Cladistic analyses of behavioural variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis[☆]

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ABSTRACT

Long-term field studies have revealed considerable behavioural differences among groups of wild *Pan troglodytes*. Here, we report three sets of cladistic analyses that were designed to shed light on issues relating to this interpopulation variation that are of particular relevance to palaeoanthropology.

In the first set of analyses, we focused on the proximate cause of the variation. Some researchers have argued that it is cultural, while others have suggested that it is the result of genetic differences. Because the eastern and western subspecies of *P. troglodytes* are well differentiated genetically while groups within the subspecies are not, we reasoned that if the genetic hypothesis is correct, the phylogenetic signal should be stronger when data from the eastern and western subspecies are analysed together compared to when data from only the eastern subspecies are analysed. Using randomisation procedures, we found that the phylogenetic signal was substantially stronger with in a single subspecies rather than with two. The results of the first sets of analyses, therefore, were inconsistent with the predictions of the genetic hypothesis.

The other two sets of analyses built on the results of the first and assumed that the intergroup behavioural variation is cultural in nature. Recent work has shown that, contrary to what anthropologists and archaeologists have long believed, vertical intergroup transmission is often more important than horizontal intergroup transmission in human cultural evolution. In the second set of analyses, we sought to determine how important vertical transmission has been in the evolution of chimpanzee cultural diversity. The first analysis we carried out indicated that the intergroup similarities and differences in behaviour are consistent with the divergence of the western and eastern subspecies, which is what would be expected if vertical intergroup transmission has been the dominant process. In the second analysis, we found that the chimpanzee cultural data are not only comparable to a series of modern human cultural data sets in terms of how tree-like they are, but are also comparable to a series of genetic, anatomical, and behavioural data sets that can be assumed to have been produced by a branching process. Again, this is what would be expected if vertical inter-group transmission has been the dominant process in chimpanzee cultural evolution.

Human culture has long been considered to be adaptive, but recent studies have suggested that this needs to be demonstrated rather than assumed. With this in mind, in the third set of analyses we investigated whether chimpanzee culture is adaptive. We found the hypothesis that chimpanzee culture is adaptive was supported by an analysis of data from the Eastern African subspecies, but not by an analysis of data from the eastern and western subspecies.

The results of our analyses have implications for the number of subspecies in *Pan troglodytes*, the relationship between hominin taxa and Palaeolithic industries, and the evolution of hominin cognition and behaviour.

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Introduction

Over the last 30 years it has become increasingly apparent that there are considerable behavioural differences among wild

populations of *Pan troglodytes* (McGrew et al., 1979; Whiten et al., 1999, 2001; Schoening et al., 2008). Certain behaviours have been observed at some sites but not others. Chimpanzees at Bossou (Guinea), Taï Forest (Côte d'Ivoire), and Gombe (Tanzania), for instance, use sticks to collect army ants for consumption, while those at Mahale (Tanzania), Kibale (Uganda), and Budongo (Uganda) do not. Likewise, chimpanzees at Gombe, Kibale, and Mahale engage in "leaf grooming" (i.e., typical chimpanzee-to-chimpanzee grooming actions directed toward leaves), whereas those at Bossou and the Taï Forest do not. The way in which some behaviours are carried out also varies among sites. Nut cracking is a case in point. At Bossou, individuals employ only stone hammers and anvils to open a single species of nut (Matsuzawa, 1994). In contrast, at Taï both wooden and stone hammers, as well as root and stone anvils, are used to crack four kinds of nut (Boesch and Boesch-Achermann, 2000). So far, at least 65 behaviours have been found to vary among wild chimpanzee populations (Whiten et al., 1999, 2001).

In this paper, we outline three sets of analyses that were carried out to shed light on issues regarding this interpopulation variation that are of particular relevance to palaeoanthropology. The first set of analyses focused on the basis of the variation. It has been hypothesised that many of the behavioural differences among chimpanzee populations are cultural (McGrew, 1992, 1998, 2004; Whiten et al., 1999, 2001; Boesch, 1996, 2003; Whiten, 2005). According to the proponents of this hypothesis, a behaviour can be considered cultural if it is exhibited by multiple members of a community and is socially learned (Whiten et al., 1999, 2001). They contend that these criteria are fulfilled by at least 39 of the aforementioned 65 behaviours (Whiten et al., 1999, 2001; Whiten, 2005).

The hypothesis that chimpanzees have culture has been criticised by two groups of researchers. One group accepts that the behaviours that vary among populations are socially learned, but considers them to be traditions rather than cultural behaviours (Galef, 1992; Tomasello, 1999; Tuttle, 2001; Richerson and Boyd, 2005). These researchers differ with respect to their reasons for rejecting the behaviours as cultural. Tuttle (2001) argues that they cannot be considered cultural because chimpanzees have not been shown to have symbolically mediated ideas, beliefs, and values. The use of symbolism, he contends, is the "*sine qua non* of culture" as far as anthropologists are concerned (Tuttle, 2001: 407). Galef (1992) challenges the hypothesis that chimpanzees have culture on the grounds that culture depends on teaching and imitation (a form of social learning in which an individual stores a mental representation of a task in their brain and then matches their motor behaviour to this stored representation) and there is no evidence that chimpanzees engage in either of these activities. Tomasello (1999) and Richerson and Boyd (2005), meanwhile, argue that the crucial feature of culture is that it is cumulative. As such, for a behaviour to be considered cultural it not only has to be prevalent within a community and socially learned, but also has to show signs of the "ratchet effect." That is, there has to be evidence of elaboration through time and across generations. The behaviours that vary among populations of chimpanzees, Tomasello (1999) and Richerson and Boyd (2005) aver, do not qualify as culture because they do not exhibit elaboration.

Another group of researchers is sceptical that the behaviours in question are even socially learned (Laland and Hoppitt, 2003; Laland and Janik, 2006). These researchers assert that the available evidence is too weak to discount the possibility that the behaviours are genetically determined. The claim that the behaviours are socially learned is based on the results of applications of the "method of exclusion" (sometimes also confusingly referred to as the "ethnographic method"). In this method, sites are compared with a view to identifying potential environmental causes of the behavioural variation. Behaviours are deemed socially learned if

the observed variation among sites cannot be explained in terms of environmental factors. Researchers who reject the social learning hypothesis contend that the method of exclusion is problematic. They point out that a third of the 39 putative cultural behaviours occur in a single subspecies, and that genetic studies suggest the subspecies represented in the sample have been genetically isolated for hundreds of thousands of years. In such circumstances, they argue, a genetic origin for the observed behavioural differences cannot be easily dismissed. Even in cases where genetic control of a specific behaviour seems implausible, it is possible that at a proximate level genetic mechanisms account for the behavioural differences among populations. Thus, results obtained via the method of exclusion may suggest that many chimpanzee behaviours are maintained by social learning, but they are not conclusive.

Tuttle's (2001) and Galef's (1992) critiques of the chimpanzee culture hypothesis have been refuted by Brumann (2002) and McGrew (2004), respectively. Brumann (2002) argues that, contrary to what Tuttle (2001) contends, there is no consensus among anthropologists that culture is based on symbolism. Rather, many of the definitions of culture that have been developed by anthropologists include both mental phenomena and behaviour, and at least one of the definitions does not mention mental phenomena at all. The only criterion that all anthropological definitions of culture agree upon, Brumann (2002) suggests, is that for something to be considered cultural it has to be shared by a group of individuals. Brumann (2002: 509) goes on to argue that since this is also a feature of the definition of culture used by the proponents of the chimpanzee culture hypothesis, the latter's definition is "not out of touch with present-day anthropology." In response to Galef's (1992) suggestion that chimpanzees cannot be considered to have culture because they do not teach or imitate, McGrew (2004) has pointed out that many human behaviours are accepted as cultural even though there is no evidence that they are the result of teaching or imitation rather than some other mechanism. As such, insisting that a chimpanzee behaviour must involve teaching or imitation to be considered cultural inappropriately holds chimpanzees to a higher standard than humans.

