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NEW WINE IN NEW BOTTLES

Prospects and Pitfalls of Cultural Primatology

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*Cultural primatology has matured in recent years from natural history to ethnography to ethnology, but new techniques of analysis and interpretation are needed to deal with new findings. Studies of the chimpanzee (*Pan troglodytes*) lead the way, both observationally in nature and experimentally in captivity. New data on elementary technology employed in extractive foraging (e.g., ant dipping) show that prevailing ideas of environmental versus cultural determinism are simplistic. Cultural primatology yields both behavioral diversity and universals. As with humans, cultural change can be maladaptive (e.g., pestle pounding, crop raiding) as well as adaptive. The future of cultural primatology depends on the ongoing survival of wild populations of primates.*

WHEN JULIAN HUXLEY (1957) REFERRED FIFTY YEARS AGO TO NEEDING NEW BOTTLES FOR NEW WINE, he argued that a synthetic treatment of evolutionary theory and humanism called for a new, scientifically based belief system. My aim is not so grand, however parasitical the choice of title, and however great my admiration for Huxley. My goal here is to ponder the successes and failures of the new field of cultural primatology, and to suggest some ways that it might develop in the future. It is also a reflection of the growth of the field that it requires constant updating (cf. McGrew 2004). As usual, I will focus on the chimpanzee, the nonhuman primate species about whose culture we know the most. To anticipate the conclusion, I will argue that the phenomena of primate behavioral variation (or lack of it) and its cognitive underpinnings (new wine) *and* the framework within which primatology seeks to make sense of these things (new bottles) call for novel approaches if we are to progress.

BACKGROUND

The idea that nonhuman primates might have something akin to human culture dates at least to Wolfgang Koehler's (1925) pioneering studies of problem-solving in captive chimpanzees. His findings made a great impact in the social sciences: Kroeber (1928) was moved to propose criteria for culture against which apes could be tested, and Hart and Panzer (1925) were compelled to conclude (with remarkable

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prescience) that animals learned behavioral complexes from one another and that these were socially accumulative. Such assertions were all the more remarkable given that Koehler had shown only individual (not social) learning in his subjects, and that his tasks were artificial ones in contrived contexts.

Before going further, a distinction must be drawn between two areas of enquiry that are sometimes confused: ethnoprimateology and cultural primatology. Ethnoprimateology is the study of human-nonhuman primate interaction, at a local level, in terms of behavior, knowledge, emotion, and meaning. In this sense, it resembles ethnomedicine, ethnohistory, and so on. Usually it is done by First World anthropologists who work in Third World traditional societies. Loretta Cormier's (2003) *Kinship with Monkeys* is a prime example, detailing the relations of Amazonian foragers and howler monkeys. This species of monkey is the main prey of the human hunters, but the hunters also rear the orphaned monkey infants as if they were children. Cormier's insightful analysis explains this apparent paradox. However, most ethnoprimateology is applied research, especially in the contexts of ecotourism (Wheatley 1999) and crop-raiding (Paterson and Wallis 2005).

Cultural primatology is simply the study of culture in nonhuman primates, as opposed to the study of primate ecology, genetics, anatomy, etc. As such, it is analogous to (and perhaps a subfield of) cultural anthropology (McGrew 2004; Perry 2006). For a lively treatise on the potential of cultural primatology, see Frans de Waal's (2001) *The Ape and the Sushi Master*.

From its recent origins to the present, cultural primatology can be said to have gone through three stages: natural history, ethnography, ethnology. Like cultural anthropology, its roots were in the natural sciences, and studies of chimpanzees echo this.

The natural history stage was one of anecdotes (that is, rare or unique events) or ad hoc, opportunistic observations in nature. Beatty's (1951) note on a Liberian chimpanzee cracking palm nuts with stone hammer and anvil is a prototypical anecdote, admirable in its clarity and brevity. The pioneering chimpanzeologists (Jane Goodall, Junichiro Itani, Toshisada Nishida, Vernon Reynolds, Yukimaru Sugiyama) who founded today's established field sites were essentially natural historians. None had anthropological training, nor had they studied apes in captivity before going to Africa. Their findings in the 1960s were spectacular in their novel discoveries—for example, tool making and use, hunting and carnivory, infanticide and cannibalism—but all moved on to ethnography. (Even at this stage, astute field researchers glimpsed potential: In only her second article, written while still a graduate student, Goodall [1963] opined that termite fishing “is a social tradition that represents the emergence of a primitive culture.”)

