

Are Behavioral Differences Among Wild Chimpanzee Communities Genetic Or Cultural? An Assessment Using Tool-Use Data and Phylogenetic Methods

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ABSTRACT Over the last 30 years it has become increasingly apparent that there are many behavioral differences among wild communities of *Pan troglodytes*. Some researchers argue these differences are a consequence of the behaviors being socially learned, and thus may be considered cultural. Others contend that the available evidence is too weak to discount the alternative possibility that the behaviors are genetically determined. Previous phylogenetic analyses of chimpanzee behavior have not supported the predictions of the genetic hypothesis. However, the results of these studies are potentially problematic because the behavioral sample employed did not include communities from central Africa. Here, we present the results of a study designed to address this shortcoming. We carried out cladistic analyses of presence/absence data pertaining to 19 tool-use behaviors in 10 different *P. troglodytes* communities plus an outgroup

(*P. paniscus*). Genetic data indicate that chimpanzee communities in West Africa are well differentiated from those in eastern and central Africa, while the latter are not reciprocally monophyletic. Thus, we predicted that if the genetic hypothesis is correct, the tool-use data should mirror the genetic data in terms of structure. The three measures of phylogenetic structure we employed (the Retention Index, the bootstrap, and the Permutation Tail Probability Test) did not support the genetic hypothesis. They were all lower when all 10 communities were included than when the three western African communities are excluded. Hence, our study refutes the genetic hypothesis and provides further evidence that patterns of behavior in chimpanzees are the product of social learning and therefore meet the main condition for culture. *Am J Phys Anthropol* 142:461–467, 2010. © 2010 Wiley-Liss, Inc.

Many behavioral differences exist among wild-living chimpanzee communities (Whiten et al., 1999, 2001; Schöning et al., 2008). Some behavioral patterns are seen at some sites but not others. Chimpanzees at Bossou (Guinea), for example, detach fronds from an oil-palm and use them to smash the plant's crown to produce a pulpy mass for consumption (Yamakoshi and Sugiyama, 1995). This activity has not been recorded at any other long-term study site, although oil-palms are common throughout sub-Saharan Africa (McGrew, 1992). The way in which some behaviors are performed also varies among sites. Nut cracking exemplifies this: Only stone hammers and anvils are used to open nuts at Bossou (Matsuzawa, 1994). In contrast, at Tai (Côte d'Ivoire) both wooden and stone hammers as well as root and stone anvils are employed to crack nuts (Boesch and Boesch-Achermann, 2000). So far, at least 65 behaviors have been found to vary among the six major chimpanzee study sites (Whiten et al., 1999, 2001).

Opinions differ regarding the nature of these behavioral differences. Some researchers contend that many of the behavioral differences among the sites are likely to be socially learned and so meet the main necessary condition for culture. This claim is based on results of the application of the "method of exclusion" (e.g. McGrew, 1992, 2004; Whiten et al., 1999, 2001; Boesch, 2003; Whiten, 2005; Möbius et al., 2008; Schöning et al., 2008).

In this method, sites are compared to identify behaviors that occur at high frequency in some but not all sites. Then, an attempt is made to exclude behaviors whose variation can potentially be explained in terms of environmental differences among the sites. The remaining behaviors are deemed to be socially learned on the grounds that social learning is the only other process that can account for a behavior being exhibited by multiple members of one group but not by the members of another group. Other researchers are skeptical that the behaviors are socially learned (Laland and Hoppit, 2003;

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Laland and Janik, 2006; Galef, 2009; Laland et al., 2009). These researchers point out that a third of the putative cultural behaviors occur in a single subspecies, and that genetic studies suggest the some of 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 behavioral differences cannot be dismissed.