There is also some evidence to challenge the claim that the ratchet effect is absent in chimpanzees. Whiten et al. (2003) have argued that the differences in invertebrate fishing techniques at the sites of Taï Forest, Gombe, and Bossou may indicate that chimpanzees engage in cumulative social learning. In the Taï Forest, short sticks are used as fishing probes and ants are then placed directly into the mouth, whereas at Gombe, long sticks are used and ants are swiped from the stick by hand prior to ingestion. At Bossou, both techniques appear to be present and are used in different contexts. The long stick method is approximately four times more productive than the short stick method. The existence of both techniques at Bossou provides circumstantial evidence that one technique is an elaboration of the other, suggesting accumulation of modifications to this socially learned behaviour (Schoening et al., 2008). Sanz et al.'s (2004) demonstration that chimpanzees at Goualougo (Republic of Congo) use one tool to fish for termites in above-ground nests and another tool to fish for termites in subterranean nests also hints at the possibility that chimpanzees engage in cumulative social learning. It suggests the Goualougo chimpanzees may have modified an existing behaviour to suit a different set of conditions.

The claim that the population-level variation in behaviour is genetically determined rather than cultural also requires further evaluation. Given the complexity of some of the chimpanzee behaviours involved in this debate (e.g., termite fishing), it may seem implausible that genetic differences could account for the population differences. However, as Whiten and van Schaik (2007)

have noted recently, studies of instinctive tool manufacture and use by hand-reared Caledonian crows (e.g., Kenward et al., 2005) demonstrate the potential for genes to control behaviours that intuitively seem unlikely to be genetically controlled. As such, the genetic explanation for the population-level variation in chimpanzee behaviour cannot simply be dismissed out of hand.

A number of studies have provided evidence that chimpanzees are not only capable of employing social learning, but do so spontaneously. For example, Whiten et al. (2005) trained two high-ranking females from two 16-individual groups to use a different tool technique for obtaining food from identical experimental apparatuses, which were dubbed "Pan-pipes." Upon gaining private expertise in their different variants of tool technique (poking a hole with a stick vs. lifting a hook with a stick), the females were returned to their respective groups. A third control group with no resident "expert" present was also studied. Thirty-two individuals from the groups with a resident expert successfully mastered the Pan-pipes. In contrast, no members of the control group succeeded. In the group where the high-ranking individual was trained to use the poke method, all tool users predominantly adopted that method. In the lift technique group, the number of individuals employing it over the alternative method was significantly above chance, although several individuals also made use of the poke method. Over time the predominant technique in the lift method group became that of their peers, a finding which was interpreted as possible evidence for conformity bias in the adoption of novel behaviours (Whiten et al., 2005). Whiten et al.'s (2005) principal finding—that chimpanzees spontaneously engage in social learning—has since been replicated in a number of different experimental studies involving captive individuals (Horner et al., 2006; Bonnie et al., 2007; Hopper et al., 2007; Whiten et al., 2007). Hence, it is unlikely to be accidental.

There is also reason to believe that spontaneous social learning is not limited to captive individuals. The chimpanzees at the site of Bossou have been the focus of a number of experimental studies designed to assess the social learning abilities of chimpanzees (Matsuzawa, 1994; Matsuzawa et al., 2001; Biro et al., 2003, 2006). In what the researchers termed an "outdoor laboratory," two species of nut cracked by neighbouring communities, *Coula* nuts and *Panda* nuts, were introduced to the Bossou group, who normally only cracked locally available oil-palm nuts (*Elaeis*). When *Coula* nuts were first introduced to the group in 1993, the reaction of several individuals was to nibble or sniff the novel items, while other individuals simply ignored them. A single adult female, however, immediately cracked the nuts without hesitation and did not pause to investigate the novel objects. It appeared, therefore, that this adult female had migrated from a neighbouring group and had prior experience with this species of nut. Her exploitation of this resource attracted attention from juveniles, and by the fourth session of *Coula* presentation, two of these juveniles had begun to crack the nuts (Matsuzawa, 1994; Matsuzawa et al., 2001). By 2002, two-thirds of the Bossou population was cracking *Coula* nuts (Biro et al., 2003, 2006). *Panda* nuts were introduced in 2000. However, they did not attract the same attention as the *Coula* nuts. Two juveniles briefly tried to crack the *Panda* nuts, but were unsuccessful. Two adult females successfully cracked them, but the behaviour did not persist (Biro et al., 2003). At the moment, it is not clear why *Coula* nut cracking spread within the Bossou population but *Panda* nut cracking did not. One possibility is that sustained exploitation of a novel food item is essential for the successful social transmission of the relevant behaviour. Regardless of the reasons for the population's different reactions to the two nut species, this body of work supports the hypothesis that chimpanzees engage in social learning and do so of their own accord.

However, to date, only one study has directly tested the claim that the interpopulation variation in chimpanzee behaviour is genetically determined rather than cultural. Lycett et al. (2007) used cladistic analysis of Whiten et al.'s (1999) cross-site behavioural data set to test one of the key predictions of the genetic hypothesis. Since genetic data indicate that chimpanzees living in East and West Africa are well differentiated from each other, while the populations within East Africa cannot be distinguished (Morin et al., 1994; Goldberg and Ruvolo, 1997; Gagneux et al., 2001; Gonder et al., 2006), they reasoned that if the genetic hypothesis is correct, the behavioural data should mirror the genetic data in terms of structure. Specifically, the phylogenetic structure yielded by a continent-wide cladistic analysis should be greater than one involving exclusively East African populations. The study involved several steps. First, Lycett et al. (2007) reviewed the published scientific literature to generate codes for the 39 putatively cultural behaviours for an outgroup, the bonobo (*Pan paniscus*). Next, they carried out a cladistic analysis of the entire data set. They identified the most parsimonious cladogram and recorded its length and Retention Index (RI). The length of a cladogram is the number of evolutionary changes that it requires to explain a given data set. The RI is a measure of the number of homoplastic changes a cladogram requires that are independent of its length (Farris, 1989a,b). Essentially, the RI is a measure of goodness-of-fit to a bifurcating tree model and, as such, is an expression of how well similarities and differences across a group of taxa can be explained by a given phylogenetic hypothesis. Then, they performed a cladistic analysis of the data for just the five East African groups, all of which are *P. t. schweinfurthii*. Again, they identified the most parsimonious cladogram and recorded its length and RI. The results of the analysis were not consistent with the prediction of the genetic hypothesis. Specifically, the RI for the cladogram obtained in the multiregion analysis was markedly lower than the RI for the cladogram derived from the East African data set. Accordingly, Lycett et al. (2007) concluded that their study refuted the genetic hypothesis.

While the results of Lycett et al.'s (2007) analyses are incompatible with the hypothesis that wild chimpanzee behavioural variation is genetically determined, they are consistent with the hypothesis that the behaviours are socially learned. One of the key features of social learning is that it is "model neutral." That is, the ability to copy the behaviour of other individuals is not confined to certain categories of model. Most significantly, individuals with the ability to acquire information socially are not limited to copying from their parents. They also have the option to copy more distantly related kin and unrelated individuals. The corollary of this is that individuals who are able to employ social learning can potentially acquire behaviours from members of one group and then disperse to mate with members of another, which opens up the possibility of patterns of transmission of socially learned behaviour being different from their genetic counterparts. Thus, a mismatch between the results of a phylogenetic analysis of a behavioural data set and the results of a phylogenetic analysis of genetic data from the same set of taxa is not unexpected if the behaviours in question are socially learned.