The ethnographic stage of cultural primatology can be likened to its counterpart in cultural anthropology: scientific description of customs, habits, and variation. At chimpanzee field sites, the transition to ethnography occurred gradually and has been documented best at Gombe, Tanzania (Goodall 1986). (Table 1 lists the best-known sites of chimpanzee field study.) Explicit comparison across populations also emerged at this stage, when field researchers (Christophe Boesch, William McGrew, Yukimaru Sugiyama, Caroline Tutin, Richard Wrangham) ventured to work at more than one site, specifically for the purpose of seeking contrasts. At this

stage, ethograms, activity budgets, dominance hierarchies, sampling schedules, daily protocols, and statistical testing became the norms. Cultural primatology turned systematic.

The third stage, ethnology, appeared more haphazardly, if one defines this as question-based, theory-driven, hypothesis-testing, comparative analysis. As in cultural anthropology, it was only feasible when a sufficient ethnographic record had accumulated (although no one in cultural primatology at the time used that phrase). However, once ethnographies were available, comparison was inevitable, even if no standardized, centralized database comparable to Murdock's *Ethnographic Atlas* existed. Even as early as 1972, writing in Menzel's (1973) ground-breaking edited volume, Goodall (1973) attempted to compare tool-use across all known field studies of chimpanzees, finding provocative similarities and differences.

Meanwhile, experimental ethnology was created by Tetsuro Matsuzawa, at Bossou, Guinea. Setting up a clearing in the forest, in the midst of the home-range of the wild chimpanzees long-studied by Sugiyama, he controlled variables. He and his colleagues augmented the naturally occurring elements of nut cracking, leaf sponging (Figure 1), and ant dipping (Matsuzawa et al. 2006). Further, he introduced new but ecologically valid variables, such as species of nuts found not at Bossou, but a few kilometers away in the nearby Nimba Mountains.

However, it was the Collaborative Chimpanzee Cultures Project (CCCP), brokered and orchestrated by Andrew Whiten (Whiten et al. 1999, 2001), that undeniably signaled the arrival of ethnology in chimpanzee research. Nine

TABLE 1
Field sites of chimpanzee studies with systematic ethnographies, in descending order of approximate duration of study (longest to shortest)

Site	Country	Subspecies	Leader(s)
Gombe	Tanzania	<i>Pan troglodytes schweinfurthii</i>	Jane Goodall
Mahale (K, M Groups)	Tanzania	<i>P. t. schweinfurthii</i>	Toshisada Nishida
Bossou	Guinea	<i>P. t. verus</i>	Tetsuro Matsuzawa, Yukimaru Sugiyama
Taï (North, South Groups)	Ivory Coast	<i>P. t. verus</i>	Christophe Boesch
Kibale (Kanyawara)	Uganda	<i>P. t. schweinfurthii</i>	Richard Wrangham
Kibale (Ngogo)	Uganda	<i>P. t. schweinfurthii</i>	John Mitani, David Watts
Budongo	Uganda	<i>P. t. schweinfurthii</i>	Vernon Reynolds
Kalinzu	Uganda	<i>P. t. schweinfurthii</i>	Takeshi Furuichi, Chie Hashimoto
Goualougo	Congo	<i>P. t. troglodytes</i>	David Morgan, Crickette Sanz
Fongoli	Senegal	<i>P. t. verus</i>	Jill Pruetz
Assirik	Senegal	<i>P. t. verus</i>	William McGrew, Caroline Tutin
Nimba (Serengbara)	Guinea	<i>P. t. verus</i>	Tatyana Humle



Figure 1. Leaf sponges used by wild chimpanzees of Semliki (Uganda) to soak up water from wells dug in dry riverbeds. (Photo courtesy of L. F. Marchant)

Top are intact leaves (raw materials); middle are processed leaves, discarded after removing material between veins; bottom is a disarticulated, damp sponge. Scale object is a tape measure.

researchers with a combined history of more than 150 years of study of wild chimpanzees across Africa coded and collated their data from six populations (Bossou, Budongo, Gombe, Kibale, Mahale, Taï). They chose 65 behavioral patterns for classification into four categories; of these, 39 showed variation across sites that could not be explained by environmental differences. The diversity of the resulting patchwork “quilts” of customs and habits called for explanation that went beyond standard natural science paradigms (McGrew 2004).

