—but not orangutans—use the prevalence of a particular location among their models as a learning cue (though they could also have copied with a bias toward any of the demonstrator chimpanzees, which would have led to the same overall effect).

Teaching in Chimpanzees

We now shift our focus away from the learner toward the model, who can facilitate the acquisition of useful practices by the learner. From an evolutionary perspective, teaching involves paying at least small costs to help another individual—so it is a type of altruism or cooperation. Evolutionary models suggest that teaching and social learning can coevolve, but 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). It is primarily expected to emerge between parents and their offspring.

Teaching is any costly behavior by the model that facilitates learning in conspecifics (Caro and Hauser 1992). Variously, 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, guiding learners via reinforcement (Castro and Toro 2002);

(3) actively draw the learners' attention to key elements of a demonstration with cues such as pointing or eye contact ("pedagogical cues"; see Csibra and Gergely 2006, 2009); (4) mold the learners' hands, position their feet, or orient their bodies; (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 (Hoppitt et al. 2008; Boesch 2012). This behavioral definition permits us to cast a wide net and to compare teaching in humans with other species.[9]

Characterizing teaching in humans is problematic, because most studies come from developmental psychologists studying children in Western societies (e.g., Tomasello 1999a; Csibra and Gergely 2009). Middle- and upper-class Westerners place immense emphasis on active and often verbal forms of teaching, molding their students' hands, and providing explicit feedback. In the smallest-scale human societies, including foragers, teaching exists—but is much less common and largely passive (Lancy 1996, 2009; Fiske 1998; Gaskins and Paradise 2010; Hewlett et al. 2011; 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 a "presence" versus "absence" debate, which frequently come down to arguments about definitions. Recent quantitative studies in Fijian villages show patterns of teaching or pedagogy 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.[10]

In nature, as expected from theory, teaching is much rarer than social learning. However, several studies furnish 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, 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 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 one and six years of age acquire these skills, observing, coding, and analyzing the behaviors of both mothers and other nearby adults and juveniles for any hint of teaching (Inoue-Nakamura and Matsuzawa 1997; Biro et al. 2003; Lonsdorf et al. 2004; Lonsdorf 2005, 2006, 2013; Humle et al. 2009).

The results are consistent across different researchers and field sites. Adults, particularly mothers, were highly tolerant of the activities of young chimpanzees (<5 yrs), permitting them to play with tools and "steal" or "scrounge" the tool and/or harvest, but they did not *actively facilitate* learning. Mothers generally reacted neutrally to their infants' efforts, provided 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.[11] In short, no teaching was found (also see Moore and Tennie 2015).

The one potential exception occurs in dipping for army ants. This foraging task can be done at more dangerous nests or on less dangerous trails. Mothers with infant learners showed a bias to ant-dip at the less productive trails (paying a cost), thereby providing a safer environment for their offspring to learn in (Humle et al. 2009). An important question is whether this is merely a by-product of mothers' concerns about their offspring being attacked by army ants (or even about themselves, as mothers are less mobile, being handicapped by 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 (under five years of age), chimpanzees, and capuchin monkeys. Dean et al. (2012) presented participants with a three-step task in which solving each step 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 at the task, and may help explain why so many children reached the final stage but so

few nonhumans advanced. We 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 (Rogers 1995; Henrich 2001; Bell et al. 2009; Jordan 2015). 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; Walker et al. 2010; Watts et al. 2015).

These cultural patterns are often adaptive, and are systematically associated with ecological variables for several reasons (Billing and Sherman 1998; Jordan and Shennan 2003; Shennan 2003; Henrich and Henrich 2010; Hruschka and Henrich 2013). First, as discussed above, human social learning has likely been honed by natural selection to use a wide range of adaptive cues, such as 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 (Diamond 1997; Henrich 2004a; Currie and Mace 2009; Richerson et al. 2016).

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 2016). 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 1991; 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 sixty-nine 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 and 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 versus wood). Each of the sixty-nine 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 2009a; Laland et al. 2009; Tennie et al. 2009; Langergraber et al. 2011) or (2) locally adaptive responses to ecological variation that depend only on individual learning or other ontogenetic responses to en-

vironmental cues (Galef 1992; Tomasello 1994; Laland et al. 2009; Tennie et al. 2009). The authors recognized these problems, and attempted to mitigate them by removing variants that were (1) universal, (2) very rare, or (3) readily explained by ecological variables, to arrive at a list of thirty-nine putative cultural variants. This catalogue of behaviors is impressive, and analyses of it have led researchers to argue that chimpanzee cultures are special (Whiten and van Schaik 2007) and more sophisticated than those of crows (McGrew 2013).