Given the implications of the claim that chimpanzees have culture for our understanding of human evolution and more generally for the way in which we conceptualise the relationship between ourselves and other animals (Corbey, 2005), there is a need for further research designed to evaluate the criticisms of the claim. With this in mind, in the first set of analyses we addressed one of the shortcomings of the study by Lycett et al. (2007), namely that they used only a single measure of phylogenetic structure to test the hypothesis that the interpopulation variation in chimpanzee behaviour is genetically determined. We

repeated their analysis with two other measures of phylogenetic structure, the permutation tail probability test and the phylogenetic bootstrap.

The second set of analyses reported in this study built on the results of the first set of analyses, which were consistent with those of Lycett et al. (2007) in refuting the genetic hypothesis. In the second set of analyses, we used cladistic methods to investigate how similar chimpanzee cultural transmission is to cultural transmission in small-scale human societies. Debate about the evolution of cultural diversity among human populations has focused on the relative importance of the inheritance of cultural information by a daughter population from a parent population versus the transfer of cultural information among contemporaneous groups through intermarriage, trade, exchange, etc. The first of these processes has been dubbed "vertical intergroup transmission," "demic diffusion," and "phylogenesis" (e.g., Durham, 1990; Guglielmino et al., 1995; Hewlett et al., 2002; Collard et al., 2006). The second has been referred to as "horizontal intergroup transmission," "cultural diffusion," and "ethnogenesis" (e.g., Moore, 1994a,b; Tehrani and Collard, 2002; Collard et al., 2006).

Since the middle of the last century, most anthropologists have believed that cultural evolution and biological evolution differ greatly as a result of the significant role played by horizontal intergroup transmission in the former. Alfred Kroeber was an early and highly influential proponent of this view. In a widely cited volume published in the mid-20th century, he argued that:

> "The course of organic evolution can be portrayed properly as a tree of life, as Darwin has called it, with trunk, limbs, branches, and twigs. The course of the development of human culture in history cannot be so described, even metaphorically. There is a constant branching-out, but the branches also grow together again, wholly or partially, all the time…A branch on the tree of life may approach another branch; it will not normally coalesce with it. The tree of culture, on the contrary, is a ramification of such coalescences, assimilations, or acculturations" (Kroeber, 1948: 138).

In recent years, Kroeber's tree of life/tree of culture dichotomy has been renamed. For example, Moore (1994a) calls the tree of life model the "cladistic model" and the tree of culture model the "rhizotic model," while Terrell (1988) refers to the former as the "family tree model" and the latter as the "entangled bank model." However, Kroeber's basic point—that human cultural evolution is much more complex and intertwined than biological evolution—remains widely accepted (e.g., Moore, 1994a,b; Dewar, 1995; Terrell et al., 1997, 2001).

Human populations have engaged in various forms of exchange for tens of millennia (McBrearty and Brooks, 2000: 530). However, the idea that this means each human language or culture should be assumed to be derived from several antecedent groups is not consistent with the available evidence. Several studies have focused on cultural variation among villages on the North Coast of New Guinea (Welsch et al., 1992; Moore and Romney, 1994; Roberts et al., 1995; Shennan and Collard, 2005). Although the first of these studies found horizontal intergroup transmission to be more important than vertical transmission (Welsch et al., 1992), subsequent reanalyses using more powerful statistical and phylogenetic methods concluded that vertical transmission was at least as important as horizontal intergroup transmission (Moore and Romney, 1994; Roberts et al., 1995; Shennan and Collard, 2005). Another group of studies have analysed cultural data from African populations (Guglielmino et al., 1995; Borgerhoff-Mulder, 2001; Hewlett et al., 2002). Two of these concluded that horizontal intergroup transmission among populations was much less important than vertical transmission (Guglielmino et al., 1995;

Hewlett et al. 2002), while the third study returned more equivocal results (Borgerhoff-Mulder, 2001). Other studies have investigated the relative contributions of vertical and horizontal intergroup transmission to Neolithic German pottery decorations (Collard and Shennan, 2000), Turkmen carpet designs (Tehrani and Collard, 2002), and Californian basketry styles (Jordan and Shennan, 2003). Horizontal intergroup transmission appears to have played a role in generating all these data sets, but only the Californian basketry study concluded that it was the dominant evolutionary process.

Recently, Collard et al. (2006) reported the most comprehensive analysis of this issue that has been carried out to date. They examined how tree-like 21 cultural data sets were in comparison to 21 biological data sets that there is reason to think have been generated by vertical intergroup transmission. They found that the cultural data sets were no less tree-like than the biological data sets, and concluded from this that the cultural data sets were also primarily generated by vertical intergroup transmission. Thus, the suggestion that horizontal intergroup transmission is a more important process than vertical intergroup transmission in the generation of human cultural diversity is not supported by the empirical studies that have been published to date. On the contrary, it appears that vertical intergroup transmission is more often the dominant cultural evolutionary process.

To determine whether chimpanzee cultural diversity is also primarily a consequence of vertical intergroup transmission, we carried out two analyses. First, we reasoned that if vertical intergroup transmission has been the dominant process, the multiregion MP cladogram should be statistically indistinguishable from a cladogram in which the eastern and western populations form separate clades. Next, we first used the RI to assess how tree-like are patterns in comparative samples of human cultural data sets and biological data sets. Given that the biological data sets can be confidently assumed to have been structured by speciation, which is a branching process, our rationale was that if the human cultural and the biological RIs are not significantly different, then it is reasonable to conclude that the human cultural data sets have been structured by vertical intergroup transmission. We also reasoned that if the chimpanzee cultural RIs fall within the range of human cultural RIs, then whichever process is found to have structured the human cultural data sets is likely to have structured the chimpanzee cultural data sets.

The third set of analyses also built on the results of the first set of analyses. In the third set of analyses, we used cladistic methods to investigate whether chimpanzee culture is adaptive. Hominin culture is widely considered to be an "extrasomatic means of adaptation," to use White's (1959: 8) well-known formulation (e.g., Binford and Binford, 1966; Shipman and Walker, 1989; Ambrose, 2001; McBrearty, 2003). It certainly seems to be the case that some of the cultural behaviours of humans are adaptive. For example, the results of several studies suggest that variation in the diversity and complexity of the toolkits of historically documented hunter-gather groups is influenced by the risk of resource failure (e.g., Torrence, 1983, 1989, 2000; Collard et al., 2005). However, a number of other human cultural behaviours appear to have evolved via the cultural equivalent of genetic drift rather than selection (Bentley et al., 2004, 2007). Still other human cultural behaviours can be seen as maladaptive from the viewpoint of inclusive fitness (Richerson and Boyd, 2005: 148–190). Thus, hominin culture cannot simply be assumed to be adaptive. Clearly, the same holds for chimpanzee culture. Accordingly, in the third set of analyses, we attempt to determine whether chimpanzee cultural behaviours might also be adaptations to differing ecological conditions.

It is important here to be clear about the distinction between environmental constraints and ecological conditions with respect to their implications for interpretations of cultural variability.

An environmental constraint would imply some factor that prevents a specific behaviour from being exhibited at a given locality (e.g., absence of certain material for tool manufacture). Patterns created by such absences cannot necessarily be interpreted as cultural (Whiten et al., 1999). Conversely, ecological conditions (e.g., rainfall, seasonality, number of daylight hours, etc.) may influence the differential representation of cultural variants such that some come to be more frequently represented in the behavioural repertoires of subsequent generations than others. That is, ecologically induced selection is acting as a sorting mechanism on cultural variation through time. In this sense, chimpanzee cultural variation could be seen as an adaptive response to ecological conditions (Boesch and Boesch-Achermann, 2000; Yamakoshi, 2001), just as some of human cultural variation appears to be adaptive.

A number of ecological factors could potentially influence the behaviour of the chimpanzee populations. For an initial assessment of potential ecological influence, we used mean annual rainfall as a proxy for ecology. Needless to say, the use of any single variable alone as a measure of ecological conditions is less than ideal. However, rainfall level has been shown to be a key ecological variable in Africa, one that influences species abundance and vegetation composition among other things (e.g., Andrews and O'Brien, 2000). In addition, rainfall data are readily available for many chimpanzee study sites. In order to assess the impact of rainfall, we constructed a hypothetical "model" cladogram that groups the chimpanzee populations on the basis of rainfall level. We then statistically compared that model tree to the most parsimonious cladograms yielded by the behavioural data. We reasoned that if ecological conditions have influenced the evolution of chimpanzee cultural behaviours, there should be no statistical difference between the rainfall model tree and the behavioural cladograms.

