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The knowns and unknowns of chimpanzee culture

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Claims of culture in chimpanzees appeared soon after the launch of the first field studies in Africa.[1] The notion of chimpanzee 'material cultures' was coined,[2] and this was followed by a first formal comparison, which revealed an astonishing degree of behavioural diversity between the different study communities, mainly in terms of tool use.[3] Although this behavioural diversity is still undisputed, the question of chimpanzee cultures has remained controversial.[4-6] The debate has less to do with the definition of culture (most animal behaviour researchers accept the notion for behaviour that is 'transmitted repeatedly through social or observational learning to become a population-level characteristic'[3]), but more with whether some key criteria are met.

The main points of contention are two. A first one has to do with the biological processes leading to observed behavioural differences. It is possible that the behavioural diversity seen in chimpanzees is the product of genetic or ecological factors, rather than cultural learning. This argument also rests on the fact that one third of all observed behavioural variants are found only in one population, the subspecies *Pan troglodytes verus*.[6] A second line of critique concerns the underlying psychology supporting the transmission of the behaviours. Crucially, the behaviours found in a community may be the product of independent individual learning, rather than complex forms of social learning, such as imitation or teaching, which are thought to be fundamental to transmission in human cultures.[7-9] Animal cultures, in other words, might differ not only in degree but also in kind from those of humans.

Until recently, research in the domain of 'cultural primatology'[10] was purely observational, although in many cases involving highly sophisticated micro-ecological or phylogenetic analyses.[11,12] Intriguing as they are, these analyses cannot decide between the main alternative hypotheses, that is, that the observed population differences in behaviour are the result of genetic or ecological factors. To address the issue, we carried out a field experiment to investigate one foundation upon which the chimpanzee culture claim rests: the difference in tool use behaviour in two Ugandan communities of the *Pan troglodytes schweinfurthii* subspecies. The study was carried out with the Sonso community of Budongo Forest and the Kanyawara community of Kibale Forest.[13] Genetic differences between the two communities are known to be negligible.[14] The two forests, separated by less than 200 km, are very similar in most relevant ecological variables. Although they have somewhat different logging histories, the sections inhabited by the two chimpanzee communities have both been heavily logged during the 20th century. Despite these similarities in ecology and genetics, however, there are a number of behavioural differences between the two communities.[3] While Kanyawara chimpanzees sometimes use sticks during foraging, this behaviour has never been recorded in the Sonso community, despite two decades of continuous observations. However, the Sonso chimpanzees regularly produce leaf sponges to retrieve water from tree holes, a behaviour also seen in other wild populations, including Kanyawara.

Figure 1. Young chimpanzees grow up in small but highly cohesive social units in which foraging and food processing is conducted as part of a group activity (Photo courtesy Florian Möllers).

In our experiment, we exposed individuals of the two communities to an identical but novel foraging problem, liquid honey trapped in a vertical hole that was drilled into a large naturally fallen horizontal tree. The hole was wide enough for chimpanzees to insert two fingers, but not shallow enough to retrieve honey during the critical experimental condition. We found that the individuals of the two communities differed radically in how they tried to solve this problem. Most Sonso individuals (unsuccessfully) inserted their fingers, but some proceeded to manufacture leaf sponges to extract honey. In contrast, most Kanyawara individuals quickly manufactured sticks and retrieved honey by inserting them into the hole. None of them produced a leaf sponge, even though this is part of their tool repertoire. The most likely explanation for this behavioural difference is that individuals resorted to their own cultural background, previously acquired in their communities, rather than individualistic trial-and-error based attempts. Their cultural knowledge, in other words, helped them to solve this novel task.[13]

Has this experiment finally resolved the controversy surrounding chimpanzee culture? Critics continue to point out that the issue of acquisition is still not addressed. We have been able to rule out that chimpanzees were looking for private ad hoc solutions, but it is still possible that the community-specific behavioural differences were acquired originally by individual learning (that is, without any kind of social influence). In sum, the chimpanzees may be relying on 'habits', acquired earlier through individual learning.[15] Although this explanation remains a theoretical possibility, we find it an unconvincing one, for the following reasons.

If trial-and-error based individual learning were the main mechanism for the acquisition of tool use behaviours, then one would expect different techniques to emerge within the same group, even when the ecological conditions are the same. Instead, we found perfect segregation: no Kanyawara individual produced a leaf sponge, while no Sonso individual manufactured a stick to access the honey. But are the two habitats really so similar? Both forests were connected until about 10,000 years ago, suggesting that the observed behavioural differences cannot be the result of different long-term ecological pressures on these populations, an explanation often proposed to explain behavioural differences between communities.[8] Second, honey produced by Apis, Meliponula and Xylocopa bees is regularly found in both forests, suggesting that the learning opportunities to extract honey have been equal for all individuals, regardless of community membership.

Another relevant point is that chimpanzees spend the first ten years of their lives in almost constant contact with their mothers and siblings,[16] suggesting that occasions for private individual learning are rare, while social influences are strong and omnipresent. In chimpanzees, foraging is a group activity and individuals are very attentive to each other's behaviours from an early age (**Fig. 1**).

Dietary habits could be responsible for rendering tool-based foraging more or less likely. As mentioned earlier, the habitats of both communities have been logged, but the destruction was greater at Kibale, compared to more selective logging at Budongo.[17] In Kibale, this has led to much secondary vegetation, which has often inhibited tree growth.[18] In Budongo, the logged gaps were often occupied quickly by fast-growing trees, such as *Celtis durandii, C. mildbraedii* and Ficus spp.,[19,20] reliable producers of high-energy fruits consumed by primates.[21] The Sonso chimpanzees heavily rely on these fruits as the main part of their diet.[22] Several of these species are absent at Kanyawara,[23] although Kanyawara chimpanzees also rely on figs but not as a major part of their diet.[24] Another relevant finding is that a neighbouring community of the Sonso chimpanzees, the Kasokwa community, has also been seen using sticks during foraging (Wallis J, personal communication). Although less than 10 km away from Sonso, the Kasokwa habitat consists of a riverine forest fragment with a different and less food-rich vegetation.[22,24]

Thus, stick-based foraging might have disappeared from the Sonso behavioural repertoire due to the human-induced advent of easily accessible, high-quality foods available throughout the year, an unusual situation for most other chimpanzee populations who face annual periods of food scarcity. Although this hypothesis puts a major emphasis on the ecology, it does not rule out a cultural explanation of behaviours. Instead, the ecological influence may act as a trigger for culturally transmitted behaviours to either emerge or disappear. According to this argument, social learning is responsible for the maintenance of potential cultural behaviours in a community, which will otherwise disappear if community members are no longer exposed to them by the original innovator and those who learnt from him.[25]

The complexities outlined above illustrate the need for an appropriate field experiment to shed light on the transmission patterns of novel behaviour, as has been done in captivity.[26] Traditionally, there has been considerable resistance to

expose wild chimpanzees to field experiments. We and others have shown that carefully carried out field experiments with wild chimpanzees are possible and that they can generate meaningful results. This commitment requires high standards in terms of minimising health risks and unethical infringement in the daily lives of these animals. In our experience, a successful field experiment needs to be designed such that the manipulation is not perceptible to subjects as man-made. Instead, it needs to melt into a natural landscape that is ecologically relevant to the individuals. It is in this spirit that scientific progress on important questions, such as chimpanzee cultures, should be most likely.

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