Pan African culture: Memes and genes in wild chimpanzees

Andrew Whiten*

Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology, University of St. Andrews, St. Andrews KY16 9JP, United Kingdom

As decades-long studies of primates and other taxa have accumulated, there has been increasing recognition of local behavioral differences that circumstantial evidence suggests are socially transmitted cultural variants or "memes" (1, 2). Field studies of chimpanzees have been particularly bountiful, revealing as many as 39 such behavioral variants across Africa (3). However, without experimental intervention, it is difficult to reject alternative explanatory hypotheses appealing to genetic differences between subspecies or to differences in local environmental opportunities. In this issue of PNAS, a study by Lycett *et al.* (4) addresses this problem by exploiting numerical methods recently used to elucidate the branching histories of human languages and material culture (5). Applying these methods to a non-human species for the first time, the authors conclude that the phylogenetic trees that best describe the affinities between the behavioral profiles of different chimpanzee communities are not compatible with a genetic explanation and instead support the cultural interpretation.

Only recently has a sufficiently rich dataset of putative cultural variants become available for a non-human species to which such an analysis can be applied. A few decades ago, we knew virtually nothing of the behavior of our closest relatives. Now, after a half-century of intensive study across multiple African field sites, we can at last address the question of chimpanzee cultural diversity, as anthropologists have long done for humans. A "cultural *Pan*thropology" (6) becomes a real prospect.

The possibility of chimpanzee culture surfaced early in Jane Goodall's pioneering studies, stimulated by youngsters' intense observations of skilled adult tool use (7). Studies at other sites later began to map local behavioral variations in tool use and social behavior. By 1992, such work merited a landmark book-length treatment by McGrew (8), one of the authors in ref. 4. However, such efforts were based on existing published information, which is often incomplete. A significant step forward was therefore made when the directors of the nine most long-term study sites pooled their records and systematically compared them. This comparison indicated a complexity of culture unprecedented in the animal behavior literature (3). Each chimpanzee community was shown to display a profile of traditions that together defined a unique local culture (Fig. 1), including tool use, foraging techniques, social behavior, and grooming methods.

However, with experimental intervention logistically and ethically problematic, it is difficult to decisively reject alternative explanations for the regional variations that appeal to genetic or environmental differences.

Most studies of animal traditions have documented only one or two behavioral variants.

The authors of the chimpanzee papers themselves recognized this and called on a variety of types of evidence to exclude such alternatives. For example, it was noted that some variations occur between geographically proximate populations, making genetic explanations unlikely. Nevertheless, debates have developed in the scientific literature between skeptics and those who weigh the various lines of evidence as converging on the existence of significant cultural variation (1, 2, 9).

Lycett *et al.* (4) have tackled the issue by applying to the chimpanzee database numerical analyses more complex than have been used before. These are referred to as "phylogenetic" or "cladistic" methods because they were originally developed to identify branching evolutionary patterns among biological taxa. More recently, they have been applied to the analysis of human cultural evolution, from the diversification of languages, to ancient arrowheads, to more recent textile designs (10, 11). One of the authors of the article by Lycett *et al.*, M. Collard, has been active in this.

Lycett *et al.* (4) used these methods to identify the branching patterns that best fit the behavioral profiles of the five East African chimpanzee communities alone, then repeated the exercise for all seven communities, now including the two from West Africa that belong to a different subspecies. Because there is extensive genetic diversity between these eastern and western forms, the authors reasoned that if behavioral variations are genetically based, there should be more evolutionary tree-like structure in the Africa-wide analysis than in the single-species eastern one. Their analysis yields an index of such "tree-ness," the retention index, which the genetic hypothesis predicts should show a higher value in the Africa-wide analysis. However, the authors found that the reverse was the case, with one East African community, Budongo, grouping with the West African communities. Accordingly, Lycett *et al.* reject the genetic explanation for the behavioral variations and instead embrace the cultural explanation.

Broadly, of course, one might expect some correlation between genetic and cultural variation. The individuals who migrate to neighboring communities (in chimpanzees, typically the females) provide the same route for the spread of their genes and their cultural repertoire of memes. Indeed, there is evidence of such a gross correlation for both orangutans and chimpanzees (12), the latter confirmed in the East Africa analysis of Lycett *et al.* (4). However, unlike its genetic counterpart, social transmission is not restricted to parent-to-offspring relationships, creating a potential disjunction between regionally distributed patterns in behavior shaped by genetic versus cultural factors. Lycett *et al.* point out that just such a behavioral–genetic mismatch is revealed in their more refined cladistic analyses. Their conclusion that the distribution patterns favor a cultural interpretation is consistent with recent observational data showing that young female chimpanzees, who watch their mother's tool use more closely than do their male peers, acquire the tech-

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*E-mail: aw2@st-andrews.ac.uk.

