

# The Evolution of Culture: New Perspectives and Evidence

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This and the next issue of *Evolutionary Anthropology* are devoted to presenting the most recent advances in our understanding of the evolution of culture in non-human primates and humans. This effort was stimulated in part by the recent explosion of comparative evidence for extensive communicative and material culture in two great apes, chimpanzees<sup>1</sup> and orangutans.<sup>2</sup> Before this evidence accumulated, it was easy for anthropologists to maintain that examples of non-human primate culture were little more impressive than those put forward for many other non-human species, and thus they could leave intact the seemingly huge gap between animal and human culture. The overall purpose of this special pair of issues of *Evolutionary Anthropology* is to ask how and why culture has changed over evolutionary time from non-primates to non-human primates to early hominins to modern humans.

As evidence accumulates for continuity in cultural abilities between animals and humans, so have disputes arisen about what exactly defines culture. These arguments arise partly from the usual lack of standardization common to many emerging disciplines, but also from the perceived need to distinguish what animals do from what humans do. Frigaszy<sup>3</sup> starts off this issue with a discussion of some of these problems and a proposed resolution, being careful to distinguish what culture is from the problem of how we recognize that it

exists in a given population or set of populations. All the contributors to these special issues agree that culture is minimally a pattern of behaviors (or their material manifestations or informational content) that is socially transmitted, rather than genetically inherited or stimulated by particular environmental conditions. Beyond that, however, debates arise about how long the pattern must persist and how widespread it must be for us to consider a particular behavioral pattern as cultural. Frigaszy argues forcefully that social transmission is the *sine qua non* of culture; just showing the existence of distinctive group- or population-specific behaviors will always leave in doubt the mechanism which accounts for the differences and thus whether the observed differences are cultural. Indeed, at the end of the second issue in this series, Laland and Hoppitt<sup>4</sup> review the scientific evidence for culture and present the surprising conclusion that the evidence is most direct for certain experimentally-tractable fish and birds with rather simple cultural differences, rather than the seemingly more interesting and complex examples from great apes and other primates. Will

the evidence for culture in non-human primates necessarily remain weak? Frigaszy<sup>3</sup> describes at least two methods to strengthen future studies of culture in species not easily amenable to population-level experiments.

If any reasonably common and persistent socially-learned behavior in an animal can qualify as cultural, then what, if anything, distinguishes the human variety? In some contributions to these issues, the word "tradition" is used as a synonym for culture in the broad sense, but is reserved for animals. In other cases, all socially-transmitted behavior patterns are called cultural, but human culture is set apart by some criterion, for instance "cumulative culture." What is the evidence of a continuum of abilities or qualities of culture that progress from animals to monkeys to apes to humans? Is the gap between all animals and man so vast that it will remain unscientific speculation to try to bridge it? Does a particular mode of learning (e.g., imitation, teaching) define human culture? Is human culture unique in being cumulative?

These and other questions are addressed empirically and theoretically in the remaining seven articles in this series of two issues devoted to cultural evolution. In doing so, the research reviewed here analyzes cultural phenomena using a wide array of methods and approaches. The evidence on non-human primates uses longitudinal studies of changing behaviors within groups, broad comparisons of group-distinctive behaviors between groups within a population and between populations, and increasingly sophisticated laboratory experiments on learning and cognition. Even the three essays focused on just *Homo sa-*

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*piens* include ethnographic observation, experiments, formal models, archaeology, and paleontology.

Following the first article by Fraszky,<sup>3</sup> the rest of the present issue is devoted to articles that summarize empirical evidence for culture in monkeys and chimpanzees. Perry and Manson<sup>5</sup> neatly summarize the growing evidence for cultural differences among populations of monkeys. They make a strong case that longitudinal studies of single populations of a species can provide convincing evidence for traditions. Although the range of foraging behaviors that might qualify as traditions is rather poor compared to that in great apes, they show that monkeys can possess relatively rich and rapidly changing repertoires of cultural behaviors in the realm of social communication. They argue that these behaviors are essentially a private channel of communication among potential partners anxious to test the strength of their social bonds with each other. This reasoning foreshadows the argument of Alvard<sup>6</sup> in the next issue that one of the benefits of symbolic cultural distinctiveness is that it facilitates coordinated action among humans who share aims and value systems.