Recently we have reported two studies in which we carried out cladistic analyses of the major, multi-site behavioral dataset (Whiten et al., 1999) to test a key prediction of the claim that the inter-community variation in chimpanzee behavior is genetically determined (Lycett et al., 2007, 2009). Whiten et al.'s (1999) dataset records the prevalence of 65 behaviors among seven chimpanzee groups. Five of these are from East Africa and are *Pan troglodytes schweinfurthii*; the other two are in West Africa and are *Pan troglodytes verus*. In our studies, we focused on 39 behaviors that meet the criteria for being considered cultural according to Whiten et al. (1999).

The prediction tested in the two studies was that the prevalence data for the 39 behaviors should mirror the available genetic data in terms of phylogenetic structure. Genetic studies indicate that chimpanzees living in East and West Africa are well differentiated from each other, while the communities in East Africa cannot be distinguished (Morin et al., 1994; Goldberg and Ruvolo, 1997; Gagneux et al., 2001; Gonder et al., 2006). Thus, we reasoned that, if the genetic hypothesis is correct, the behavioral data should exhibit more phylogenetic structure when communities from both eastern and western Africa are included in the sample than when the sample is restricted to eastern African communities.

In the first study, we ran cladistic analyses with and without the western African communities, and then compared the Retention Indices of the most parsimonious cladograms. The Retention Index (RI) is a measure of the number of homoplastic changes a cladogram requires that are independent of its length (Farris, 1989a,b). As such, it indicates how well the similarities and differences among a group of taxa can be explained by a given phylogenetic hypothesis. The results of the analysis contradicted the prediction of the genetic hypothesis. The RI for the cladogram obtained in the continental analysis was markedly lower than the RI for the cladogram derived from the East African dataset.

In the second study, we repeated the comparison of the continental and East African datasets with two additional means of evaluating the phylogenetic structure of a dataset, the permutation tail probability (PTP) test and the bootstrap. The results we obtained were consistent with the results of our RI analysis: the eastern African dataset exhibited more phylogenetic structure than the continental dataset.

Although these studies cast doubt on the validity of the genetic hypothesis, they suffered from an obvious shortcoming, namely that Whiten et al.'s (1999) sample did not include groups from central Africa. Here, we report a third evaluation of the genetic hypothesis that addressed this shortcoming. We carried out the study in the same manner as our previous tests of the genetic hypothesis, but used a dataset that focused on tool use. The dataset was restricted to tool-use behaviors because central African chimpanzees have been studied much less intensively than those in east and west Africa, and tool use is the only category of behavior for which sufficient data have been published to enable a robust cladis-

tics-based test of the genetic hypothesis to be carried out. Focusing on tool use reduced the number of behaviors compared to our previous attempts to test the genetic hypothesis but allowed us to include a larger number of groups, including two from central Africa.

As noted above, genetic studies indicate that chimpanzees living in western and eastern Africa are well differentiated from each other. The genetic evidence also suggests that western and central African chimpanzees are well differentiated from each other (Gonder et al., 2006). Conventionally, chimpanzees from central and eastern Africa have been assigned to different subspecies. However, this is not supported by phylogenetic analyses of mitochondrial DNA, which suggest that central and eastern African chimpanzees are not reciprocally monophyletic (Gagneux et al., 1999, 2001; Gonder et al., 2006). Given that genetic studies suggest there is a phylogenetic split between western African chimpanzees on the one hand, and central and eastern African chimpanzees on the other, but no such split between central and eastern African chimpanzees, we reasoned that, if the genetic hypothesis is correct, the tool-use data should exhibit more phylogenetic structure when all the communities are included than when just the central and eastern African communities are included.