We are sympathetic to this effort, but the approach has several interpretive limitations. First, cultural evolution is adaptive, at least in humans, so removing things that are universal or explained by ecology potentially removes important cultural variants (Laland and Janik 2006; Byrne 2007). Second, in removing the "rarities," the authors suggest that social learning will cause traits to be common in groups—implying that rare traits are not socially learned. Theoretically, this is not true. How common a cultural trait becomes within a group depends on many factors, including 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. These first two limitations suggest that the number of cultural traits may in fact be underestimated by Whiten et al. Third, however, the local forces that shape individual learning or other noncultural ontogenetic responses may arise from nonobvious or even subtle ecological differences (e.g., differences in the number of available nuts to crack). Indeed, a recent review concluded that ecological opportunities were one of the main drivers of 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 range, and can be classified into three subspecies, with much internal genetic structure. Thus, genes are a potentially important competing explanation for the behavioral variation. These last two limitations imply a tendency toward overestimating the number of cultural traits.

Subsequent analyses of these putative cultural variants have shown that it is difficult to exclude genetic variation as a potential cause. Langergraber et al. (2011) assembled mitochondrial DNA data 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, suggesting that genes might be important. However, when the data are analyzed at the level of particular variants, the authors establish that genetic

variation is unlikely to explain five, and possibly as many as twenty, of the variants. It is still possible that most or all of these variants are cultural, but we 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) was 0.96. Some argue that this means that genes and culture were merely moving together as populations expanded, a common pattern in human migration. This would mean that correlations between genes and behavior revealed by Langergraber et al. were noncausal associations created by a spreading population. However, this view overlooks 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 in chimpanzees (and both are much lower in fidelity than genetic transmission). This implies, given the temporal depths involved in the spread of chimpanzee populations, that 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, correlations between culture and genes exist only because the temporal depths of human expansions are recent, and the fidelity of cultural transmission is high. A firmer answer to this question awaits proper modeling, but on a first pass, the correlation between genes and culture in chimpanzees is unlikely to be due to persistence created by high-fidelity inheritance.[12]

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) analyzed Whiten et al.'s thirty-nine 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. Given the low fidelity of chimpanzee cultural transmission, high rates of both loss and reinvention, and the deep time scales associated 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 to chimpanzee subspeciation occurred over a million years ago, and 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? For the reasons given above, this seems unlikely. 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 percent 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 these 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. (2011) evaluated as unlikely to be due to genetic differences among chimpanzee groups, and it is widespread across Africa (Whiten et al. 1999), but not found in some populations where termite mounds do exist. In termite fishing, chimpanzees fashion simple tools out of vegetation found near 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 Pruetz 2009), particularly among populations living in savanna-woodlands (Bogart and Pruetz 2011). Meanwhile, in locales with more limited opportunities for exploiting termites

relative to other resources, the practice is nonexistent (Koops et al. 2013; Sanz and Morgan 2013). Overall, termite fishing is indeed 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 learning is enhanced by social factors. Detailed studies of the acquisition of termite fishing skills in East Africa have helped illuminate the process. As mentioned above, Lonsdorf (2006) studied termite fishing by following eleven infants (unweaned, typically less than age five) and juveniles, along with their five mothers, for sixty-five 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 six) was 0.63. This correlation may be due, entirely or in part, to genetic similarities between mothers and their offspring. However, this seems unlikely since mother-offspring correlations on other such tasks are generally small or zero. This is consistent with other work suggesting that the complexity of termite fishing rods depends on direct experience and learning opportunities (Sanz and Morgan 2011).

All of this is consistent with at least "exposure" learning (Thorndike 1911), meaning that youngsters were aided in learning to fish because hanging around their mothers provided access to termite mounds, tools, and opportunities to practice (similar to 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 analyses 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—see Moore 2013), while their sons did not (Lonsdorf et al. 2004; Lonsdorf 2005). In a manner consistent with the theoretical expectations discussed above, this suggests that more may be afoot than mere exposure or local enhancement.