Boesch<sup>7</sup> then addresses directly the question of whether the evidence for culture in chimpanzees is sufficiently strong, and its manifestations sufficiently diverse, to cross the apparently vast chasm between animal and human culture. Boesch starts with a small set of traits that arguably set out the three minimal requirements for a human level of culture: social transmission, group distinctiveness, and shared symbolic content. He then shows that chimpanzees in the wild show suggestive evidence for all three. He adds to previous evidence of population distinctiveness in foraging and social behaviors with exciting new evidence for significant differences among neighboring groups of the same population in Tai National Park. He also fleshes out the evidence for social transmission of nut-cracking behaviors in these chimpanzees, and discusses whether some of these foraging traditions could be the result of cumulative cultural evolution.

In the final contribution on non-

human primates, Whiten<sup>8</sup> and colleagues take a different approach to the question of the continuity of animal and human culture. They set out a comprehensive list of ten defining characteristics of human culture, expanding beyond Boesch's set to include cultural complexity, advanced aspects of social transmission (imitation, teaching, conformity, selective retention based on meaning), and the particular content of human culture. They then ask if there is evidence for each of these characteristics in chimpanzees, whether wild or captive. Perhaps not surprisingly, given our close similarity, chimpanzees show at least some evidence for each of these. What is less clear is if chimpanzees are unique in doing so—would equally detailed studies of birds or fish show at least some evidence for all these characteristics? Which specific ones would fail to show up in animals less similar to us? Several of the articles presented here focus on the ability of humans and chimps to imitate complex sequences of hand movements and they note the lack of evidence for direct imitation in other animals. However, Laland and Hoppitt<sup>4</sup> question whether imitation is as ubiquitous in humans or as rare in other animals as is currently suspected.

In a recent article presenting evidence for orangutan culture, van Schaik and colleagues<sup>2</sup> present yet another "taxonomy" of culture by focusing on the *domains* of cultural phenomena, which they list as: labels (e.g., commonly shared responses to predators), signals (conventional communicatory signs or displays), skills (including tools), and symbols (arbitrary signals that serve to define group membership). They conclude that humans are unique in possessing the last of these domains, but that great apes are also unique among animals in showing all of the first three domains.

Whatever the evolutionary and psychological continuities between non-human primate and human culture, no one disputes that *Homo sapiens* displays a unique degree of dependence upon and elaboration of cultural inheritance and its products (particularly technology and social institutions). Three contributions in the

next issue of *Evolutionary Anthropology* focus on human culture and delineate various aspects of this unique development. In the first article, Foley and Lahr<sup>9</sup> use the archaeological record to demonstrate that the technological manifestations of cultural evolution (as classified into different stone tool "modes") emerged in fits and starts at various points in the hominin phylogeny. Indeed, early change in hominin material culture was so slow that it appears to have been essentially static for at least 500,000 years. These episodic increases in tool sophistication and variability presumably reflect evolutionary innovations in cognitive mechanisms underlying cultural transmission. Unfortunately, reliably inferring these mechanisms from the archaeological record is extremely difficult at best.

The articles by Henrich and McElreath<sup>10</sup> and by Alvard<sup>6</sup> draw primarily on ethnographic evidence, and are correspondingly able to make more headway in delineating possible cognitive mechanisms underlying our species' unique reliance on culture. Henrich and McElreath<sup>10</sup> raise a variety of questions that they address mostly with theoretical models: 1) How does social learning increase adaptability? 2) Why is reliance on such a diverse array of transmission mechanisms so rare outside our species? 3) What cognitive processes guide cultural transmission? 4) Given low copying fidelity and the lack of any clear particulate basis to cultural traits, how can culture in fact evolve? 5) Do genes (and the basic cognitive mechanisms for which they code) and culture co-evolve, and if so, over what time scales and in what directions?

Following in the tradition pioneered by Boyd and Richerson<sup>11</sup> and Cavalli-Sforza and Feldman,<sup>12</sup> Henrich and McElreath<sup>10</sup> emphasize the population-level dynamics of cultural transmission and change, dynamics that can be fruitfully analyzed using modified versions of various population-genetic models. Henrich and McElreath also incorporate psychological mechanisms that purportedly underlie human cultural transmission (e.g., conformity to local norms or beliefs, preferential imitation of locally successful individuals), and which are

presumed to be pan-human and genetically-evolved adaptations. If their hypotheses are correct, these mechanisms provide at the same time a bio-evolutionary basis to cultural transmission, a link to studies of primate culture and cognition, and a framework for explaining why human behavioral evolution follows some unique trajectories, including ones that sometimes produce maladaptive outcomes in terms of the genetic fitness of their individual bearers.

