

Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task

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Summary

Population and group-specific behavioral differences have been taken as evidence for animal cultures [1–10], a notion that remains controversial. Skeptics argue that ecological or genetic factors, rather than social learning, provide a more parsimonious explanation [11–14]. Work with captive chimpanzees has addressed this criticism by showing that experimentally created traditions can be transmitted through social learning [15–17]. Recent fieldwork further suggests that ecological and genetic factors are insufficient to explain the behavioral differences seen between communities, but the data are only observational [18, 19]. Here, we present the results of a field experiment [20, 21] that compared the performance of chimpanzees (*P. t. schweinfurthii*) from two Ugandan communities, Kanyawara and Sonso, on an identical task in the physical domain—extracting honey from holes drilled into horizontal logs. Kanyawara chimpanzees, who occasionally use sticks to acquire honey [4], spontaneously manufactured sticks to extract the experimentally provided honey. In contrast, Sonso chimpanzees, who possess a considerable leaf technology but no food-related stick use [4, 22], relied on their fingers, but some also produced leaf sponges to access the honey. Our results indicate that, when genetic and environmental factors are controlled, wild chimpanzees rely on their cultural knowledge to solve a novel task.

Results and Discussion

Some of the strongest evidence for animal culture comes from studies on wild chimpanzees comparing the behavioral patterns of different populations in Africa [4, 5]. Population-specific behavioral differences are particularly evident in tool use. However, the observational nature of most field studies makes it difficult to draw definitive conclusions, because it is impossible to rule out all potential ecological or genetic explanations for behavioral variation attributed to culture [12]. Although social transmission has been observed in captivity, with good evidence that chimpanzees can socially learn

arbitrary behaviors [16], it is currently unclear to what degree this finding can be applied to the wild. For example, it is possible that chimpanzees resolve a particular problem with trial-and-error learning because they operate under the same conditions every time they confront it, not because they have acquired cultural knowledge. Testing cultural knowledge, therefore, requires field experiments by which individuals of the same genetic background are tested with a novel problem under the same environmental conditions, thus controlling for all other potential sources of explanations.

We conducted a field experiment with two communities of East African chimpanzees, *P. t. schweinfurthii*, to investigate how their cultural knowledge determined the way they solved a simple cognitive task under identical ecological conditions. The genetic differences between the two communities are negligible and insufficient to assign an individual to a particular community, making it unlikely that any difference in behaviors is the result of underlying genetic differences [23]. Individuals of the Sonso community of Budongo Forest and the Kanya-wara community of Kibale National Park, Uganda, were allowed to encounter an artificial hole of 4 × 5 cm, drilled into a horizontally situated log, which was filled with natural honey. Honey, produced by bees of the *Apis*, *Meliponula*, and *Xylo-copa* genera, is found in both forests and consumed by members of both communities ([22], M.N.M. and R.W., unpublished data). A rectangular shape was chosen to provide a visually novel stimulus that differed from the entrance of the beehives chimpanzees naturally encounter in the wild. In another difference, the hole was presented in the horizontal plane. Natural beehive entrances are usually found on the vertical sides of trunks (see the Supplemental Data available online), but chimpanzees may also access the hives after the supporting trees have fallen down. In such cases, honey is easily accessible and chimpanzees do not use sticks on such trees (T.G., unpublished data). Finally, experimental honey was provided as a liquid substrate as opposed to the waxy honey naturally encountered by the chimpanzees. This accumulation of differences generated a task sufficiently different from what chimpanzees usually encounter in the forest, while conserving the basic natural features. This way we were able to ensure that individuals could not rely blindly on simple stimulus-response algorithms acquired previously for example by operant conditioning. Moreover, we made sure, by filling the holes when no individual was present, that chimpanzees could not associate the presence of honey with humans.

The experimental logs were selected so that they were located in a relatively open area of at least 5 × 5 m often visited by the chimpanzees. Individuals had unrestricted access to the hole during the experimental phase, and no efforts were made to attract individuals or to encourage engagement with the hole.

Two types of hole were drilled at each site. The first was 11 cm deep with honey filled up to 6 cm below the surface. This allowed the chimpanzees to get most of the honey by using their fingers only. Tool use was not required. Honeycombs were scattered around the hole to provide a visual cue (Figure 1A). In the second experiment, the same hole was re-drilled to a 16 cm depth, with honey filled up to 10 cm beneath

