Phylogenetic analyses of behavior support existence of culture among wild chimpanzees

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Culture has long been considered to be not only unique to humans, but also responsible for making us qualitatively different from all other forms of life. In recent years, however, researchers studying chimpanzees (*Pan troglodytes*) have challenged this idea. Natural populations of chimpanzees have been found to vary greatly in their behavior. Because many of these interpopulation differences cannot be readily explained by ecological factors, it has been argued that they result from social learning and, therefore, can be regarded as cultural variations. Recent studies showing social transmission in captive chimpanzee populations suggest that this hypothesis is plausible. However, the culture hypothesis has been questioned on the grounds that the behavioral variation may be explained at a proximate level by genetic differences between subspecies. Here we use cladistic analyses of the major cross-site behavioral data set to test the hypothesis that the behavioral differences among the best-documented chimpanzee populations are genetically determined. If behavioral diversity is primarily the product of genetic differences between subspecies, then population data should show less phylogenetic structure when data from a single subspecies (*P. t. schweinfurthii*) are compared with data from two subspecies (*P. t. verus* and *P. t. schweinfurthii*) analyzed together. Our findings are inconsistent with the hypothesis that the observed behavioral patterns of wild chimpanzee populations can be explained primarily by genetic differences between subspecies. Instead, our results support the suggestion that the behavioral patterns are the product of social learning and, therefore, can be considered cultural.

social learning | cultural transmission | *Pan troglodytes* | cladistics
nature (genes) vs nurture (culture)

The behavioral repertoires of wild chimpanzee populations vary greatly (1, 2). Some behavioral patterns occur at certain sites, but not at others. For instance, chimpanzees at Bossou, Taï Forest, and Gombe use sticks and stems to collect army ants for consumption, whereas chimpanzees at Mahale, Kibale, and Budongo do not. Other behaviors are performed differently at different sites, such as the use of hammers and anvils to crack open nuts. Habitual nutcracking has been recorded at only two of the sites where long-term field studies have been conducted, Bossou and Taï Forest. At Bossou, individuals employ only stone hammers and anvils to open one species of nut, whereas at Taï, both wooden and stone hammers and root and stone anvils are used to crack three kinds of nuts.

Researchers disagree about the interpretation of these intersite differences in behavior. Some researchers argue that many of the differences are cultural (1–6). According to these authors, a behavior can be considered cultural if it is exhibited by multiple members of a community and is socially learned (1, 2). They contend that these criteria are fulfilled by at least 39 behavioral patterns that vary among the best-documented wild chimpanzee populations (1, 2, 7).

Other researchers argue that the patterns in question need not be cultural (8, 9). According to these researchers, the crucial feature of culture is that it is cumulative. As such, for a behavior 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. These researchers contend that the behaviors that vary among wild chimpanzee populations are too simple to qualify as cultural.

Other researchers are skeptical that the behaviors in question are even socially learned (10, 11). These researchers assert that the available evidence is too weak to discount the possibility that the behaviors are genetically determined. The claim that the behaviors are socially learned is based on the application of the "method of exclusion" (sometimes also erroneously referred to as the "ethnographic method"). In this method, sites are compared with a view to identifying potential environmental causes of the behavioral variation. Behaviors are deemed to be 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 one third of the 39 putative cultural behaviors occurs 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 (12). In such circumstances, they argue, a genetic origin for the observed behavioral differences cannot be dismissed. Even in cases where genetic control of a specific behavior seems implausible, it is possible that, at a proximate level, genetic mechanisms account for the behavioral differences among populations. Thus, results obtained by the exclusion method may suggest that many chimpanzee behaviors are maintained by social learning, but they are not conclusive.

Recently, Sanz *et al.* (13) sought to refute the notion that the behaviors cannot be considered cultural because they do not show signs of the ratchet effect. They suggested that certain behavioral patterns shown by some populations of wild chimpanzees have become more elaborate through time (e.g., termite-fishing strategies). So far, however, the question of whether the natural behavioral variation in chimpanzees is socially learned or genetically determined has not been addressed directly. 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 conceptualize the relationship between ourselves and other animals (14), there is a pressing need to do so.

Positive correlations between geographic distance and behavioral similarities among populations of nonhuman primates are consistent with those behaviors being cultural (15). However, although it is plausible that groups adjacent to each other

exchange more socially learned information, populations closer to each other in space also exhibit higher levels of gene flow (16). Hence, a correlation between behavioral repertoires and geographic distance does not exclude the possibility that the behaviors are genetically determined, especially when chimpanzee subspecies designations appear to be supported at a genetic level (17–19).