MATERIALS AND METHODS

The character state data matrix used in the study is presented in Table 1. It records the occurrence of 19 tool-use behavioral patterns at 10 chimpanzee study sites and also in an outgroup, the bonobo (*Pan paniscus*). The chimpanzee study sites are Bossou, Tai Forest, Assirik (Senegal), Gombe (Tanzania), Mahale K-group (Tanzania), Mahale M-group (Tanzania), Kibale Forest Kanyawara community (Uganda), Budongo Forest (Uganda), Goualougo (Republic of Congo), and Lopé (Gabon). The locations of these sites are shown in Figure 1. The bonobo was chosen as the outgroup because it is the chimpanzee's closest living relative. The 19 tool-use behaviors are a subset of the 39 behaviors that meet Whiten et al.'s (1999) criteria for being considered cultural. Thus, their intercommunity variation does not seem to be influenced by environmental constraints (i.e. biotic or abiotic factors that prevent behaviors from being expressed at all sites where they are absent). Table 2 gives details of the behaviors. Following Sanz and Morgan (2007), character states were coded as 0 = absent, 1 = rare, 2 = regular, and ? = status uncertain. The chimpanzee data were obtained from Whiten et al. (1999, 2001) and Sanz and Morgan (2007). The bonobo data are Hohmann and Fruth's (2003) pooled data for the *Pan paniscus* communities of Lomako and Wamba (Democratic Republic of Congo).

As in our other tests of the genetic hypothesis, the data were analyzed with cladistic methods. We carried out three analyses. These were conducted with the aid of PAUP* 4.0 (Swofford, 2003) and MacClade 4.02 (Maddison and Maddison, 1998). PAUP* 4.0's branch-and-bound search algorithm was used to identify the most parsimonious cladograms, and characters were treated as ordered and freely reversing (Slowinski, 1998).

The first analysis employed the RI. As mentioned earlier, the RI quantifies the number of homoplastic changes a cladogram requires independent of its length (Farris, 1989a,b). The RI of a single character is calculated by subtracting the number of character state changes

TABLE 1. Character matrix used in phylogenetic analyses

	Tai	Bossou	Assirik	Goualougo	Lopé	Gombe	Mahale M	Mahale K	Kibale	Budongo	Bonobo
Ant dip, single	2	2	0	2	0	1	0	0	0	0	0
Ant dip, wipe	0	1	2	2	0	2	0	0	0	0	0
Ant fish	0	1	2	?	2	1	2	2	0	0	0
Bee probe	2	0	?	?	?	0	0	1	0	0	0
Expel/stir	2	0	?	?	?	2	2	2	0	0	0
Fluid dip	2	0	2	1	2	2	2	2	2	0	0
Lever open	2	0	?	2	2	2	0	0	0	0	0
Marrow pick	2	0	?	1	?	0	0	0	0	0	0
Nut hammer	2	2	0	0	0	0	0	0	0	0	0
Pestle pound	0	2	0	0	0	0	0	0	0	0	0
Termite fish	0	1	2	2	0	2	0	2	0	0	0
Leaf dab	1	0	?	1	?	1	0	0	2	0	0
Leaf napkin	1	0	1	1	?	2	1	0	2	2	0
Self tickle	0	0	?	1	?	2	0	0	0	0	0
Fly whisk	2	0	?	?	?	1	0	0	0	2	1
Seat vegetation	2	1	?	1	0	0	0	0	1	0	1
Aimed throw	2	2	1	2	?	2	2	0	1	1	1
Club	2	1	?	?	?	2	1	0	0	0	0
Leaf clip	2	2	?	?	0	0	2	2	2	2	1