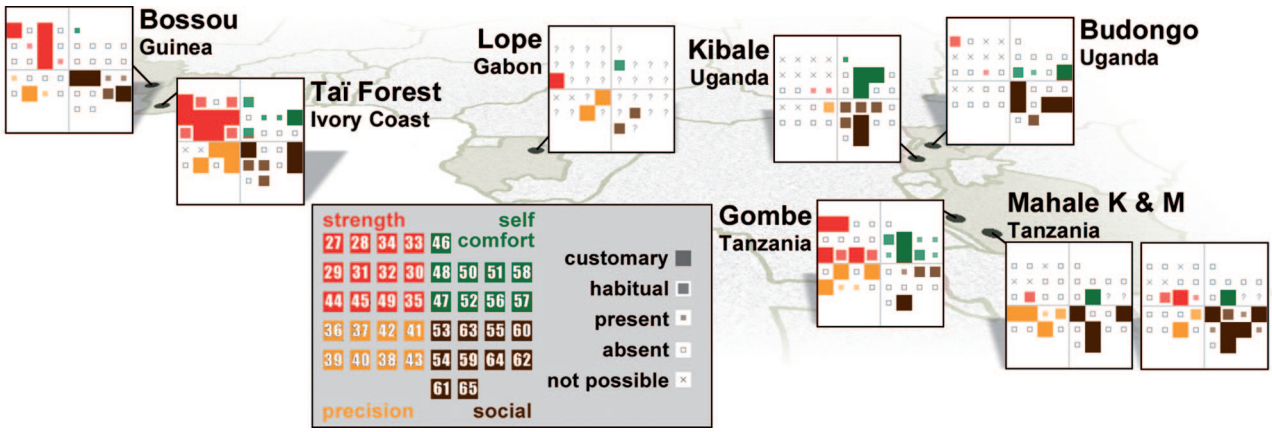

Fig. 1. The putative cultures of wild chimpanzees (after ref. 18). ''Customary'' acts are those that are typical in a community; ''habitual'' acts are those that are less frequent yet consistent with social learning. Each community displays its own profile of such local behavioral variants, providing evidence of a unique culture for each locality. Numbers identify behavior patterns in the catalog attached to ref. 3 and illustrated at http://culture.st-and.ac.uk/chimp.

niques earlier and even display aspects of the style of their mother (13). Recent studies that experimentally seeded alternative foraging techniques showed that they diffused differentially not only within but also between groups of captive chimpanzees (14).

The contribution by Lycett *et al.* (4) is timely, for it comes at a time when other studies are beginning to document a richness of putative cultural variation in non-human species to which the cladistic analyses may be applicable. Most studies of animal traditions have documented only one or two behavioral variants, such as bird-song dialects, rather than the multiple patterns that begin to make cladistic analysis rewarding; more recently, however, other studies have taken the chimpanzee research as a template and described more complex arrays of variation. Such studies are becoming taxonomically more diverse, extending to orangutan tool use and communication patterns [with results approaching the complexity of those for chimpanzees (12)], social and foraging patterns among capuchin monkeys (15), Japanese macaque stone-play (16), and variations in bowerbirds' decoration preferences (17). More generally, the new study may reinforce bridge-building between the work of those focused on human and non-human forms of culture and further the exciting prospect of a more integrated "science of culture" (11).

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1. Fragaszy DM, Perry S, eds (2003) *The Biology of Traditions: Models and Evidence* (Cambridge Univ Press, Cambridge, UK).
2. Whiten A, van Schaik CP (2007) *Philos Trans R Soc London Ser B* 362:603–620.
3. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) *Nature* 399:682–685.
4. Lycett SJ, Collard M, McGrew WC (2007) *Proc Nat Acad Sci USA* 104:17588–17592.
5. Mace R, Holden CJ (2005) *Trends Ecol Evol* 20:116–121.
6. Whiten A, Horner V, Marshall-Pescini S (2003) *Evol Anthropol* 12:92–105.
7. van Lawick-Goodall J (1973) in *Precultural Primate Behaviour*, ed Menzel EW (Karger, Basel), pp 144–184.
8. McGrew WC (1992) *Chimpanzee Material Culture: Implications for Human Evolution* (Cambridge Univ Press, Cambridge, UK).
9. Laland KN, Janik V (2006) *Trends Ecol Evol* 21:542–547.
10. Collard M, Shennan S, Tehrani JJ (2006) in *Mapping Our Ancestors: Phylogenetic Methods in Anthropology and Prehistory*, eds Lipo CP, O'Brien MJ, Shennan S, Collard M (de Gruyter, New York), pp 53–63.
11. Mesoudi A, Whiten A, Laland KN (2006) *Behav Brain Sci* 29:329–383.
12. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M (2003) *Science* 299:102–105.
13. Lonsdorf EV, Pusey EA, Eberly L (2004) *Nature* 428:715–716.
14. Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM (2007) *Curr Biol* 17:1038–1043.
15. Panger MA, Perry S, Rose L, Gros-Luis J, Vogel E, Mackinnon KC, Baker M (2002) *Am J Phys Anthropol* 119:52–56.
16. Leca J-B, Gunst N, Huffman MA (2007) *Behaviour* 144:251–281.
17. Madden JR (June 6, 2007) *Anim Cognit*, 10.1007/s10071-007-0092-5.
18. Whiten A (2005) *Nature* 437:52–55.