Here we present the results of a study designed to test the hypothesis that the behaviors are genetically determined in such a way as to avoid the criticism leveled at the exclusion method and also the shortcomings of the geographic distance/behavioral difference correlation approach. We used cladistic analyses of the major multisite behavioral data set (1) to test the hypothesis that the behavioral differences among the best-documented chimpanzee populations are genetically determined. We focused on this hypothesis because it has been argued that it should be treated, with respect to culture, as the null hypothesis (11).

The Whiten *et al.* (1) data set records the prevalence of 65 behavioral patterns among seven chimpanzee groups. Five of these groups are from East Africa and are *Pan troglodytes schweinfurthii*; the other two groups are in West Africa and are *P. t. verus*. Thirty-nine of the behaviors meet the criteria for being considered cultural according to Whiten *et al.* (1). Cladistics is currently the main method of phylogenetic reconstruction used in biology (20–22). In recent years, anthropologists and archaeologists also have used it successfully to address questions concerning human culture (e.g., refs. 23–31). Based on a null model, in which new taxa arise from the bifurcation of existing ones, cladistics defines phylogenetic relationships in terms of relative recency of common ancestry. Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that also is not shared by the third taxon. The evidence for exclusive common ancestry is evolutionarily novel or derived character states. Two taxa are inferred to share a common ancestor to the exclusion of a third taxon if they exhibit derived character states that also are not exhibited by the third taxon.

Our study involved four steps. First, we reviewed the published scientific literature to generate codes for the 39 putatively cultural behaviors for an outgroup (see *Materials and Methods*). The bonobo (*Pan paniscus*) was selected for this role because it is the closest living relative of the chimpanzee (32). Next, we carried out a cladistic analysis of the entire data set. We 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 (33, 34). 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 we performed a cladistic analysis of the data for the five East African groups, all of which are *P. t. schweinfurthii*. Again, we identified the most parsimonious cladogram and recorded its length and RI. Lastly, we compared the results of the two analyses in light of recent research on the genetics of chimpanzees. These genetic data indicate that chimpanzees living in East and West Africa are well differentiated from each other, whereas the populations within East Africa cannot be distinguished (17–19). If the genetic hypothesis is correct, the behavioral data should mirror the genetic data in terms of structure. Specifically, the RI yielded by the continental analysis should be higher than the RI yielded by the East African analysis.

Results and Discussion

Analysis of the total data set produced a single-most parsimonious tree (Fig. 1) with a length of 177 and an RI of 0.44. The
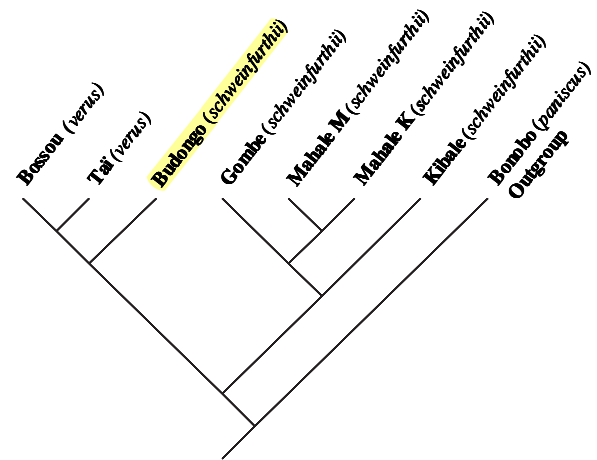

Fig. 1. Maximum parsimony tree produced by cladistic analysis of full data set (tree length = 177, RI = 0.44).

cladogram divides the populations into two major clades. One group comprises the two West African study populations, Bossou and Taï, and one of the East African populations, Budongo. Within this group, Budongo is suggested to be the sister taxon of a clade consisting of Bossou and Taï. The second major clade comprises the remaining East Africa populations: Gombe, Kibale, Mahale M, and Mahale K. Mahale M and K groups are shown to be sister taxa, with Gombe being the next most closely related, followed by Kibale. This cladogram is generally consistent with the results of phylogenetic analyses of the genetic evidence (17–19). Adding the geographically misplaced Budongo group to the East African (*P. t. schweinfurthii*) clade increased the overall tree length by only one step (from 177 to 178).

Analysis of the East African data set also produced only a single-most parsimonious cladogram (Fig. 2). This cladogram suggests that the Mahale M and K populations share the most recent common ancestry. Gombe is indicated to be the next most closely related population to the (Mahale M, Mahale K) clade, followed by Kibale and then Budongo. The cladogram is 107 steps long and has an RI of 0.53.