Materials and methods

Testing the genetic hypothesis

As noted earlier, in the first set of analyses we repeated the analysis reported by Lycett et al. (2007) but with different measures of phylogenetic structure. The data set utilised by Lycett et al. (2007) comprises codes for 39 behaviours for seven chimpanzee populations, two from West Africa and five from East Africa. Also included in the data set are codes for the same 39 behaviours for an outgroup, Pan paniscus. Lycett et al. (2007) obtained the chimpanzee data from Whiten et al. (1999) and the P. paniscus data from Hohmann and Fruth (2003). The codes for the behaviours are absent (0), present (1), habitual (2), customary (3), or status uncertain (?).

The data set was employed in two sets of analyses. The first utilised the permutation tail probability (PTP) test. The degree to which the structural properties of a given character matrix determine a tree topology produced via parsimony analysis can be defined as its "cladistic structure" or phylogenetic signal (Kitching et al., 1998). In order to assess the strength of phylogenetic signal within the data, a PTP test was undertaken. The PTP test permutes the original character matrix without replacement, creating a predefined number of pseudoreplicate character matrices. Thereafter, a maximum parsimony (MP) cladogram is computed for each pseudoreplicate character matrix, the lengths of which are compared to the most parsimonious cladogram(s) computed for the unpermuted character matrix. If 95% or more of the cladograms produced from the pseudoreplicate character matrices are longer than the original MP cladogram(s), the original character matrix is considered to contain a significant phylogenetic signal (Kitching et al., 1998). The PTP test was originally designed to be employed as a statistical test for the strength of phylogenetic signal within

a given character matrix (Archie, 1989; Faith, 1991; Faith and Cranston, 1991). However, criticism of the PTP test (e.g., Carpenter, 1992; Kitching et al., 1998) has led to suggestions that it should be considered a heuristic device rather than a means of statistically accepting or rejecting a given cladogram (Kitching et al., 1998). It is in this capacity that the PTP test is applied here.

Two PTP tests were performed, one at the continental level that included both western P. t. verus and eastern P. t. schweinfurthii populations, and one with only the five eastern P. t. schweinfurthii populations. Fischer et al. (2006) found that none of the conventionally recognised subspecies of P. troglodytes are genetically distinct. However, Fischer et al.'s (2006) results are not consistent with the results of the other analyses of wild chimpanzee genetic variation that have been carried out to date (Morin et al., 1994; Goldberg and Ruvolo, 1997; Gagneux et al., 2001; Gonder et al., 2006; Becquet et al., 2007). These studies differ with respect to the distinctiveness of P. t. troglodytes and P. t. schweinfurthii (e.g., Gonder et al., 2006; Becquet et al., 2007). But they have all found marked genetic divergence between the subspecies to which our study populations are assigned, P. t. schweinfurthii and P. t. verus. Accordingly, we reasoned that if the genetic hypothesis is correct, we should see less evidence of phylogenetic structure in the data set at the East African level than when both subspecies are included together. Following recent permutation-based analyses (e.g., Collard and Wood, 2000; Gibbs et al., 2000; Tehrani and Collard, 2002; Lycett 2007, 2009), 10,000 pseudoreplicate character matrices were examined. PTP tests were undertaken with the aid of PAUP* 4.0 (Swofford, 1998). All characters were treated as ordered and freely reversing (Slowinski, 1993).

A second set of analyses employed a technique called bootstrapping. In phylogenetics, bootstrapping assesses the level of support for individual clades within a given cladogram (Felsenstein, 1985; Kitching et al., 1998). The bootstrap procedure randomly samples characters with replacement and forms a pseudoreplicate data matrix with the same number of characters and character states as the original. Thereafter, each pseudoreplicate character matrix is subjected to parsimony analysis, with results typically presented in the form of a majority rule consensus cladogram as a means of displaying the proportion of pseudoreplicate character matrices that support individual nodes. Like the PTP test, phylogenetic bootstrapping was initially introduced as a statistical test of support for clades. According to Felsenstein (1985), if a clade appears in ≥95% of bootstrap replicates, the clade is supported at the 95% (i.e., $\alpha = 0.05$) confidence level. On the basis of simulation analyses, Hillis and Bull (1993) argued that bootstrap values of 70% are enough for a clade to be considered significantly supported. However, recent criticism of the assumptions of bootstrapping—in particular the assumption that the characters to be bootstrapped represent a random sample of all possible characters—have left its status as a statistical test in doubt (Kitching et al., 1998; Page and Holmes, 1998; but see Sanderson, 1995; Felsenstein, 2004). As a consequence, the procedure is now generally considered to be a heuristic method of investigating clade robusticity rather than a statistical test (e.g., Kitching et al., 1998; Page and Holmes, 1998).

Two bootstrap analyses were conducted. Again, one was carried out at the continental level and one with only the five East African populations. The prediction in this analysis was that if the genetic hypothesis is correct, there should be less support for individual clades at the East African level than when both subspecies are included together. The bootstrap analyses were carried out in PAUP*4.0 (Swofford, 1998). In line with recent studies (Collard and Wood, 2000; Tehrani and Collard, 2002; Strait and Grine, 2004; Lycett 2007, 2009), the character matrix was bootstrapped a total of 10,000 times. Thereafter, minimum length cladograms were computed for the pseudoreplicate matrices with PAUP*'s branch-

and-bound algorithm, which is guaranteed to find the most parsimonious cladogram(s) for a given data set. All characters were treated as ordered and freely reversing (Slowinski, 1993). A majority-rule consensus cladogram was subsequently determined for each data set in order to determine which clades were supported in ≥50% of the bootstrap replicates.

Cultural transmission processes among chimpanzees

We carried out two analyses to evaluate the importance of vertical intergroup transmission in the evolution of chimpanzee cultural diversity. In the first analysis we assessed the extent to which the multiregion MP cladogram reflects the divergence between eastern and western populations that has been repeatedly documented in genetic studies. We reasoned that if vertical intergroup transmission has been the dominant process, the multiregion MP cladogram should be statistically indistinguishable from a cladogram in which the eastern and western populations form separate clades. To test this prediction, we used *MacClade* 4.02 (Maddison and Maddison, 2001) to create a cladogram reflecting the east-west split between the seven ingroup taxa (eastern and western groups were each represented by a multifurcating or "polytomous" clade). We then subjected the data set to a parsimony analysis in PAUP* 4.0 (Swofford, 1998) using the MacClade-generated cladogram to constrain the search (i.e., cladograms that were inconsistent with the constraint cladogram were rejected). Subsequently, the topologies of the resulting cladogram and the multiregion MP cladogram were compared with the aid of the Kishino-Hasegawa (K-H) test (Kishino and Hasegawa, 1989). The K-H test allows an MP cladogram to be statistically compared with one or more other cladograms. Thus, it can be used to test hypotheses regarding processes that may explain the structure of a cladogram by comparing the MP cladogram with cladograms constructed to reflect the hypothesised processes. The test uses the standard deviation of changes in each character and the *t*-statistic in order to determine if the MP cladogram is statistically different from that of the explanatory cladogram. If the cladograms are significantly different, the hypothesised process can be discounted.