The practice of ant dipping shows patterns that parallel termite fishing. Like termite fishing, ant dipping is widespread across Africa, often sea-
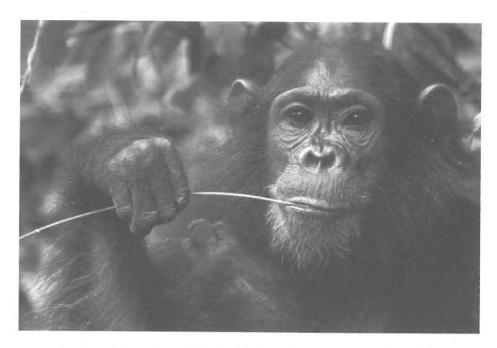
FIGURE 18.1. Termite fishing by an eight-year-old female chimpanzee (Gaia) in the Kasekela community in Gombe National Park, Tanzania (2001). Photo by Ian Gilby.

sonal, 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 thirteen mother-offspring pairs at Bossou in East Africa. Young chimpanzees tended to watch their 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 at 0.87 between mothers and their juvenile offspring. Mom provides access to ants and tools as well as time and tolerance. This permits offspring to learn through direct experience. The more time mom provides, the better both she and her offspring get.

Humle et al. looked for correlations between mother-offspring (1) dipper stick lengths and (2) techniques used, but did not find any—unlike in the

termite fishing study above. This is not altogether surprising, given that in an earlier study, Humle and Matsuzawa (2002) had already found 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. 2011). Many other wild chimpanzees inhabit environments with the requisite nuts, stones, and wood, but 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 (Yamakoshi 1998; Biro et al. 2003), 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 Taï National Park, Côte d'Ivoire. Though they found few or no differences in ecology between these three communities, they did observe some differences in the nut cracking behavior. These differences were relatively subtle, being related to the selection of hammer material and size, rather than to the technique of nut cracking itself. Nevertheless, such differences are unlikely to be related to genetic variation among these neighbors, since they are known to interbreed.

As with both ant dipping and termite fishing, observational studies reveal that it is the exposure to, and possibly the observation of, nut crackers, their tools, and the fruits 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 three and five years (Inoue-Nakamura and Matsuzawa 1997; Biro et al. 2003; 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 evidence showing the existence of experimentally induced "traditions" and field evidence of patterns of behavioral differences among captive chimpanzee populations. This evidence seems sufficient to establish that social learning can facilitate the spread of novel prac-

FIGURE 18.2. Nut cracking by an adult male chimpanzee (Jeje) at Bossou, Guinea, West Africa (2012). Photo by Kathelijne Koops.

tices. And, without it, novel inventions disappear. But, as noted above, what the studies of captive 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 their distribution (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 2016). 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). 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 (Aoki 1986; Laland et al. 2010; Richerson et al. 2010; Henrich 2016). 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 and McElreath 2007; Wrangham and Carmody 2010; Henrich 2016). More broadly, researchers have suggested that this process of cumulative cultural evolution created genetic selection pressures for our long-distance running abilities (e.g., foot anatomy), folkbiological and artifact cognition, "overimitative" tendencies, status psychology (prestige), and verbal mimicry, among other aspects of our species (Henrich 2016).

Applying this theoretical work, we next ask how much cumulative cultural evolution exists in chimpanzees. Since our answer is that little or no cumulative cultural evolution has emerged, we then 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 (Tomasello 1999a; Tennie et al. 2009). 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 reinvent everything, but can anyone in the group reinvent it?

In the field, the existence of variation in tool-using skills, as discussed with nut cracking, termite fishing, and ant dipping, among populations suggests 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 variants 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 captivity, this issue has recently been put to the test by giving naïve chimpanzees opportunities to independently invent practices that have been observed in the field. "Leaf swallowing" behavior, a proposed tool against internal parasites, develops fully in naïve chimpanzees (Huffman and Hirata 2004; Huffman et al. 2010; Menzel et al. 2013). Similarly, food washing and food mining behavior—that is, the classic cases of primate culture—also spontaneously reemerge in naïve chimpanzees (Allritz et al. 2013). The same is true for other behaviors and/or for other primates. For example, mountain gorilla nettle feeding behavior—a complex non-tool-use behavior—reappeared in naïve captive gorillas (Tennie et al. 2008; Masi 2011).[13] Similarly, leaf swallowing also occurs in naïve bonobos (Menzel et al. 2013), and both food washing and food mining behaviors reemerge in naïve orangutans (Allritz et al. 2013).