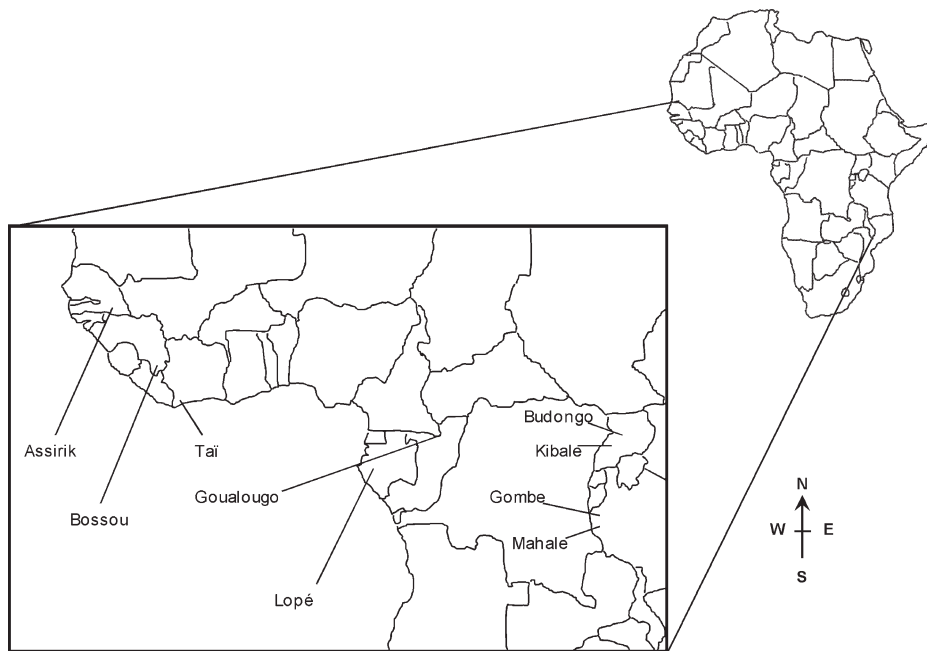


Fig. 1. Study-sites of *Pan troglodytes* communities used in this study.

required by the focal cladogram (*s*) from the maximum possible amount of change required by a cladogram in which all the taxa are equally closely related (*g*). This figure is then divided by the result of subtracting the minimum amount of change required by any conceivable cladogram (*m*) from *g*. The RI of two or more characters is computed as $(G - S)/(G - M)$, where *G*, *S*, and *M* are the sums of the *g*, *s*, and *m* values for the individual characters. An RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0. The RI is a useful goodness-of-fit measure when comparing different datasets because, unlike some alternative measures, it is not affected by number of taxa or characters.

We began by identifying the most parsimonious cladogram with all 10 chimpanzee communities included in the data matrix. We then ran another parsimony

analysis after removing the three western African study groups (Assirik, Bossou, and Tai) from the data matrix. Next, we computed the RIs for the most parsimonious cladograms. Lastly, we compared the two RIs. The prediction was that the RI of the most parsimonious cladogram yielded by the continental data matrix should be higher than the RI of the most parsimonious cladogram yielded by the central and eastern African data matrix.

In the second analysis, we employed the permutation tail probability (PTP) test. The PTP test is designed to indicate the strength of the phylogenetic signal in a given data matrix (Archie, 1989; Faith, 1991; Faith and Cranston, 1991). The PTP test reshuffles the original data matrix without replacement, creating a predefined number of pseudo-replicate data matrices. A most parsimonious cladogram is then computed for each pseudo-

TABLE 2. Tool-use behavioral patterns employed in cladistic analyses

Behavior	Description
1. Ant dip, single	Use stick to collect army ants, then pick off with lips and eat
2. Ant dip, wipe	Use wand to collect army ants, then manually wipe ants off wand and eat
3. Ant fish	Probe to extract arboreal ant from tunnels in nests
4. Bee probe	Test for presence and subsequent disabling of bees by probing nest entrance with stick
5. Expel/stir	Insert and probe vigorously with stick to expel or stir up insects or other prey in cavity
6. Fluid dip	Probe to extract fluid (e.g. honey)
7. Lever open	Lever with stick to enlarge insect or bird nest-entrance
8. Marrow pick	Probe to extract contents from bones or crania of prey
9. Nut hammer	Stone/wood hammer on stone/wood/hard-ground anvil to crack open nut
10. Pestle pound	Mash palm crown with petiole
11. Termite fish	Use probe to extract termites from tunnels in mounds
12. Leaf dab	Touch leaves to wound, then examination or chewing of leaves
13. Leaf napkin	Clean body surface with leaf
14. Self tickle	Use object to tickle self
15. Fly whisk	Use twig with leaves to drive away flies
16. Seat vegetation	Detach large leaves and place on (wet) ground, then use as seat
17. Aimed throw	Throw deliberately object with clear aim at target
18. Club	Strike forcefully with stick
19. Leaf clip	Noisily rip leaf to gain attention