In the second analysis, we used the RI to assess how tree-like are 25 human cultural data sets and 25 biological data sets, the latter of which have been used to reconstruct the relationships of species and higher-level taxa. We then calculated RIs for the most parsimonious cladograms derived from the multiregion and East African chimpanzee cultural data sets, and compared these with the RIs for the human cultural data sets. Given that the biological data sets can be confidently assumed to have been structured by speciation, which is a branching process, our rationale was that if the human cultural and the biological RIs are not significantly different, then it is reasonable to conclude that the human cultural data sets have been structured by vertical intergroup transmission. Conversely, if the human cultural RIs are significantly lower than the biological RIs, then it is reasonable to conclude that the human cultural data sets have been structured by horizontal intergroup transmission. We reasoned that if the chimpanzee cultural RIs fall within the range of human cultural RIs, then whichever process is found to have structured the human cultural data sets is likely to have structured the chimpanzee cultural data sets too.

The RIs for the 25 human cultural data sets were taken from the literature (Table 1). RIs for 21 of the biological data sets were also taken from the literature (Table 2). The remaining four were calculated from published data using PAUP* 4.0 (Swofford, 1998). In all four analyses, the characters were treated as unordered and the most parsimonious cladogram was detected via the heuristic search routine. The statistical significance of the difference between the RIs of the 25 human cultural data sets and the RIs of the 25

Table 1
Retention Indices associated with most parsimonious cladograms derived from 25 human cultural data sets[a]

#	Data set	RI	Source of RI
1	Gulf of Georgia Salish food taboos and prescriptions	0.57	Collard et al. (2006)
2	Neolithic pottery	0.71	Collard et al. (2006)
3	Californian Indian basketry	0.71	Collard et al. (2006)
4	Eastern North American projectile points	0.70	Collard et al. (2006)
5	Coast and inland Salish cultural practices	0.63	Collard et al. (2006)
6	New Guinea material culture	0.51	Collard et al. (2006)
7	Turkmen weaving designs	0.44	Collard et al. (2006)
8	Northwest Coast tribal religion and ritual	0.65	Collard et al. (2006)
9	Early Christian doctrinal beliefs	0.61	Collard et al. (2006)
10	Iranian tribal weavings	0.60	Collard et al. (2006)
11	Northwest Coast archaeology	0.50	Collard et al. (2006)
12	Pomo structures	0.52	Collard et al. (2006)
13	Oregon Coast tribal puberty rites	0.55	Collard et al. (2006)
14	Southern Sierra Nevada tribal death and mourning practices	0.48	Collard et al. (2006)
15	Nevada Shoshoni tribal mutilations	0.78	Collard et al. (2006)
16	Southern California tribal body- and dress-related practices	0.52	Collard et al. (2006)
17	Yuman-Piman warfare-related practices	0.69	Collard et al. (2006)
18	Apache-Pueblo houses	0.63	Collard et al. (2006)
19	African cultural practices	0.42	Collard et al. (2006)
20	Northern Paiute birth rituals	0.43	Collard et al. (2006)
21	Northeastern Missouri projectile points	0.66	Darwent and O'Brien (2006)
22	Baltic psaltery	0.54	Temkin and Eldredge (2007)
23	Cornets	0.80	Temkin and Eldredge (2007)
24	Palaeolithic stone tools	0.66	Lycett (2007)
25	Linear B scripts	0.65	Skelton (2008)

[a] RI = Retention Index. A maximum RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0.

biological data sets was assessed with the Mann-Whitney U-test function of SPSS 12.0.1. The RIs for the two chimpanzee cladograms were computed in MacClade 4.02 (Maddison and Maddison, 2001).

Chimpanzee culture and adaptation

To investigate whether chimpanzee culture is adaptive, two phenograms were constructed via a cluster analysis (nearest neighbour method) of the mean annual rainfall at the seven ingroup study sites. Rainfall data were taken from McGrew et al. (1996). One of the phenograms included all seven populations and the outgroup; the other used just the five East African (*P. t. schweinfurthii*) study groups and the outgroup. The phenograms were then converted into cladograms by rooting them on the outgroup (Figs. 1 and 2). This was carried out in MacClade 4.02 (Maddison and Maddison, 2001). Subsequently, the model cladograms were imported into PAUP* 4.0 (Swofford, 1998) and compared to the relevant MP cladogram using the Kishino-Hasegawa (K-H) test (Kishino and Hasegawa, 1989). In this study, it was predicted that if chimpanzee culture is adaptive, the MP cladograms should not be statistically different from the rainfall cladogram ($\alpha = 0.05$).

Results

Testing the genetic hypothesis

During the PTP test of the multiregion character matrix, 9513 cladograms were found to be longer than the MP cladogram (MP TL [tree length] = 177; shortest tree = 167; longest tree = 193). Hence, 95.13% of the 10,000 trees drawn from the permuted data matrix

Table 2
Retention Indices associated with most parsimonious cladograms derived from 25 biological data sets[a]

#	Data set	RI	Source of RI
1	Australasian teal mtDNA	0.94	Collard et al. (2006)
2	Corbiculate bee behaviour	0.94	Collard et al. (2006)
3	Pelecaniforme bird behaviour	0.84	Collard et al. (2006)
4	Anoles lizards morphology	0.79	Collard et al. (2006)
5	Primate behaviour	0.73	Collard et al. (2006)
6	Strepsirhine primate morphology	0.72	Collard et al. (2006)
7	Fossil hominid morphology	0.71	Collard et al. (2006)
8	New World monkey morphology	0.70	Collard et al. (2006)
9	Ungulate morphology	0.70	Collard et al. (2006)
10	Phalacrocoracid bird mtDNA	0.65	Collard et al. (2006)
11	Phocid seal morphology	0.60	Collard et al. (2006)
12	Hawaiian fruitfly mtDNA	0.50	Collard et al. (2006)
13	Hominoid primate cranial morphology	0.49	Collard et al. (2006)
14	Carnivore mtDNA	0.47	Collard et al. (2006)
15	Mammal mtDNA with emphasis on Malagasy primates	0.47	Collard et al. (2006)
16	Carnivore mtDNA with emphasis on Malagasy taxa	0.47	Collard et al. (2006)
17	Mammal mtDNA	0.44	Collard et al. (2006)
18	Insectivore mtDNA	0.44	Collard et al. (2006)
19	Lagomorph mtDNA	0.39	Collard et al. (2006)
20	Hominoid primate soft-tissue morphology	0.38	Collard et al. (2006)
21	Anoles lizard mtDNA	0.35	Collard et al. (2006)
22	Tetrapod ribosomal RNA	0.75	Calculated from Hedges et al.'s (1990) data.
23	Fossil hominin craniodental data	0.68	Calculated from Strait et al.'s (1997) data.
24	Annelid DNA	0.63	Calculated from Halanynch et al.'s (2001) data.
25	Fossil hominin craniodental data	0.45	Calculated from Wood's (1992) data.

[a] RI = Retention Index.

were longer than the MP cladogram. This indicates that the data set contains a significant phylogenetic signal, which in turn indicates that the topology of the multiregion MP cladogram obtained by Lycett et al. (2007) was not merely the result of random factors but driven by the internal structure of the data set. During the PTP test including only the five East African populations, 9844 cladograms
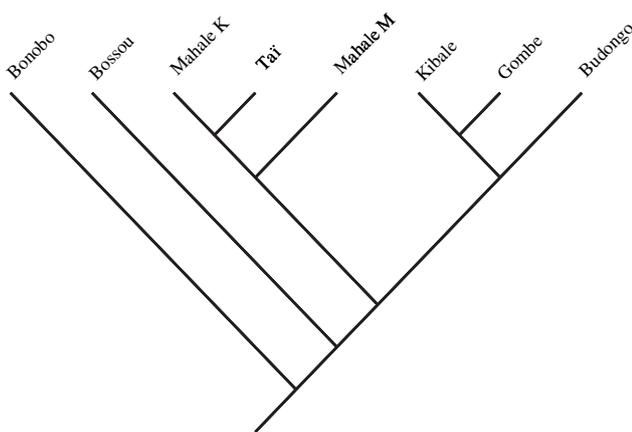
Fig. 1. Model cladogram based on nearest neighbour clustering of mean annual rainfall at the five Eastern African (*P. t. schweinfurthii*) and two Western African (*P. t. verus*) chimpanzee study sites.
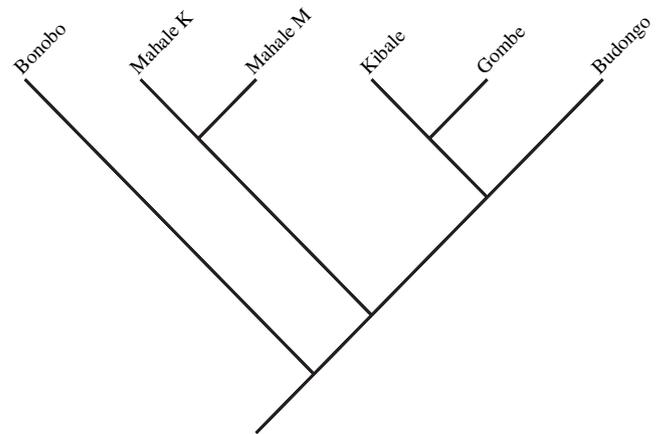
Fig. 2. Model cladogram based on nearest neighbour clustering of mean annual rainfall at the five Eastern African (*P. t. schweinfurthii*) study sites.