Once the precedent was set, the CCCP approach was adopted for other taxa: for example, cetaceans (Rendell and Whitehead 2001), orangutans (van Schaik et al. 2003), and capuchin monkeys (Perry et al. 2003). The ethnographic record for the bonobo is more sparse, so that only preliminary, qualitative efforts can yet be made (Hohmann and Fruth 2003). Further, Carel van Schaik (Schaik et al. 2003; van Schaik and Pradhan 2003) has led the way in the application of theoretically based modeling of cultural processes. Starting with simple tests of geographical propinquity, he and his colleagues went on to look at the influence of social factors (e.g., tolerance) and of inferred cognitive constraints.

Finally, in parallel with field studies, experimental behavioral studies aimed at elucidating the underlying mechanisms of cultural transmission are underway. Andrew Whiten and Frans de Waal, working at the Yerkes Primate Center in the U.S., have tackled conformity, fidelity, and arbitrary acquisition of new behavioral patterns in captive groups of chimpanzees (Bonnie et al. 2007; Horner et al. 2006;

Whiten et al. 2005). Meanwhile, Matsuzawa and his colleagues (2006) at Inuyama, Japan, have done a series of studies simulating natural tasks (e.g., nut cracking, leaf sponging, honey dipping) under controlled conditions. Such data on cultural processes, ranging from stimulus enhancement through emulation and imitation to teaching in captive apes, can sometimes be directly compared with those shown by their wild counterparts.

DETERMINISM AND VARIATION

If behavior varies from population to population of apes, how is this to be explained? Perhaps the simplest starting point is the logically pleasing but otherwise impoverished paradigm of nature versus nurture. In this dichotomy, either genetic or environmental determinism can in principle account for diversity. In the gross sense, each of these alternatives can be easily dismissed:

- If two neighboring groups of primates regularly exchange genes, and especially if they have polygynandrous mating (i.e., each male mates with several females, and vice versa), yet the groups have different customs, then it is unlikely that there is a genetic explanation for any differences found. Elementary population genetics alone rules out genetic determinism, without needing to invoke genomics.
- If two groups live side-by-side in the same type of habitat yet show different customs, it is unlikely that environmental factors, whether biotic or abiotic, at least at the macro-level, can explain this variation.
- If two groups live on opposite sides of a river wide enough to be an impassable barrier to gene flow, and if the habitats on either side are essentially identical, then we are entitled to rule out environmental factors but cannot dismiss genetic differences owing to divergence (depending on the time depth of the present allopatry).
- Finally, if neighboring groups exchange genes but live in different habitats (e.g., adjoining primary vs. secondary forest blocks), then we can rule out genetic but not environmental determinism.

All four of these combinations of nature and nurture are known for wild chimpanzees, and behavioral variation across groups exists for all of them.

If customary behavioral variation occurs across groups that cannot be explained simply by genes or environmental factors, then what is left are sociocultural determinants of differential learning. That is, behavior varies collectively because members of groups learn particular variants from one another. (This does not apply to individual learning. If Susie in Group A and Fred in Group B act differently, this need not have anything to do with sociocultural processes, for obvious reasons. Idiosyncrasy is but one reason to be wary of anecdotes.) In this framework, group-typical behavioral diversity results from comprehensible processes (e.g., conformity) that can be modeled in some detail (Boyd and Richerson 1985; Richerson and Boyd 2005).

CASE STUDY: ANT DIPPING

A specific example may make the issues clearer: Chimpanzees and army ants (*Dorylus* spp.) are apparently sympatric throughout the range of the apes. About half of known populations of chimpanzees eat the ants, but others do not. Those that do sometimes use tools to do so, and elementary technology varies by correlated technique and artifact (McGrew 1992). Gombe chimpanzees use a bipedal, bimanual technique that entails skilled use of a long tool (McGrew 1974). Taï chimpanzees use a non-bipedal, unimanual technique that entails unskilled use of a short tool (Boesch and Boesch 1990). At Bossou, chimpanzees use both techniques and tool types (Sugiyama et al. 1988). All variants have been termed “ant dipping” because the predatory ape dips the tool into a visible mass of ants on the ground, but the Gombe type is more efficient and complex than the Taï one. The raw materials needed for making the ant-dipping tools are readily available everywhere: all that is needed is a long-enough, straight-enough stem, stalk, or branch that can be stripped of leaves or twigs to make a wand.

Based on these ethnographic data, in 1992 I inferred that variation across populations in ant dipping was likely to be cultural. Since nearby populations of apes (e.g., Gombe vs. Mahale in Tanzania; Kalinzu vs. Kibale in Uganda) did or did not prey on the ants, and given the ubiquity of the prey and the raw materials, neither genetic nor environmental influences were thought to be enough to explain the observed diversity. Similarly, the motor skills needed for the standardized Gombe technique (e.g., while one hand or foot [!] holds the wand steady and vertical, the other hand simultaneously sweeps its length, collecting the ants in a jumbled mass) are unlikely to have been learned on an individual-by-individual basis by trial-and-error.