Further descriptions of these behaviors are in Whiten et al. (2001) and in Sanz and Morgan (2007).

replicate data matrix. Thereafter, the lengths of the cladograms generated from the permuted data matrices are compared with the length of the most parsimonious cladogram(s) yielded by the original data matrix. The number of most parsimonious cladograms produced from the pseudo-replicate data matrices that are the same length as or shorter than the most parsimonious cladogram(s) yielded by the original data matrix indicates the strength of the phylogenetic signal in the dataset.

We ran two 10,000-replication PTP tests. In the first, we included all 10 chimpanzee communities. In the second, we included only the central and eastern African communities. Subsequently, we compared the numbers of cladograms derived from the permuted data matrices that are shorter than the most parsimonious cladogram derived from the original data matrix. The prediction was that fewer MP cladograms derived from the permuted matrices should be shorter than the MP cladogram when all the communities are included than when just the central and eastern African communities are included.

In the third analysis, we used bootstrapping. In cladistics, bootstrapping is used to assess the level of support for the clades of a given cladogram (Kitching et al., 1998). Bootstrapping proceeds by randomly sampling with replacement from the original data matrix to create a large number of new data matrices with the same number of characters as the original data matrix. Next, the bootstrap data matrices are subjected to parsimony analysis. Subsequently, a consensus cladogram is generated from the most parsimonious cladograms yielded by the bootstrap data matrices. The number of bootstrap cladograms in which a given clade appears is taken to indicate how well the clade is supported.

We began by subjecting the continental data matrix to a 10,000-replication bootstrap analysis. We then repeated the analysis after removing the three West African chimpanzee communities. Lastly, we calculated the average bootstrap value for the two consensus bootstrap cladograms. The prediction was that the average bootstrap value for the continental data matrix should be higher than the average bootstrap value for the central and eastern African data matrix.

RESULTS

The continental data matrix yielded three equally parsimonious cladograms. These had a length of 69 steps and an RI of 0.56 (see Fig. 2). The central and eastern African data matrix produced a single most parsimonious cladogram (see Fig. 3). This cladogram was 43 steps long and had an RI of 0.68. Thus, contrary to expectation, the RI yielded by the continental data matrix was lower than the RI yielded by the central and eastern African data matrix.

In the continental PTP test, 52 cladograms derived from the permuted data matrices were shorter than the most parsimonious cladogram yielded by the original data matrix ($P = 0.0128$). In the central and eastern African PTP test, only one cladogram derived from the permuted data matrix was shorter than the most parsimonious cladogram yielded by the original data matrix ($P = 0.0006$). This indicates that the continental data matrix contains a weaker phylogenetic signal than the central and eastern African data matrix. Thus, the results of the PTP analysis were also inconsistent with the predictions of the genetic hypothesis.

Figure 4 shows the majority-rule consensus cladogram derived from the bootstrap analysis of the continental data matrix. None of the clades in this cladogram was supported by more than 50% the bootstrap replicates. The majority-rule consensus cladogram obtained in the bootstrap analysis of the eastern and central data matrix is presented in Figure 5. All of the clades in this cladogram were supported by more than 50% of the bootstrap replicates. Thus, the average bootstrap value for the bootstrap cladogram derived from the continental data matrix was lower than the average bootstrap value for the bootstrap cladogram derived from the central and eastern African data matrix. Again, this is contrary to the predictions of the genetic hypothesis.