were found to be longer than the MP tree (MP TL = 107; shortest tree = 102; longest tree = 120). Thus, 98.44% of the cladograms drawn from the permuted data matrix were longer than the MP cladogram. These results indicate a stronger phylogenetic signal within the character matrix when only the five East African populations are analysed. This in turn suggests that the regional, within-subspecies phylogenetic signal is stronger than the phylogenetic signal present in the multiregion, two-subspecies data set. This contradicts the predictions of the genetic hypothesis.

Figure 3 shows the 50% majority rule consensus cladogram computed from the bootstrap cladograms yielded by the 10,000 pseudoreplicates of the multiregion data set. Only one clade (the Mahale M and K group clade) was supported in more than 50% of the bootstrap replicates, and only in 52% of the cases. This indicates that the topological structure of the MP cladogram is not robustly supported. In contrast, Figure 4 shows the 50% majority rule consensus cladogram computed from the cladograms yielded by the 10,000 bootstrap pseudoreplicates of the regional data set. All of the nodes of this cladogram are more robustly supported than the nodes of the 50% majority rule cladogram obtained when both East and West African populations were analysed together. These results are also contrary to the predictions of the genetic hypothesis.

Thus, the results of our first set of analyses are consistent with the results of our previous study (Lycett et al., 2007). They also refute the genetic hypothesis and offer support for the hypothesis that the interpopulation differences in chimpanzee behaviour that have been observed are the result of social learning. Accordingly, there are grounds for considering at least one nonhuman primate species to have culture, and to begin the process of developing an integrated approach to the study of culture in modern humans, fossil hominins, and apes.

Cultural transmission processes among chimpanzees

A single most parsimonious cladogram was returned by the parsimony analysis in which only cladograms that contained a clade comprising eastern populations and one consisting of western populations were accepted (Fig. 5). The K-H test indicated that this cladogram and the multiregion MP cladogram are not significantly different (length difference = 1; s.d. difference = 3.36; $t = 0.298$; $p = 0.77$). This is consistent with the hypothesis that the evolution of chimpanzee cultural diversity has been dominated by vertical intergroup transmission.
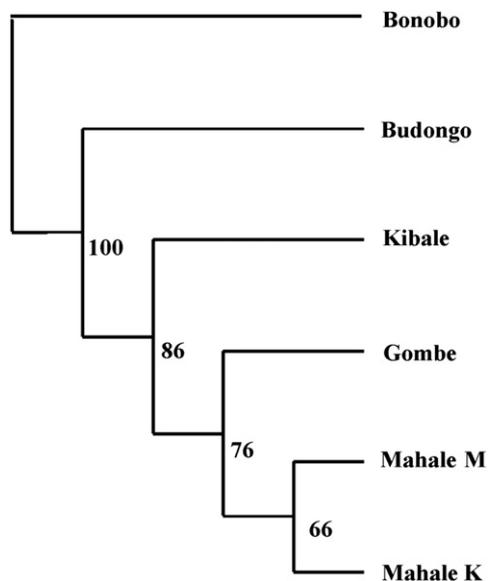
The RIs associated with the most parsimonious cladograms derived from the human cultural and the biological data sets suggest
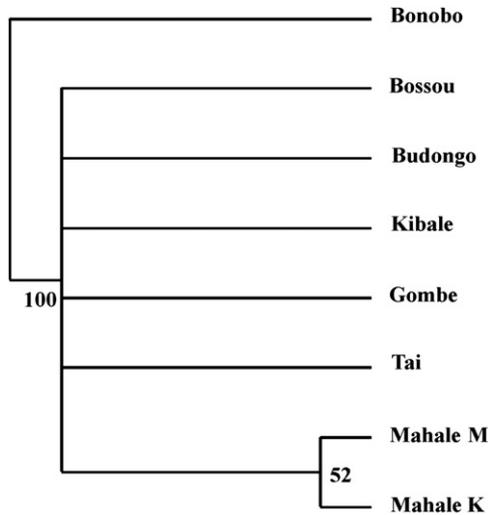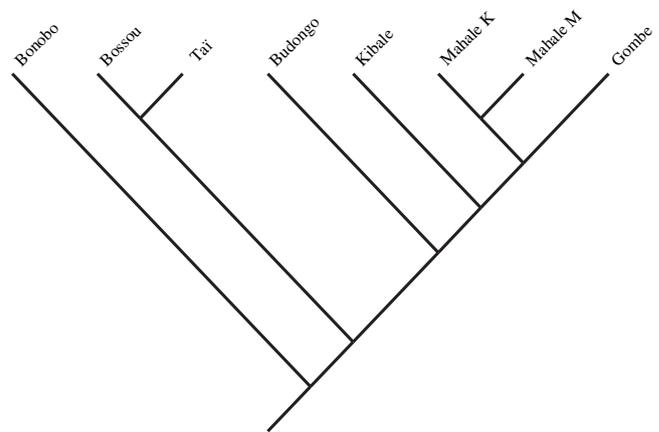
Fig. 3. 50% Majority Rule consensus cladogram of 10,000 bootstrap replications using five Eastern African (*P. t. schweinfurthii*) and two Western African (*P. t. verus*) chimpanzee groups.

Fig. 5. Model cladogram that clusters chimpanzee groups into eastern and western subspecies. This cladogram was constructed by importing a cladogram with an unresolved eastern clade and a western clade into PAUP* as a constraint cladogram and searching for the MP cladogram within those constraints. The cladogram shown in this figure is not significantly different from the MP cladogram yielded by the multiregion data set when constraints were not employed, according to the K-H test.

that the fit between the bifurcating tree model and the human cultural data sets is little different from the fit between the bifurcating tree model and the biological data sets. Not only are the averages similar, but also the ranges are comparable. The RIs for the 25 human cultural data sets range from 0.42 to 0.80. The mean RI for the human cultural data sets is 0.60. The RIs for the biological data sets range from 0.35 to 0.94. Their mean RI is 0.61. Thus, on average, the human cultural data sets appear to be no more reticulate than the biological data sets. The result of the Mann-Whitney U-test is in line with the descriptive statistics. The biological and cultural RIs are not significantly different according to the test (Mann-Whitney U = 308, p = 0.930). These results are consistent with the hypothesis that the human cultural data sets have been structured by vertical intergroup transmission.

The multiregion chimpanzee culture cladogram returned an RI of 0.44, while the regional chimpanzee culture cladogram returned an RI of 0.53. Thus, both chimpanzee RIs fall within the range of RIs

yielded by the human cultural data sets, and the RI for the regional chimpanzee cultural cladogram is close to the mean of the human cultural RIs. This suggests that the chimpanzee cultural data are as tree-like as human cultural data sets. This in turn implies that the differences in cultural behaviour among chimpanzee groups are also primarily the result of vertical intergroup transmission rather than horizontal intergroup transmission.