However, this tidy consensus crumbled when Humle and Matsuzawa (2002) reported within-site variation in ant dipping at Bossou. They found that characteristics of technique and tool were correlated with type of ant. Instead of army ants being a single taxon, they were several species that varied morphologically and in their anti-predator responses. The black army ants were more aggressive and required longer (i.e., safer) wands and the two-handed technique; the red army ants were more docile and so could be harvested by the shorter tools and one-handed technique. Thus, it appeared that the apes’ behavioral variation across sites was after all environmentally determined. No need to invoke complex ape culture if the predator-prey relationship was being driven by the tiny insects and not by the large-brained primate! Critics of cultural primatology (e.g., Byrne 2007; Laland and Janik 2006) pounced on this result, especially when Humle (2006) presented more extensive data strengthening the prey-related contrasts.

Missing was a comprehensive, systematic analysis of many co-occurring populations of chimpanzees and ants, across Africa, in terms of predator-prey relations. This was remedied by Schoening and colleagues (n.d.), who collected data from 13 populations of chimpanzees, representing all four subspecies, from Senegal to Uganda (Figure 2). Intensive collections of ants were identified, and four morphological proxy measures of aggressiveness were recorded from each of 13 taxa. Data on ant consumption came from observations or fecal samples, and

tools were collected and measured. Finally, whenever possible, behavioral data on the apes' harvesting techniques were recorded.

Up to six taxa of army ants were present at a chimpanzee study site, and at six of the 13 sites, the apes ate more than one species of ant; at five sites, they ate none (Schoening et al. n.d.). Thus, there was much diversity to be explained! Luckily, some populations of chimpanzees were matched in terms of having exactly the same suite of ant taxa available. At Gombe, both species present were eaten, whereas at Mahale, the same two species were ignored. At Bossou, Seringbara, and Taï, the same five taxa of ants were present; all were eaten at Bossou and Taï, but only two at Seringbara (only a few kilometers from Bossou). Thus, availability does not determine consumption.

On the technology front, Humle and Matsuzawa's (2002) findings on within-site variation at Bossou in tools and techniques were confirmed. However, the differences found between Bossou and Taï cannot have been due to differential availability of types of ant, as these were the same. Overall, Schoening and colleagues' (n.d.) results suggest that both cultural and environmental factors interact to produce cross-population variation in chimpanzees' ant dipping.

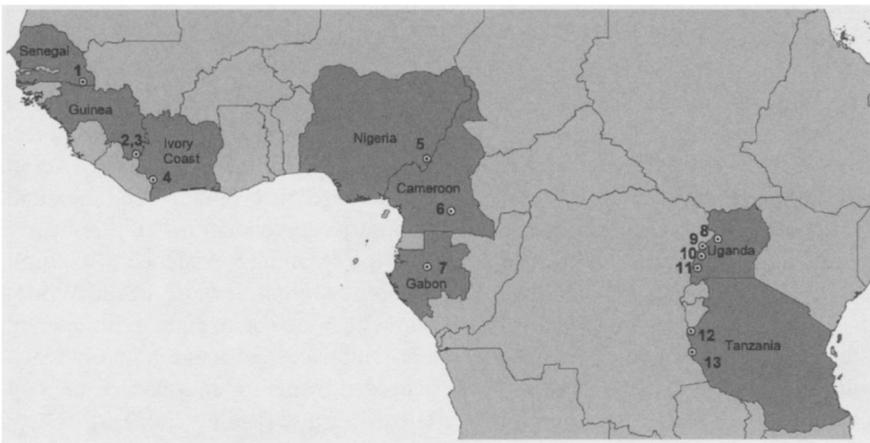


Figure 2. Field sites of studies of wild chimpanzees.

1: Assirik (Senegal), 2: Bossou (Guinea), 3: Nimba (Guinea), 4: Taï (Ivory Coast), 5: Gashaka (Nigeria), 6: Dja (Cameroon), 7: Lope (Gabon), 8: Budongo (Uganda), 9: Semliki (Uganda), 10: Kibale (Uganda), 11: Kalinzu (Uganda), 12: Gombe (Tanzania), 13: Mahale (Tanzania)

DURKHEIM'S DICTUM

Early efforts by cultural primatologists (e.g., McGrew and Tutin 1978) simplistically sought to show the existence of chimpanzee culture by excluding other, non-social causes of variation. This argument-by-exclusion stated that if genetic, environmental, and individual learning factors could be ruled out, then by default, sociocultural factors must be invoked. This approach echoed Durkheim's (1938) dictum that the social realm is an emergent phenomenon, that culture and society transcend the constraints of nature.