The RI produced by the full data set is lower than the RI yielded by the East African data set. Hence, the fit with the tree model is lower at the continental level than at the regional level. This finding is contrary to the genetic hypothesis, which predicts that the behavioral data should mirror the genetic data in terms
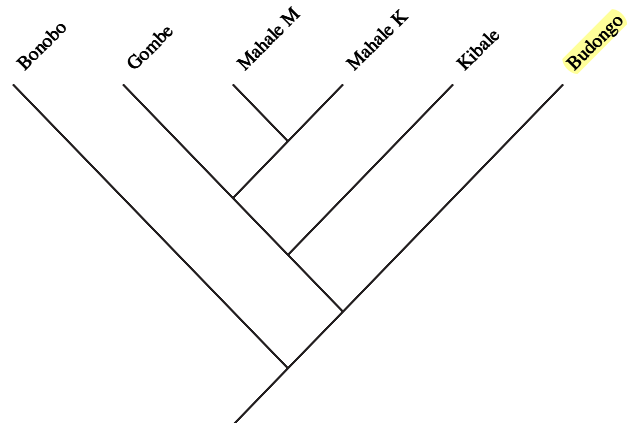

Fig. 2. Maximum parsimony tree produced by cladistic analysis of East African (*P. t. schweinfurthii*) study groups (tree length = 107, RI = 0.53).
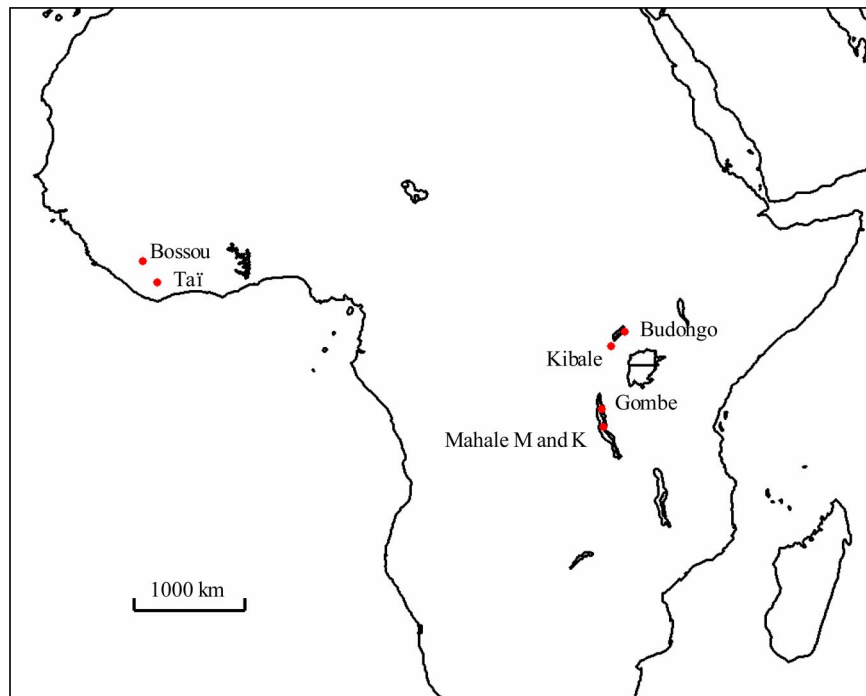
Fig. 3. Location of the seven study groups used in the analyses: Bossou (Guinea), Taï Forest (Côte d'Ivoire), Gombe (Tanzania), Mahale K and M groups (Tanzania), Kibale Forest–Kanyawara (Uganda), and Budongo Forest (Uganda).

of structure and, therefore, should have a more treelike structure at the continental level than at the regional level. Thus, our analyses refute the hypothesis that the behavioral variation reported by Whiten *et al.* (1) is determined primarily by genetic factors.

Although the results are incompatible with the hypothesis that the 39 behaviors are genetically determined, they are consistent with the hypothesis that the behaviors are socially learned. One of the key features of social learning is that it is model-neutral. That is, the ability to copy the behavior 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 biological parents. They also have the option to copy more distantly related kin and unrelated individuals. The corollary of this notion is that individuals who are able to employ social learning potentially can acquire behaviors from members of one group and then disperse to reside and mate with members of another, which opens up the possibility of patterns of transmission of socially learned behavior being different from their genetic counterparts. Thus, a mismatch between the results of a phylogenetic analysis of a behavioral data set and the results of a phylogenetic analysis of genetic data from the same set of taxa is not unexpected if the behaviors in question are socially learned.