Chimpanzee culture and adaptation

The K-H test in which the multiregion cultural and environmental cladograms were compared suggested that the topologies of the two cladograms are significantly different (length difference = 23; s.d. difference = 10.98; t = 2.095; p = 0.043). In contrast, the K-H test in which the East African cultural and environmental cladograms were compared suggested that the topologies of the cladograms are not significantly different (length difference = 10; s.d. difference = 5.109; t = 1.9572; p = 0.06). Hence, the hypothesis that chimpanzee culture is adaptive is supported by the East African data set but not by the multiregion data set.

Discussion

In the first set of analyses reported here, we tested the hypothesis that intergroup variation in chimpanzee behaviour results from genetic differences as opposed to being the product of social learning. We reasoned that if the genetic hypothesis is correct, the phylogenetic signal should be stronger when data from two subspecies are analysed together compared to when data from one subspecies are analysed. Using randomisation procedures, we found that the phylogenetic signal was substantially stronger within a single subspecies rather than with two, which is contrary to the predictions of the genetic hypothesis. Thus, the first set of analyses refuted the genetic hypothesis and supported the suggestion that wild chimpanzee behavioural variation is cultural.

Having found additional support for the hypothesis that chimpanzees have culture, we then investigated how the processes that produce cultural variation among chimpanzee populations compare to the processes that give rise to cultural variation among human populations. The first analysis we carried out indicated that the similarities and differences in the behaviour of chimpanzee groups are consistent with the divergence of the western and eastern subspecies, which is what would be expected if vertical

Fig. 4. 50% majority rule consensus cladogram of 10,000 bootstrap replications using the five Eastern African (*P.t.schweinfurthii*) chimpanzee groups.

intergroup transmission has been the dominant process. Comparison of RI values from 25 human cultural data sets with 25 biological data sets revealed no significant difference. This implies that, on average, human cultural data fit a tree-like model as well as biological data, and that the former is no more reticulate than the latter. This in turn suggests that vertical intergroup transmission is the dominant mechanism involved in generating human cultural diversity. Both RIs from our cladistic analyses of chimpanzee behavioural data (i.e., both the RI for the multiregion data set and the RI for the East African data set) fall within the range of RIs yielded by the human cultural data sets. Moreover, the RI for the regional (*P. t. schweinfurthii*) cultural cladogram is close to the mean RI of the human cultural data sets. This suggests that the chimpanzee cultural data are as tree-like as the human cultural data sets, and in turn implies that chimpanzee cultural diversity is also primarily a result of vertical intergroup transmission.

Since aspects of human culture are frequently interpreted as being adaptive, we subsequently turned to the question of whether chimpanzee culture may also be fitness enhancing. We used the K-H test to compare the multiregion and East African cultural cladograms with cladograms constructed to reflect variation in a key environmental variable, rainfall. We found that the topologies of the East African cultural and environmental cladograms were not significantly different from each other, whereas the topologies of the multiregion cultural and environmental cladograms were. Thus, the hypothesis that chimpanzee culture is adaptive was supported by the analysis of the East African data set but not by the analysis of the multiregion data set.

Two issues need to be addressed before we discuss the implications of our results. One is how the behavioural/genetic mismatch that was documented by Lycett et al. (2007), and has been confirmed here, can be explained in terms of social learning. As we noted earlier, because social learning is model neutral, a phylogenetic mismatch between behavioural data and genetic data from the same set of taxa is not unexpected if the behaviours in question are socially learned. But it is still necessary to explain the divergence in terms of social learning processes.

Two observations need to be taken into account in any explanation of the behavioural/genetic mismatch. One is that chimpanzee males remain in their natal group (philopatry), while females usually emigrate on reaching sexual maturity. The other is that relations among males from different communities are (sometimes fatally) aggressive, and therefore not conducive to pro-social interaction. These observations are important because they constrain the possible routes of transmission of both genes and culture. The former suggests that females are the primary vectors of genetic transmission among populations, while the latter implies that females are also the primary vectors of interpopulation cultural transmission. Thus, the behavioural/genetic mismatch is likely a consequence of females transmitting genes among populations at a greater rate than they transmit culture.

One possible explanation for females transmitting genes among populations at a greater rate than they transmit culture is that after females disperse they abandon the behavioural patterns learned in their natal community and adopt the behaviours they encounter in their new community (McGrew et al., 2001). Another possibility is that females continue to employ the behaviours they learned from members of their natal community after they disperse, but are only rarely copied by members of their new community (Biro et al., 2006). A combination of the two is also feasible. All three hypotheses are consistent with recent experimental demonstrations that chimpanzees can engage in conformity biased cultural transmission (Whiten et al., 2005, 2007). However, discriminating among these hypotheses will require further longitudinal fieldwork. Specifically, it will require data on individual social learning strategies in wild chimpanzee populations in a similar manner to the way evolutionary anthropologists have begun to document individual social learning strategies in human populations (e.g., Hewlett and Cavalli-Sforza, 1986; Aunger, 2000; Tehrani and Collard, 2009).

The other issue that needs to be addressed before we consider the implications of our results is the higher level of homoplasy in the multiregional data set compared to the East African data set. One possible explanation for this finding is cultural adaptation to similar conditions. According to this hypothesis, shared characteristics of the environment have selected for the same cultural behaviours in at least one West African population and one East African population. While this hypothesis is plausible, it is not supported by the results of the analyses in which we compared the MP behavioural cladograms with cladograms constructed to reflect average annual rainfall. To reiterate, in these analyses we found that the topology of the East African behavioural cladogram was not significantly different from the topology of the East African rainfall cladogram, while the topology of the multiregion behavioural cladogram was significantly different from the multiregion rainfall cladogram. The latter finding is the reverse of what we would expect if the homoplasy in the multiregional behavioural data set is a result of cultural adaptation to shared environmental conditions.

This finding suggests either that the homoplasy in the multiregion data set is a result of cultural adaptation to some other ecological variable, or that cultural adaptation to shared ecological conditions does not explain the homoplasy in question. Other ecological variables that it would seem worth investigating include overall species diversity, number of plant species consumed, length of dry season, elevation, and habitat type. An alternative explanation for the higher level of homoplasy in the multiregion data set relative to the East African data set is demographic decline due to habitat loss (van Schaik, 2002; Wrangham, 2006). The idea that fluctuating demography influences cultural diversity has recently received attention in the anthropological and archaeological literature with regard to both human populations and Pleistocene hominins (Shennan, 2000, 2001; Henrich, 2004; Lycett and von Cramon-Taubadel, 2008). Sharp changes in chimpanzee demography, coupled with fragmentation of habitat, could accentuate stochastic processes of cultural variant loss analogous to those seen in the genetic structure of populations undergoing fragmentation and demographic decline (Gagneux, 2002). Population decline may have led to character losses in chimpanzee populations stochastically across Africa, resulting in homologies being erroneously identified as homoplasies. This hypothesis can be tested with correlation analysis. If it is correct, there should be a significant positive correlation between the number of cultural behaviours and population size.

The results of our first set of analyses have implications for the evolution of hominin cognition. It has long been assumed that the appearance of the first stone tool industry, the Oldowan, represents a significant event in human evolution and that this event is the result of an important cognitive change (e.g., Oakley, 1958; Tobias, 1991; Plummer, 2004). Our results are not inconsistent with either of these hypotheses, but they do cast some light on the nature of the putative cognitive change. By showing that wild chimpanzee behavioural variation is more consistent with the culture hypothesis than the genetic hypothesis, our results join a growing body of research on nonhuman primates challenging the assumption that culture is unique to hominins (e.g., Biro et al., 2003, 2006; van Schaik et al., 2003; Whiten et al., 2005, 2007). This in turn implies that if the appearance of the Oldowan reflects a cognitive change, that change is not the appearance of the cognitive machinery responsible for social learning (see also Wynn and McGrew, 1989; Panger et al., 2002; Toth et al., 2006).