In retrospect, this argument was misguided and naive, on both theoretical and practical grounds. No organism, human or not, exists in a vacuum, and so it cannot be free of environmental constraints. Put another way, this means that unrecognised non-social influences logically can never be excluded. No matter how many ecological variables are controlled, from climatic to metabolic, there could always be one more yet-to-be measured one that is crucially deterministic. This is equally true of the chemical secretions of termites that might deter potential ape predators from termite fishing to the absence of adhesible pigments that might constrain potential Upper Palaeolithic artists faced with damp cave walls.

Despite this realization, anthropologists are still more impressed by social than environmental diversity when it comes to attributing cultural capacity. Differences in diet are always less compelling than differences in communication, however value-laden are the former (e.g., food taboo) or mechanical the latter (e.g., hand clapping). Thus, we are moved by human oral traditions of storytelling, especially if the content is symbol-rich, as in origin myths. (This recalls another Durkheimian essential, that of collective consciousness, which, however beguiling, is apparently empirically untestable.) The grooming-hand-clasp, a seemingly functionless aspect of chimpanzee social grooming (McGrew and Tutin 1978; Nakamura and Uehara 2004), varies across populations in ways that seem to have nothing to do with hygiene, or any other environmental constraints.

Why has cultural primatology sought, grail-like, for behavioral variation that is free of ecological limitations? At the outset, this was likely a bending-over-backwards by natural scientists seeking acknowledgement from social scientists, in venturing onto their turf. It was as if emphasis on social facts (another Durkheimian phrase!) could advance the candidature of apes as contenders for culture-bearer status. Such misplaced idealism ignored the long-standing existence of cultural evolutionary ecology or ecological anthropology (Julian Seward, Leslie White) and cultural materialism (Marvin Harris), in which the social and environmental arenas were inextricable. This confusion is reminiscent of naive nature-versus-nurture dichotomizing, which has been succeeded by nature-and-nurture, then by nature-via-nurture, and finally by nature-equals-nurture (Ridley 2003).

DIVERSITY AND UNIVERSALS

Early cultural primatology (just like early cultural anthropology?) was obsessed with variation. Field researchers scrutinized the behavior of their subjects, seeking new patterns or new variations on old themes. These novelties were promptly reported, even if only anecdotal, sometimes with what seemed to be an air of the proud parent, as accomplishments of “my apes” (cf. “my people”). In this mindset, exciting diversity is cultural whereas, by implication at least, lack of diversity is boring, and even non-cultural. At its worst, this neophilia becomes a sort of culturological competition, in which one’s chosen study population (and therefore one’s research project) earns points, especially for unique and exotic patterns. (For a recent example of such advocative ethnography, see Sanz and Morgan 2007.)

Lost in the shuffle of rich diversity was the other side of the coin: universality. In one sense, this is not surprising, as something need be seen only once to be new, although the greater the background of familiarity, the more notable the novelty. An ape who picks his teeth with a porcupine quill is all the more salient if many other apes have been seen to encounter quills but have ignored them. To establish universality in a species, one needs to have a decent (statistically representative) sample of populations that have been observed enough, and then to find a behavioral pattern present in all. "Absence of evidence is not evidence of absence," and so false-negative results are the bane of someone seeking universals. The ethnographic record for apes was not substantial enough for such an exercise until now (see below), which may explain the total absence of publications on the subject of universals in nonhuman primates.

The subject of human (behavioral) universals, once the bailiwick of anthropological giants such as George Murdock and Clyde Kluckhohn, is no longer fashionable, perhaps because it suggests an underlying "human nature," the putative existence of which is deemed politically incorrect. It is surely noteworthy that the definitive treatise on the topic, Donald Brown's (1991) *Human Universals*, never went into a second edition (although it has never gone out of print, either).

The potential for seeking universals in chimpanzee behavior now exists in CCCP Phase 2 (Whiten et al. unpublished data). As outlined above, the CCCP was originally based on six populations of apes showing 65 behavioral patterns, as taken from the western (*Pan troglodytes verus*) and eastern (*P. t. schweinfurthii*) subspecies. Now the expanded CCCP-2 covers 12 populations and 571 behavioral variants, though the latter can be grouped into functional "complexes"—for example, meat eating covers 23 categories. The intersection of 12 sites and 571 categories yields a master matrix of almost 6,900 cells. Each of these is assigned one of six codes, thus generating more than 40,000 coding options. (This may not yet be equivalent to Murdock's Cross-Cultural Sample, but surely it provides the basis for empirical ethnology!)