The particular behavioral/genetic mismatch we have identified is explicable in terms of cultural transmission when two factors are taken into account. One factor is that chimpanzee males generally stay in their natal group (philopatry), whereas females usually emigrate on reaching sexual maturity. The other factor is that relations among males from different communities are (sometimes fatally) aggressive and, therefore, not conducive to prosocial interaction. These factors 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, whereas the latter implies that females must also be the primary vectors of interpopulation cultural transmission. Thus, the behavioral/genetic

mismatch we have identified can reasonably be assumed to be a consequence of females transmitting genes among populations at a greater rate than they transmit culture. One possible explanation for this finding is that, after females disperse, they abandon some of the behavioral patterns learned in their natal community and adopt the behaviors they encounter in their new community (35). Another hypothesis 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 (36). A combination of the two also is feasible. All three hypotheses are consistent with the recent experimental demonstration that chimpanzees can engage in conformity-based cultural transmission (37, 38). However, discriminating among the hypotheses will require further longitudinal fieldwork. Specifically, it will require data on individual social learning strategies in wild chimpanzee populations to be collected, similar to the way evolutionary anthropologists have begun to document individual social learning strategies in human populations (e.g., refs. 39–41).

Conclusions

The hypothesis that patterns of behavioral variation in wild chimpanzees are the product of cultural learning mechanisms has hitherto proved difficult to test *in situ*. In particular, it has been suggested that putative cultural variation among wild populations of *P. troglodytes* can be explained proximately by genetic differences between subspecies. Our cladistic analyses show that there is a better fit between population-level behavioral patterns and the phylogenetic tree model when populations from a single subspecies (*P. t. schweinfurthii*) are analyzed than when data from two subspecies (*P. t. verus* and *P. t. schweinfurthii*) are analyzed together. These findings are inconsistent with the hypothesis that patterns of behavioral differences at the population level are genetically determined. Instead, they are in line with a growing number of studies involving captive groups (e.g., refs. 37, 38, and 42–44) and wild populations (e.g., refs.

3–6, 36, and 45) that suggest many chimpanzee behaviors are socially learned and can be considered cultural.

Materials and Methods

We took as our starting point the data set on *P. troglodytes* produced by Whiten *et al.* (1) during the first phase of their multisite comparative behavioral analysis (Fig. 3). This data set listed 39 putative cultural behaviors of seven study groups from the six long-term study sites at Bossou (Guinea), Taï Forest (Côte d'Ivoire), Gombe (Tanzania), Mahale K and M groups (Tanzania), Kibale Forest–Kanyawara (Uganda), and Budongo Forest (Uganda) (Fig. 3). Hohmann and Fruth's (32) pooled data for the *Pan paniscus* populations from Lomako and Wamba (Democratic Republic of Congo) were used for the purposes of outgroup comparison. Following Whiten *et al.* (1), the putative cultural behaviors were coded as 0, absent; 1, present; 2, habitual; 3, customary; ?, status uncertain.

In its simplest form, cladistic analysis proceeds via four steps. First, a character state data matrix is generated. This matrix shows the states of the characters exhibited by each taxon. Next, the direction of evolutionary change among the states of each character is established. Several methods have been developed to facilitate this process, including communality (46), ontogenetic analysis (47), and stratigraphic sequence analysis (48). The currently favored method is outgroup analysis (49), which entails examining a close relative of the study group. When a character occurs in two states among the study group, but only one of the states is found in the outgroup, the principle of parsimony is invoked, and the state found only in the study group is deemed to be evolutionarily novel with respect to the outgroup state. Having determined the probable direction of change for the character states, the next step in a cladistic analysis is to construct a branching diagram of relationships for each character. This step is done by joining the two most derived taxa by two intersecting lines and then successively connecting each of the other taxa according to how derived they are. Each group of taxa defined by a set of intersecting lines corresponds to a clade, and the diagram is referred to as a cladogram or evolutionary tree. The final step in a cladistic analysis is to compile an ensemble

cladogram from the character cladograms. Ideally, the distribution of the character states among the taxa will be such that all of the character cladograms imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character cladograms will suggest relationships that are incompatible. This problem is overcome by generating an ensemble cladogram that is consistent with the largest number of characters and therefore requires the smallest number of ad hoc hypotheses of character appearance or homoplasies to account for the distribution of character states among the taxa.

The cladistic analyses were undertaken by using *PAUP* 4.0 (50) and *MacClade* 4.02 (51). We used *PAUP* 4.0 to identify the most parsimonious trees. All characters were treated as ordered and freely reversing (52). Searches were conducted by using the branch-and-bound algorithm, which is guaranteed to yield the most parsimonious trees for a data set. *MacClade* 4.02 was used to calculate an ensemble RI value for the most parsimonious trees. The RI of a single character is calculated by subtracting the number of character state changes required by the focal cladogram (S) from the maximum possible amount of change required by a cladogram in which all of 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. A maximum 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 data sets because, unlike some other measures (e.g., the consistency index), it is not affected by the number of taxa or characters.

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