However, tests in captivity on naïve individuals still remain outstanding for most cases of purported cultural traits in wild chimpanzees (e.g., ant dipping). In the case of termite fishing, Lonsdorf and colleagues (2009) ran a 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). 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, that is, without the need to observe others engage in it. For other 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

learn individually have been largely neglected (Sumita et al. 1985; Hayashi et al. 2005). 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.[14] Given that capuchin monkeys develop nut cracking *without* social cues (Visalberghi 1987), it would be surprising if chimpanzees could not also figure it out by themselves.

Recent field evidence converges with this captive work, indicating that chimpanzee behavioral traits can be individually invented and reinvented. Nut cracking, once thought to be locally restricted, has now also been found in chimpanzees living 1,700 km 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 (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 (e.g., Bogart and Pruetz 2011).

To be clear, we are not arguing that social learning plays no role in these practices. On the contrary, it likely plays a big role in spreading behaviors that are only occasionally reinvented by some individuals (Tennie et al. 2009); for example, nut cracking can spread socially 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 a leaf swallowing behavior, others who beforehand resisted reinvention expressed the same behavior themselves (Huffman and Hirata 2004; Huffman et al. 2010; Menzel et al. 2013). Nevertheless, the fact that these behaviors appear in some naïve individuals without any social input means that it is not so complicated or nonintuitive that no single individual can reinvent it in their lifetime. Thus, it is not cumulative culture.[15]

Currently, the best candidate for a cumulative cultural evolutionary product is a particular ant dipping rod used in the Goualougo 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.[16] 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.

Finally, recent analyses by Kamilar and Atkinson (2013) of Whiten et al.'s thirty-nine traits, while not showing evidence of cumulative cultural evolution, do reveal a kind of nested structuring of traits, which the authors argue presents a 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 thirty-nine traits include several versions of different variants (five forms of nut cracking, six types of dipping, and three types of food pounding), it is not hard to see why this might be. Work by Gruber et al. (2011, 2009), for example, 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. Finally, we also worry that the tendency of different researchers to either split or lump variants into subvarieties 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, captive apes have readily reinvented the behaviors seen in the field.[17] Moreover, bonobos and gorillas invented traits that their wild brethren don't perform. Whatever the final score turns out to be on cumulative cultural evolution in chimpanzees, the important theoretical point already seems clear: chimpanzees have 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.

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.[18]

Cognitive abilities for, or motivations to, individually figure out novel practices foster greater cumulative cultural evolution (van Schaik and Pradhan 2003; Henrich 2004b, 2009b; Kobayashi and Aoki 2012). 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). Captive 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 (Nagell et al. 1993; Horner and Whiten 2005). Moreover, field studies have repeatedly shown 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 humanlike cumulative cultural evolution, 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; Kobayashi and Aoki 2012; 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 (Tennie et al. 2009; Whiten et al. 2009). Notably, 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; Kolodny et al. 2015). 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 (Nagell et al. 1993; Whiten et al. 1996; Call et al. 2005; Herrmann et al. 2007; Tennie et al. 2010b). Thus, compared with humans, chimpanzees are worse at copying motor patterns (Tomasello and Call 1997; Tennie et al. 2012), but also at inferring underlying goals, strategies, and motivations (Tennie et al. 2010a; Dean et al. 2012), 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; Nielsen and Tomaselli 2010). Consistent with this, recent neuroimaging studies have found major deficits in brain structures enabling detailed action copying in chimpanzees[19] relative to humans (Hecht et al. 2013). These action-copying 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)—but they can also have detrimental effects on the overall copying fidelity of tasks that additionally involve other types of information (Acerbi and Tennie 2016).

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 "overimitation," which involve copying apparently unnecessary steps, are a persistent and potent feature of social learning (Lyons et al. 2007; Nielsen and Tomaselli 2010; Herrmann et al. 2013). By contrast, chimpanzees readily drop any unnecessary steps once they perceive that specific steps are superfluous (Horner and Whiten 2005)—including steps consisting of specific actions (Tennie et al. 2012). 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. 2008).

Cultural evolutionary models also show how *sociality* influences the emergence and rate of cumulative cultural evolution (Henrich 2016; Muthukrishna and Henrich 2016). 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 (Derex et al. 2013; Muthukrishna et al. 2014), field studies (Kline and Boyd 2010;

Collard et al. 2013), and ethno-historical cases (Henrich 2004b; Boyd et al. 2011). Strikingly, when populations suddenly shrink or become 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 percent at six months of age to a mere 10 percent 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 (Wiessner 2002; Henrich and Broesch 2011; Hill et al. 2011, 2014; Apicella et al. 2012; Salali et al. 2016).