Superficial examination of the preliminary results of CCCP-2 yields a staggering array of behavioral diversity, much of it totally unexpected and some of it apparently arbitrary (Whiten et al. unpublished data). However, at least 35 behavioral patterns emerge that are found at all sites, and if near-universals (i.e., absent at only one of the 12 sites) are added, this total almost doubles. Furthermore, these universals come from all areas of chimpanzee daily life: self-maintenance ('bed make'), communication ('drum'), subsistence ('leaf sponge'), agonism ('branch drag'), sexuality ('copulatory interference'), play ('invitation tag'). They are shown by young and old, male and female, dominant and subordinate.

To what extent are these universal patterns of behavior identical in form (stereotyped or fixed-action-patterns) across all populations? No one knows. It is likely that, as with human universals, they will show nuanced variation from group to group. No one knows if chimpanzee shelters (nest/bed/sleeping platform; Figure 3) are the same or not, in Uganda, Gabon, or Senegal, or if they vary, how and why? Much as been written on cross-cultural variation in the human universal of shelter construction, but chimpanzee shelter construction awaits comparative study.



Figure 3. Adult male chimpanzee from Gombe (Tanzania) asleep in day nest. All great apes build these simple structures for resting. (Photo courtesy of C. E. G. Tutin)

MALADAPTATION

Culture is generally thought to be a good thing. Cultural organisms can respond flexibly and quickly to new challenges, and new solutions to problems can spread horizontally (peer-to-peer), vertically (parent-to-offspring, or vice-versa), or obliquely (older-to-younger, or vice-versa) (Figure 4). Thus, transmission of cultural knowledge is not limited to genetic information encoded in germ lines, but can spread memetically in Lamarckian fashion. Finally, cultural evolution is not constrained by individual, Darwinian selection, but can advance by group selection, sometimes dramatically. Given this halo effect, it is not surprising that culture is sometimes presented as being all benefits and no costs. However, there is a flip-side.

Consider a particular behavioral pattern that is both customary and unique to the chimpanzees of Bossou: pestle-pounding. The chimpanzee detaches one of the petioles (fronds) in the crown of an oil palm (*Elaeis guineensis*), then uses it mortar-and-pestle style to pound to a pulp the “heart” of the palm (its apical growth tip). In the cavity created by this pounding, the tissue is converted to a nutritious, stringy soup, sometimes to a depth of a half meter, which the ape “fishes” out by hand (Yamakoshi and Sugiyama 1995). The repeated action is hard work, and the pounder may rear up bipedally, before slamming down the pestle in an overarm motion reminiscent of similar motor patterns used to pulverize grain in nearby villages. (Whether apes learned the pattern from humans, or humans from apes, or each developed it independently, remains to be established.) The overall impression given to the first-time observer is one of an enterprising technique that enables the efficient exploitation of an otherwise unavailable resource. What clever apes, one thinks.

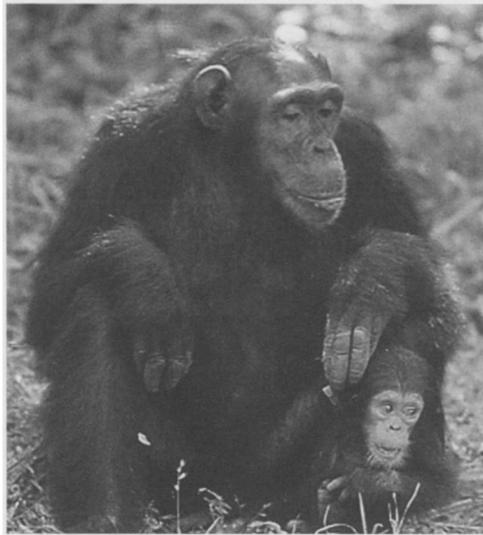


Figure 4. Adult female chimpanzee and infant at Gombe. A youngster learns foraging skills such as termite fishing literally at the mother's knee. (Photo by the author)