DISCUSSION

The results of the three analyses were congruent. In the RI analysis, the continental data matrix yielded a lower RI than the central and eastern African dataset, which is the reverse of the pattern predicted by the

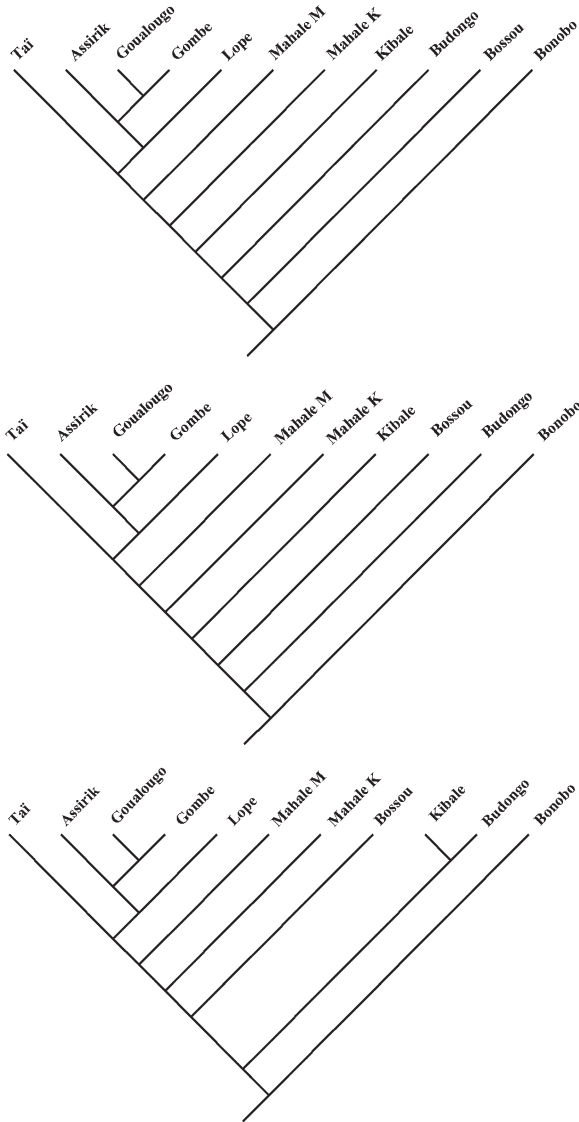


Fig. 2. Maximum parsimony (MP) trees for all taxa (Tree Length = 69; RI = 0.56).

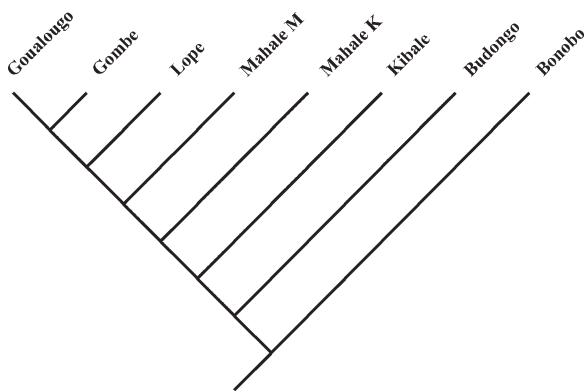


Fig. 3. Single MP tree produced during analyses of central and east African taxa only (Tree Length = 43; RI = 0.68).

genetic hypothesis. In the PTP test, a larger number of the cladograms derived from the permuted data matrices were shorter than the most parsimonious cladogram

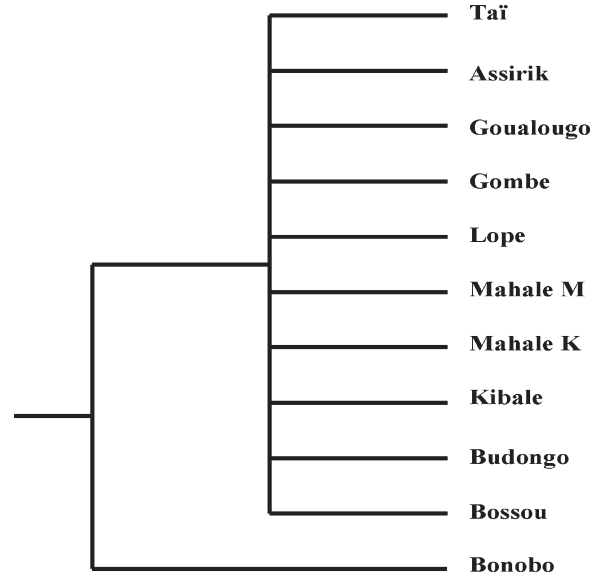


Fig. 4. Fifty percent majority-rule bootstrap consensus tree (10,000 bootstrap replications) including all 10 ingroup taxa.