This last question—how human culture developed along an apparently unique evolutionary path—is answered distinctively in each of the final three articles in the next issue. Henrich and McElreath<sup>10</sup> elaborate an earlier model<sup>13</sup> that pointed out that social learning based on inference (which they term “true imitation”) is not generally favored when it is rare, so that a population must traverse a fitness “valley” to reach a situation that leads to predominant imitation-based learning. Because imitation is widely held to be a prerequisite for cumulative culture, this evolutionary barrier could explain why cumulative culture is so rare in nature. Simpler forms of social learning do not require such synergism and so can spread when rare, but also they do not lead to cumulative cultural adaptation. This is an intriguing hypothesis, but as these authors recognize, it does not in itself explain how and why it was that this threshold was surmounted in the hominin lineage but not in others.

Alvard<sup>6</sup> presents a distinct answer to the puzzle of human cultural uniqueness by addressing several related questions: 1) how does human culture benefit humans, 2) what particular ability does this benefit require, and 3) how could natural selection have favored this particular ability in the absence of the cumulative cultural evolution which it eventually enabled? Alvard emphasizes the important role that culture may have in facilitating coordinated action among mutually interested actors, either by presenting signs of shared goals (the “symbolic” domain listed by van Schaik et al.<sup>2</sup> as uniquely human) or by promoting direct communication (primarily via language). This co-

ordination hypothesis allows the trait of imitative social transmission to be favored even when rare, as long as the group of individuals that adopts such mutual conventions is able to achieve better control of its environment or defend itself more effectively against groups that do not possess such coordinated actions.

Finally, Laland and Hoppitt<sup>4</sup> take a more gradualistic approach. They suggest that humans are not unique, but just happen to be the beneficiaries of a positive feedback process between cumulative cultural modification of our environment (“niche construction”) and the set of conditions that favor increasing degrees of social learning (environmental change that is rapid, but not too rapid). They posit that this process is not different in kind for humans, but merely more advanced in degree, than that present among non-human animals.

Whichever of these views is correct, it is clear that 1) culture has emerged as a subject for serious study by evolutionary scientists, 2) there is some degree of continuity between animals and man in cultural capacities, and 3) a great deal of new data will be required to distinguish among the alternative explanations. As Alvard<sup>6</sup> discusses, the idea that culture fundamentally changes the dynamics and outcome of human behavioral evolution is resisted by many evolutionary anthropologists, who prefer to study human populations using the same acultural adaptive arguments employed in non-human behavioral ecology. Perhaps these skeptics are right, but they may be as mistaken as those evolutionists over thirty years ago who resisted the proposal that sexual selection required a serious rethinking of the workings of Darwinian evolution.

Why is culture an important, perhaps even critical, factor for evolutionary anthropology? Based on the research and arguments presented in these special issues, we suggest there are at least three reasons. First, the means by which humans and our closest primate relatives adapt behaviorally to various social and natural environments cannot be understood without including cultural transmission. Second, the dynamics of adapta-

tion—the rates and patterns of change—differ under cultural evolution as compared to either genetic evolution or phenotypic plasticity. Finally, in the case of *Homo sapiens*, the existence of many observed outcomes of behavioral adaptation (and maladaptation) could not be understood without substantial cultural evolution. For example, as Henrich and McElreath<sup>10</sup> point out, even a tiny sample of pre-industrial human societies can encompass “a greater range of subsistence behavior than the rest of the Primate Order combined.” In addition, the ability of humans to engage in monumental cooperative tasks (including warfare) may depend critically on shared symbols that are transmitted culturally, as postulated by Alvard in his article. If this line of argument, also developed extensively by others,<sup>14–18</sup> is correct, then some aspects of human cooperation may have more in common with social insects than with our close primate relatives.

Arguably the biggest gap in cultural-evolutionary research is the paucity of empirical tests of the formal theory that has developed over the last two decades. As Alvard<sup>6</sup> notes, “[e]volutionary anthropologists who have studied cultural processes, while developing a very rich theoretical program, have left untested many of the predictions generated by this theory.” This results in a field with a quite unbalanced ratio of theory to (relevant) empirical findings. Perhaps the example provided by primatologists,<sup>1–3,5,6,8</sup> plus the provocative suggestions from archaeologists like Foley and Lahr,<sup>9</sup> added to the recent spate of cross-cultural experimental research<sup>19</sup> will inspire a concerted effort to rectify this imbalance. If so, we can look forward to exciting new vistas in *Evolutionary Anthropology's* repeat special issue on cultural evolution a decade from now.

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