However, judging from the mangled appearance of many of the palms in the chimpanzees' home range, the plants suffer damage, and some may die. Even if they survive being pounded, it is likely that their productivity is curtailed, for like any organism, vegetative growth takes priority over reproduction. Survival trumps fitness. (Of course, to test this hypothesis requires following the long-term fate of individual oil palms, both pounded and unpounded.) But why does it matter if the palms pay this price for being exploited? It could matter a lot, because the palm fruit (nut) is a staple food of the apes (Yamakoshi 1998), and they have developed a whole technological complex to harvest this foodstuff. Bossou's chimpanzees use a lithic technology that is arguably the most advanced of all such extractive foraging, with stone-on-stone percussion, and meta-tool anvils (Matsuzawa 2001). To sacrifice the long-term, sustainable productivity of a key resource in order to consume what may be a one-time, immediate payoff sounds disturbingly like a common feature of human culture. This shortsightedness seems to be analogous, at least from the viewpoint of the individual ape, to the "tragedy of the commons," in which resources in common but unrestricted ownership are overused, sometimes to total depletion, because prudent users who exercise restraint will always lose out to profligate ones (Hardin 1968). That is, "If I don't pound, someone else will, so why not do so, as it's happening anyway?" (Of course such strategizing need not be done consciously or even intentionally, so long as the organism acts "as if" it were so motivated.) So, such innovative cultural exploitation as pestle-pounding may be ultimately maladaptive.

A more equivocal form of maladaptation may be crop-raiding. Primates exposed to cultivars may come to prefer them to their natural foodstuffs, and so come into conflict with human cultivators. For common, fecund plants that

require little or no care, such as papaya, the occasional theft of a fruit may be easily overlooked by local farmers. Similarly, losing a proportion of a fast-growing, perennial field crop such as sugarcane to a variety of agricultural “pests,” including primates, may be tolerated, so long as enough remains for the humans. However, slow-growing, K-selected cash crops such as pineapple may be fiercely defended, as a year’s work may be lost in minutes. Such depredation may be especially galling if the crop-raiders merely sample and discard many fruits, thus rendering them unsaleable. In the latter circumstances, it is not surprising that farmers may trap, poison, or shoot apes in defense of their crops.

(This conflict should be distinguished from human vs. nonhuman scramble competition over wild plant products, which presumably has been underway for millennia and may have reached some kind of equilibrium. In southeastern Senegal, both local people and chimpanzees prize the orange-sized fruits of *Saba senegalensis*, which grows in tall vine “towers” in gallery forest. Humans harvest terrestrially, using bamboo poles no more than 4–5 m long, thus inadvertently leaving fruits higher up in the vines to the arboreal apes.)

So, is it culturally maladaptive for chimpanzees to take up crop-raiding? Would a rational creature risk its life for an orange? The answer remains unknown until systematic, quantitative research that includes probabilistic risk assessment is done on the overall foraging strategies of crop-raiders. It is likely to be a multivariate optimality problem that requires data ranging from caloric (energy budgeting) to ethological (an arms race between human defenders and primate raiders?). It may be that the chimpanzees raid selectively in optimal foraging terms, maximizing benefit-cost ratios that include risks. Some evidence, admittedly tentative (Maples et al. 1976), suggests that primates may use cognitively complex tactics—for example, deceptive distraction in crop-raiding forays. Or, it may be that large-brained creatures become addicted or lazy when exposed to the “easy” calories and irresistible tastes of high-sugar, highly digestible, low-toxin cultivars, such as bananas. (If humans cannot resist such “empty” calories, why expect apes to do so?) Or, it may be a simple matter of opportunism: In an area where humans practice shifting, slash-and-burn horticulture, primates may arrive at a traditionally used grove of fruiting trees at the right time of year, expecting to feast. If instead they find that the trees have been cut down and pineapples are growing in their stead, is it really surprising that they then eat what they find?

Such issues are more than academic as, *in extremis*, such cultural maladaptation may lead to local extinction: for example, baboons being exterminated as vermin (personal observation). Acquired dependence on human food may have unexpected and fatal results: for example, baboons scavenging from garbage dumps have contracted tuberculosis (Sapolsky 2004). As well, such conflict is not limited to traditional, subsistence agriculture: for example, historical cycles of imposition and relaxation of bounties on Barbadian green monkeys reflect oscillations of the rise and fall of crop-raiding pressures on sugarcane plantations (Denham 1987).

Finally, great apes exhibit some acquired behavioral patterns that at first glance look dangerous, and that can be interpreted as deliberate risk-taking. Chimpanzees, gorillas, and orangutans typically drink daily from surface water sources, usually streams or springs. However, they tend to avoid larger, deeper bodies of water,

such as rivers or lakes. There are at least two potentially good reasons for this: crocodiles and drowning. The former risk is obvious, as for example *Crocodilus niloticus* is an ambush predator that can take prey even larger than an ape. The latter hazard is likely to be more deadly, however, because great apes cannot swim; rather, they sink like stones (Nishida 1980). This problem is tragically well-known from fatal accidents in water-moated exhibits in zoological gardens. (Monkeys, on the other hand, are excellent swimmers, like most mammals.) Thus, it is not surprising to find an anecdotal report of a wild gorilla using a stick to test the depth of a pool before entering it (Breuer et al. 2005).