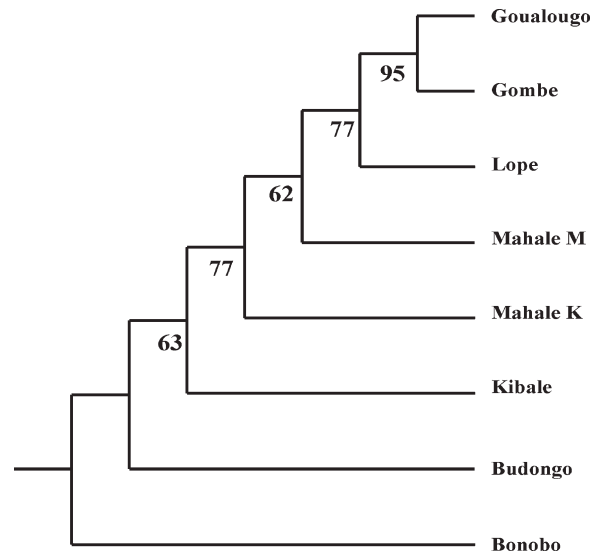


Fig. 5. Fifty percent majority-rule bootstrap consensus tree (10,000 bootstrap replications) including only central and western communities.

derived from the original data matrix in the analysis of the continental data matrix than in the analysis of the central and east African data matrix. This too is the reverse of what is predicted by the genetic hypothesis. The bootstrap analysis returned lower average bootstrap values for the continental data matrix than for the central and east African data matrix. Once again, this is the reverse of what is predicted by the genetic hypothesis. Thus, all three analyses contradicted the predictions of the genetic hypothesis.

It is important to note that it is not necessary for the RI, PTP, and bootstrap values yielded by the central and east African dataset to be statistically significantly higher than the RI, PTP, and bootstrap values yielded by the continental dataset in order for the analyses to dis-

prove the genetic hypothesis. The genetic hypothesis predicts a *decrease* in phylogenetic structure when using the central and east African dataset compared with the continental dataset. Thus, even if the RI, PTP, and bootstrap values yielded by the two datasets were statistically indistinguishable, they would still contradict the predictions of the genetic hypothesis.

It thus appears that the results of our previous assessments of the genetic hypothesis were not biased by the lack of data from central African communities. The analyses reported here show that even when data from central African communities are included, the intercommunity variation in behavior is not consistent with the predictions of the genetic hypothesis. Given that the genetic hypothesis was proposed as an alternative to Whiten et al.'s (1999) suggestion that the 39 behaviors they found to vary among wild chimpanzee communities independent of environmental constraints are socially learned and therefore cultural, the obvious corollary of this is that there is now more reason to accept the idea that wild chimpanzees engage in social learning and have culture.

The notion that chimpanzees have culture has a number of important implications. Many of these have been discussed by McGrew (1992, 2004) and Whiten (2005). Here, we will highlight one that seems to have been overlooked so far for apes, although it has been broached for cetaceans (Whitehead, 1998). If chimpanzees engage in social learning in the wild, then they effectively have two inheritance systems, a genetic one and a cultural one (Boyd and Richerson, 1985). This is important because it increases the number of processes that have to be considered when trying to explain chimpanzee gene frequencies and phenotypic characteristics. Most obviously, it means we have to allow for the possibility that a given behavior is prevalent as a consequence of social learning processes rather than differential reproduction. Less obviously but equally importantly, it means we also have to consider the possibility that a given gene, morphological feature, or physiological process may have coevolved with a socially learned behavior. Many examples of this phenomenon have been documented in modern humans, and it is clear that it can have important effects (Richerson and Boyd, 2005). In short, if chimpanzees are cultural animals, we have to change the way we analyze their evolution.