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 four to five 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 five to six (Inoue-Nakamura and Matsuzawa 1997; Biro et al. 2003; Marshall-Pescini and Whiten 2008; Lonsdorf 2013). 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, 2016; Muthukrishna and Henrich n.d.), 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 gives 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 help explain why bonobos and gorillas do not show the repertoires seen in chimpanzees and orangutans (Tennie et al. 2009; Henrich 2016) despite showing substantial individual-level cognitive abilities in captivity. 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 (van Schaik et al. 2003; Lind and Lindenfors 2010), though in chimpanzees it is the number of females that matters. Gorillas tend to live in small groups with only a silverback, his mates, and one or two other males. The particulars of their social life also seem less suited for social transmission than those of chimpanzees (Lonsdorf et al. 2009; Robbins et al. 2016). Meanwhile, though bonobos live in larger groups (mean size twenty-three), their average group size is half that of chimpanzees (mean size forty-six).[20] 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 that greatly facilitates the evolution of culture (Tennie et al. 2009; Dean et al. 2012). There is now a substantial literature comparing the sociality of chimpanzees to that of 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 (Henrich 2004c; Silk et al. 2005; Jensen et al. 2006, 2007a, 2007b; Warneken et al. 2006; Warneken and Tomasello 2006; Vonk et al. 2008; Brosnan et al. 2009; Silk

and House 2011; House et al. 2012, 2013; Henrich and Silk 2013; Tennie et al. 2016).

Experimental work described above highlights how important sociality is for cumulative cultural evolution. Dean et al. (2012) not only show that children teach and act prosocially toward each other and chimpanzees do not, but that children's success in acquiring a multistep 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.

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 2011; van Schaik et al. 2012; Henrich 2016). 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; Henrich 2016). 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; Muthukrishna and Henrich n.d.). 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 is highly adaptive information already out there in the minds of others, perhaps in the form of numerous valuable practices related to tool making and food processing, 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 would not have been very much out there, in terms of valuable practices, in the minds and behavior of others. What there was could have been discovered on one's own, using individual learning (Tennie et al. 2009). 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. Early 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, 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 inhibits cumulative cultural evolution.

To bypass the start-up problem, Henrich (2016) 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 (as predicted by theory; see 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 (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 would not have involved the continuous improvements in technical know-how and skills that many paleoanthropologists seem to expect (Henrich 2016). Instead, it would have had many fits and starts, with some groups occasionally surging ahead and other groups losing tools and know-how.[21] This is because both the size of tool kits 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 (before about 2 Ma) 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 two 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 Gesher Benot Ya'aqov, Henrich argues that some populations were clearly reliant on diverse behavior repertoires that, taken together, no single individual could reinvent in their lifetime. These repertoires may also have included individual tools or techniques (e.g., perhaps hand axes) that represented true cumulative cultural evolution.[22]

Inferences to the Last Common Ancestor

What can we say about cultural evolution in our last common ancestor with chimpanzees and bonobos? Cultural evolutionary theory predicts that the selection pressures for more sophisticated forms of social learning will increase with environmental variability (Boyd and Richerson 1985). Empirically, the available data from lake and ice cores suggest that after about three million years ago, paleoclimates increased in variability, plausibly on 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 chimpanzees split from the LCA, climatic changes may have increased selection pressures for social learning in both 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 in both primates and birds (Reader and Laland 2002; Reader et al. 2011). 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 2016, n.d.).

The upshot of this is that chimpanzees likely set an upper boundary for the social learning abilities, traditions, and culturally evolved patterns that we might expect in the LCA. The LCA likely had some social learning abilities, as we observe in other apes, and these abilities probably help foster community differences in local traditions. But, unlike in humans, these traditions were probably only ephemeral—subject to periodic disappearances and reinventions over time. There was likely little scope for culture-driven genetic evolution.