It is thus perplexing that great apes enter the water at all, especially to depths great enough for immersion, and so for potential drowning. Yet, western gorillas do this customarily (Blake et al. 1995), and some even hurl themselves into water deep enough to produce a splash display (Parnell and Buchanan-Smith 2001). In captivity, escaping western gorillas ducked underwater in order to avoid electrified fencing floating on the surface of a moat (Golding 1972). Free-ranging, rehabilitated Bornean orangutans stole pirogues and paddled them across deep and wide rivers (Russon and Galdikas 1993). Wild chimpanzees at Mahale do streambed displays by seeking out the deepest pools into which they toss boulders in order to produce impressive splashes (although they do not enter the pools) (Nishida et al. 1999). At Fongoli, chimpanzees congregate to sit up to their chests in rain-filled pools while eating, grooming, or just resting (P. Bertolani, personal communication 2005). Wild bonobos at Lukuru wade bipedally into waist-deep water to harvest algae for food (Myers Thompson 2002).

Thus, it seems that at least the largest-brained primates have enough cortical control to court disaster, that is, to take apparently maladaptive risks for functional or hedonistic purposes. None of this risk-taking has been studied in enough depth to confirm cultural processes, but the putative underlying motives might ring true to human bungee-jumpers!

CONCLUSIONS

This essay has raised both prospects and pitfalls. The prospect of full-blown ethnology on another species, especially one of our two nearest living relations, the chimpanzee, is exciting. Questions of diffusion or convergence, of the various potential mechanisms of cultural transmission from imitation to teaching, and of the possibility of “chimpanzee nature,” as enabled by the painstaking revelation of chimpanzee behavioral universals, are now on the table.

Other prospects are still only hypothetical and remain to be tackled, but they are now engageable challenges: Is chimpanzee culture cumulative, so that each new development builds upon its predecessors, in some kind of complexifying way? Do chimpanzees depend on culture in the way that humans are said to do? Is chimpanzee culture constrained in some crucial way by lack of human-like language, and if so, how? Given a chimpanzee archaeological record, how can we disentangle it from the human one? All of these questions, and many more, are awaiting investigation. It is humbling to recall that when Huxley’s book appeared, fifty years ago, none of them had even been imagined.

If the new bottles are the varied faces of cultural primatology, whether natural history, ethnography or ethnology; observational or experimental; or in nature or captivity, what are the new wines that require vessels? For example, wild primates have been seen for the first time to use hunting technology: Fongoli chimpanzees make and use “spears” (sharpened jabbing sticks) to disable bush babies as prey (Pruetz and Bertolani 2007). In field and zoo contexts, chimpanzees use referential vocal communication to signal about food and social roles (Slocombe and Zuberbuehler 2005a, 2005b). One of the oldest-known, regionally bounded chimpanzee customs, percussive lithic technology restricted to far western Africa, has fallen. Wild apes in Cameroon, 1,700 km east of the supposed “information barrier” of the N’Zo-Sassandra River in Ivory Coast, have been found using stone hammers and anvils to crack nuts (Morgan and Abwe 2006). Captive apes show signs of planning for the future: They select, transport, and cache tools for future use (Mulcahy and Call 2006). It seems that every month, provocative and unanticipated findings emerge, many of which have direct relevance to issues of human cultural emergence and evolution.

Academically, the future of cultural primatology is bright. The phenomenon, if not always the label, is included in every current introductory textbook of biological anthropology, and even in many general ones. Cultural primatologists feel confident enough to proselytize and even to prescribe, in anthropology’s mainstream (e.g., Perry 2006). So, what is wrong with this rosy picture?

The very subjects who give us the material upon which cultural primatology depends are in decline. Wild populations of all great ape species are plummeting: for example, western gorillas in the Congo Basin (Bermejo et al. 2006). At the present rate of attrition, all wild populations of great apes not in protected areas will probably be extinct by the end of the current century. At the same time, especially in ape habitat countries, human population numbers continue their inexorable rise. If this nightmare amounts to a question of “cultural survival,” then all students of culture, not just primatologists, are obliged to join the fight to save our nearest living relations.

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