With regard to further research, the issue that stands out is how the mismatch between the behaviors and genes arose. Because individuals with the ability to acquire information socially have the option to copy distantly related kin and even unrelated individuals, a mismatch between behavioral and genetic data from the same set of taxa is not unexpected if the behaviors in question are socially learned. However, 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 behavioral/genetic mismatch. One is that chimpanzee males remain in their natal group, while females usually emigrate on reaching sexual maturity. The other is that relations among males from different communities are aggressive and therefore not conducive to pro-social interaction (Manson and Wrangham, 1991). 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 across communities, while the latter implies that females are also the primary vectors of intercommunity cultural transmission. Thus, the

behavioral/genetic mismatch is likely a consequence of females transmitting genes among communities at a greater rate than they transmit culture.

There would seem to be a number of potential explanations for females transmitting genes among communities at a greater rate than they transmit culture. One is that females continue to employ the behaviors they learned from members of their natal community after they disperse but are only rarely copied by members of their new community. A second is that after females disperse they abandon behaviors learned in their natal community and adopt behaviors they encounter in their new community. A combination of these two is also feasible. Currently, it is not possible to say with certainty which of these explanations is correct. In a recent review of the occurrence of novel behaviors among the chimpanzees of Mahale over 40 years, Nishida et al. (2009) found that it was rare for a new behavioral pattern to propagate from a single immigrant to multiple members of a community. However, Biro et al. (2003) outline an example of a female employing one of her natal community's behaviors and serving as a model for members of her new community. So, there is evidence both for and against the first hypothesis. The available data also conflict with regard to the second hypothesis. On the one hand, experiments with captive *Pan troglodytes* have found that chimpanzees tend to resist learning alternatives to a behavior they have already mastered (Marshall-Pescini and Whiten, 2008; Hrubesch et al., 2009). On the other, the aforementioned review of novel behaviors in the Mahale community identified cases in which individuals rapidly acquired new behaviors (Nishida et al., 2009). Given the importance of this issue, there is clearly a pressing need for fieldwork studies specifically designed to examine the role played by immigrant females in the propagation of novel behavioral patterns.

CONCLUSIONS

Over 30 years of fieldwork have demonstrated rich behavioral diversity in wild chimpanzees, and community-specific behaviors are now documented across equatorial Africa (e.g. Whiten et al., 1999, 2001; Sanz and Morgan, 2007; Schöning et al., 2008). Some researchers claim that these intercommunity behavioral patterns are socially learned and therefore are candidates for cultural status (McGrew, 2004; Whiten et al., 1999, 2001; Boesch, 2003; Whiten, 2005; Whiten and van Schaik, 2007). Others, however, contend that a genetic origin for the observed behavioral differences cannot be dismissed and that such variation should therefore not be defined as cultural (Laland and Hoppit, 2003; Laland and Janik, 2006; Galef, 2009; Laland et al., 2009).

Here, we report the results of phylogenetic analyses designed to test this genetic hypothesis directly. Our analyses use three independent measures of phylogenetic signal. In all three cases—contrary to expectations derived from genetic data—we found that phylogenetic signal was lower in a dataset containing chimpanzee communities from western, central, and eastern Africa, as opposed to when western chimpanzee communities were excluded. Hence, we reject a genetic explanation as an underlying cause of the tool-use diversity documented in wild chimpanzees. Rather, our results are in line with a growing body of evidence from both captive studies (e.g. Horner et al., 2006; Hopper et al., 2007; Whiten et al., 2007) and from the wild (e.g. Biro et al., 2003, 2006)

suggesting that these behaviors are socially learned and cultural.

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