Summary

We have applied a culture-gene coevolutionary approach to compare humans to one of our closest living relatives. In doing so, we pointed out a few potential theoretical pitfalls—which we aimed to avoid—and focused instead on what we argue to be the most ecologically valid type of data: namely that derived from either wild chimpanzees, or from what we call "enriched captive apes." Focusing in this way illuminated some clear differences between the two species: humans, in contrast to chimpanzees, show higher fidelity in their social learning, clear evidence for teaching, and a wider range of adaptive social learning biases (e.g., conformist transmission). In addition, human social structures, effective population sizes, and life history traits are all much better suited for cumulative cultural evolution than their equivalents in chimpanzees. Perhaps resulting from these differences, there is currently no clear evidence for cumulative cultural evolution in chimpanzee populations. Instead, these behaviors seem to be (re)inventable at the individual level. This line of research suggests that small initial differences between proto-humans and proto-chimpanzees after the LCA led our lineage into a regime of culture-driven genetic evolution that has not been experienced by any other ape, including chimpanzees. Since cultural evolution created a series of autocatalytic selective pressures on the genes

in our lineage (e.g., due to cultural products such as fire, cooking, projectile weapons, cutting edges, and plant knowledge), humans have diverged much further from the LCA than chimpanzees. The human species alone has become "addicted to culture."

Endnotes

1. For the earliest model of the genetic evolution of a cultural learning ability, see Feldman and Cavalli-Sforza (1976).

2. For chimpanzee observers, the species of the demonstrator does not seem to have a significant impact on the outcome (Boesch 2007; Marshall-Pescini and Whiten 2008; Dean et al. 2012). For humans, the impact of other-species demonstrators has not been explored, though efforts to co-rear humans and chimpanzees suggest that infants and young children will readily copy older, more physically skilled apes (Kellogg and Kellogg 1933; Henrich and McElreath 2003).

3. 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).

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

5. Nevertheless, for evidence against normative conformity in chimpanzees, see Haun et al. (2014).

6. 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 2001). 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 is that chimpanzees will continue selectively copying those they have 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.

7. Data on wild great tits is consistent with conformist transmission (Aplin et al. 2015), though other important alternative interpretations exist for these findings (van Leeuwen et al. 2015; Acerbi et al. 2016).

8. 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.

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

10. 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.

11. These otherwise consistent patterns, showing no teaching, contradict earlier work on nut cracking at Taï forest (Boesch 1991, 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 the mother "giving" by Boesch (Lonsdorf 2013). Similarly, a recent study of wild chimpanzees argues for "teaching" via the transfer of a needed tool from mother to juveniles in the context of termite fishing (Musgrave et al. 2015, 2016)—but here, too, the youngsters and tool recipients were the active force in the transfer of these tools. Most importantly, even though the recipients showed increased rates of termite fishing following tool transfers, it is unclear whether the development of the underlying technique required, or even benefited, from these transfers.

12. For more on the debate see Langergraber et al. (2011) and Langergraber and Vigilant (2011).

13. But see also Byrne et al. (2011).

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

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

16. 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 Taï chimpanzees are made prior to use. Thus, modifications prior to use may actually be common in chimpanzees.

17. Incidentally, this also fits great ape gestures and vocalizations; see Slocombe and Scott-Philips (this volume) for an overview. Thus, great ape communication does not seem to require high-fidelity social transmission, either.

18. Some argue that language explains cumulative culture. While language certainly increases the fidelity and volume of cultural transmission in some domains, languages are themselves clearly the product of cumulative cultural evolution. So pointing to language to explain culture would be like pointing to archery technology to explain hunting success. Language likely first developed as a consequence of cumulative cultural evolution before it began increasing

transmission fidelity and fostering further cumulative cultural evolution (Henrich 2016: chapter 13).

19. Importantly (as far as we know), these data stem from enriched captive chimpanzees.

20. These averages were generated using the data in Wilson et al. (2014).

21. In any case, recent findings suggest that anatomy, especially hand anatomy, was not the bottleneck for early stone tool production (e.g., see Rolian and Carvalho, this volume)

22. The pathway to full-blown cumulative cultural evolution, in which individuals acquire specific skills, techniques, or bodies of know-how that no single individual could figure out in their lifetime, has a number of less sophisticated way stations along the way (Dean et al. 2014). For example, individuals may acquire a diverse repertoire of different skills, techniques, and bits of knowledge that they would be unlikely to assemble on their own despite the fact that they could individually figure out each trait in the set. More specifically, suppose a total repertoire consisted of ten different tool-using and tool-making skills, and each individual has a 30 percent chance of figuring out each skill on his or her own. This, nevertheless, makes the chances of figuring out all ten skills by themselves vanishingly small, at 0.00006 percent. Thus, social learning skills can play a big role in building up the cultural aggregations before tipping into full-blown cumulative cultural evolution; see Henrich (2016) for further discussion.

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