The results of our first set of analyses also have implications for the use of chimpanzee and bonobo behavioural data in work on the evolution of hominin behaviour. As our closest extant relatives, members of the genus *Pan* have the potential to provide insights into the character states that are plesiomorphic for the hominin lineage (McGrew, 1992; Joulian, 1996; Moore, 1996; Stanford, 1996; Wrangham and Pilbeam, 2001). However, the results of our analyses indicate that a number of important chimpanzee behaviours have evolved since the chimpanzee and bonobo lineages separated from one another. The corollary of this is that the behaviours in question are unlikely to have been exhibited by the common ancestor of chimpanzees, bonobos, and hominins. This in turn suggests that early hominin species cannot simply be assumed to have behaved like contemporary chimpanzees or bonobos. We therefore need to model the evolution of hominin behaviour in such a way that we take into account the fact that chimpanzee and bonobo behaviour has changed in the five to eight million years since their lineage and the hominin lineage diverged. What this means in practice is that the reconstruction of behaviours that are plesiomorphic for hominins must incorporate a broader range of extant taxa than just chimpanzees and/or bonobos, and employ methods for explicitly reconstructing ancestral states on a phylogeny (e.g., Stevens and Heesy, 2006; Dalerum, 2007).

The results of our second set of analyses have implications for the taxonomy of *Pan*. Currently, there is considerable disagreement regarding the number of species and subspecies within the genus. For most of the 20th century, the conventional approach was to assign chimpanzees to *P. troglodytes* and bonobos to *P. paniscus*, and to then recognise three subspecies within *P. troglodytes*; *P. t. verus* in Western Africa, *P. t. troglodytes* in central Africa, and *P. t. schweinfurthii* in Eastern Africa (Schwarz, 1934; Hill, 1969; Fleagle, 1999). In recent years, a number of alterations to this scheme have been proposed. Some researchers have argued in favour of recognising greater taxonomic diversity within *Pan*. For example, Morin et al. (1994) have proposed raising *P. t. verus* to species status on the basis of its marked genetic differentiation from *P. t. troglodytes* and *P. t. schweinfurthii*, while Groves (2001), Grubb et al. (2003), and Gonder et al. (2006) have suggested that it may be appropriate to divide *P. t. verus* into two subspecies, *P. t. verus* and *P. t. vellerosus*. Other researchers have argued that the conventional scheme overstates the taxonomic diversity of *Pan*. For instance, Gagneux et al. (1999) and Won and Hey (2005) have suggested that *P. t. troglodytes* and *P. t. schweinfurthii* are insufficiently genetically distinct to be considered separate subspecies. Fischer et al. (2006) have gone further. They have averred that the genetic differentiation among the conventionally-recognised subspecies of *P. troglodytes* is so limited that none of them is valid.

It has been suggested in the context of this debate that there are no consistent behavioural differences among the conventionally-recognised subspecies of chimpanzee (Fischer et al., 2006). If this were the case, it would support the idea of abandoning the subspecies. However, the results of the first analysis we carried out to evaluate the relative contribution of vertical intergroup and horizontal intergroup transmission to the diversification chim-panzee cultural behaviour suggest this claim is incorrect. That we found the multiregion MP cladogram and the constraint cladogram to be statistically indistinguishable indicates there are in fact consistent differences between *P. t. schweinfurthii* and *P. t. verus*. Thus, when the cultural data are analysed phylogenetically they support the existence of at least two subspecies of chimpanzee, contrary to the claims of Fischer et al. (2006).

The results of our second set of analyses also have implications for the link between hominin taxa and archaeological industries. The finding that the chimpanzee cultural diversity tracks the divergence of subspecies (Fig. 6) lends credibility to the notion that variability in

Palaeolithic material culture may, to some extent, reflect species and subspecies variation in hominin populations (Foley, 1987, 2002; Kuhn, 2004; Delagnes and Roche, 2005). While it is still necessary to demonstrate the existence of links between Palaeolithic archaeological variability and fossil hominin taxa, the results of our study suggest that rejecting such links a priori (e.g., Clark, 1989; Lieberman and Bar Yosef, 2005) is perhaps unwise. Rather, it should be a legitimate goal within palaeoanthropology to determine those instances in which cultural patterns match biological evolutionary patterns, as well as identifying instances in which they do not.

Lastly, like our first set of analyses, our second set of analyses have implications for the evolution of hominin cognition. As noted earlier, in recent years it has become clear that contrary to what archaeologists and anthropologists assumed for much of the 20th century, vertical intergroup cultural transmission is important in humans. It has been hypothesised that vertical intergroup transmission is important in humans because their cognition has been uniquely shaped by natural selection to preferentially copy behaviours exhibited by the majority of the members of their group (Henrich and Boyd, 1998; Efferson et al., 2008; McElreath and Strimling, 2008; O'Gorman et al., 2008). However, on the basis of transmission experiments undertaken in captive chimpanzee groups, Whiten et al. (2005) suggest that chimpanzees are also capable of modifying a learned behavioural pattern to conform with a dominant alternative. Our finding that vertical intergroup transmission has been more important than horizontal intergroup transmission in generating the cultural similarities and differences
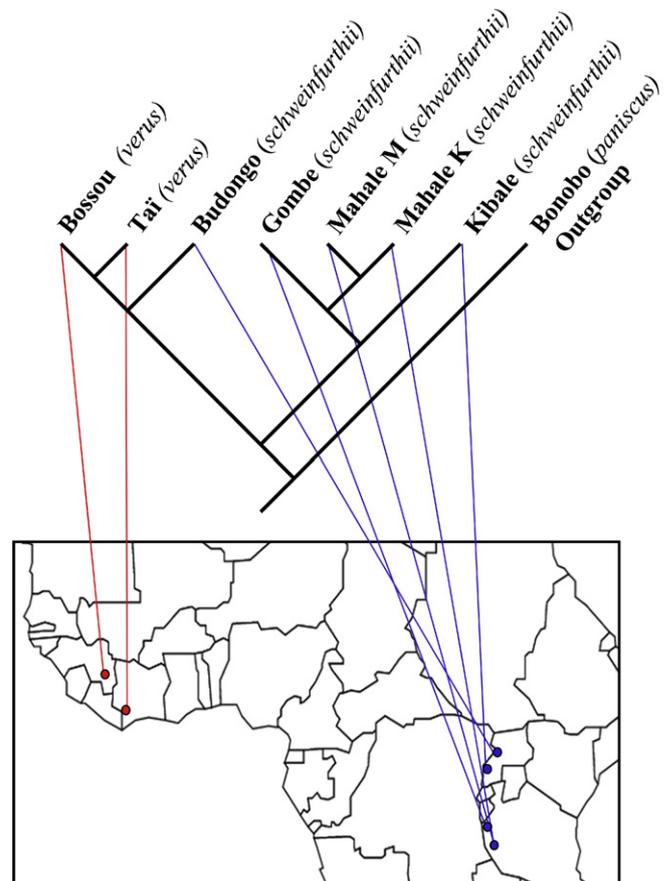
Fig. 6. The phylogeography of chimpanzee cultural variation. The most parsimonious cladogram yielded by the multiregion data set is consistent with the subspecies/geographic division between *P. t. schweinfurthiii* in Eastern Africa and *P. t. verus* in Western Africa, apart from the position of the *P. t. schweinfurthii* group from Budongo.

among chimpanzee populations is also consistent with the possibility that an evolved cognitive bias for conformist transmission is not unique to modern humans. Together, the results of our study and those of Whiten et al. (2005, 2007) suggest that such a cognitive bias may be present in chimpanzees and bonobos and, in turn, have been present in the common ancestor of chimpanzees and the other fossil hominins that form the human lineage.

Acknowledgements

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