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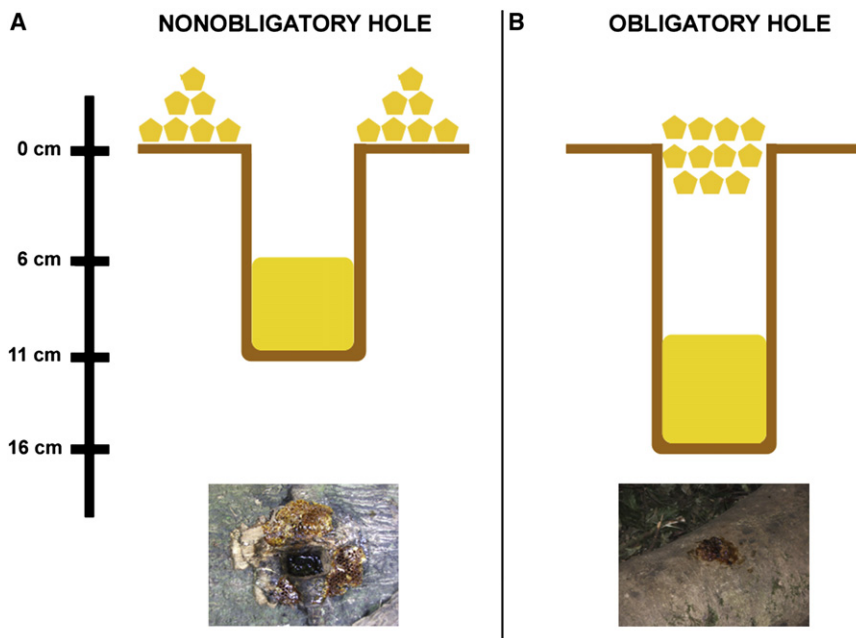


Figure 1. Schematic Representation of the Two Experimental Conditions of Honey Presentation

(A) Experiment 1. A hole of 11 cm was drilled into a tough, recently fallen log. Natural honey was filled up to 6 cm below the surface, which could be reached by inserting one or several fingers. Honeycombs were placed around the entrance to attract the chimpanzees (picture taken at Budongo).

(B) Experiment 2. The same hole was redrilled to a depth of 16 cm, and honey was filled up to 10 cm beneath the surface. Honeycombs were used to cover the entrance to the hole and prevent wild bees from entering and harvesting the honey (picture taken at Kibale).

For predicting tool use, we obtained lambda values of 0.400 (shallow condition) and 0.857 (deep condition). For predicting the response category, we obtained lambda values of 0.6 and 1 (see Experimental Procedures). Although in the shallow condition the range of response choices was larger than in the

deep condition, both lambda values demonstrated that group identity was a strong predictor of behavior in both conditions.

The Kanyawara chimpanzees engaged significantly longer ($n = 18$, mean time of 1177 s, standard deviation [SD] = 2044 s) with the two holes than the Sonso chimpanzees ($n = 22$, mean time of 126 s, SD = 132 s) (Mann-Whitney test, $Z = -3.453$, $p = 0.001$), but this difference could not explain why Sonso chimpanzees never used sticks. Because time before manufacturing a tool did not differ significantly between the two conditions in Kanyawara (shallow hole, $n = 4$, mean = 30.5, SD = 41.5; deep hole, $n = 7$, mean = 20, SD = 15.6; Mann-Whitney test, $Z = -0.38$, $p = 0.704$), we pooled the data and excluded cases where an individual had engaged previously with the hole before manufacturing a tool. The mean Kanyawara duration from first encounter to choosing a tool was 23 s ($n = 11$, range 0–88 s). Most chimpanzees at Sonso spent more than 23 s engaging with the hole, so that they would have had sufficient time to select a stick. Moreover, the three Sonso individuals who produced tools during their first engagement with the hole did so in the time range of the Kanyawara chimpanzees ($n = 3$; range 4–61 s). Crucially, Sonso chimpanzees have never been observed using sticks to acquire food in over 15 years of continuous observations.

It is theoretically possible that the stick use by the Kanyawara chimpanzees is the result of prior individual rather than social learning. Although our study does not address the previous learning history of our animals, a number of points make individual learning a less likely ontogenetic mechanism. First, the speed, determination, and accuracy of the tool-using individuals in both communities strongly suggest that ad hoc individual learning on a trial-and-error basis is an unlikely explanation for the observed differences. Affordance learning can also be ruled out by the fact that the physical properties of the task were kept identical by the design of the experiment, yet the chimpanzees responded in community-specific ways. Finally, because of the ecological and genetic similarities between the two communities, the individual-learning hypothesis predicts that individuals in both groups should be equally likely to learn stick use to obtain natural honey,

the surface. In this condition, it was no longer possible to access the honey with the fingers. Again, honeycombs were positioned to provide visual cues, this time covering the hole to prevent insects from exploiting the honey before the chimpanzees arrived (see Experimental Procedures) (Figure 1B).

At both sites, individuals initially showed similar responses to the artificial holes by consuming all available honeycombs. However, their subsequent behaviors differed in striking ways. At Sonso, most individuals relied on their hands only to access the honey in both experimental conditions (Table 1), but some of them also used leaves (Figure 2A; see Supplemental Data). For the 11 cm hole, tool use was not required, but two of 13 individuals nevertheless inserted leaves to extract honey (RE and PS). In the second condition, tool use was necessary and two further individuals of 11 in total were observed to compress leaves in their mouth to produce a leaf sponge. One of them, a subadult male (HW), proceeded to sponge the honey. In comparison, most chimpanzees at Kanyawara prepared sticks to access the honey (Figure 2B; 11 cm hole: 6 of 10 individuals; 16 cm hole: 11 of 12 individuals; see Supplemental Data). No individual at Kanyawara used leaf sponging, although the behavior is customary in the community in other contexts [4].

Overall, there was significantly more tool use at Kanyawara than Sonso in both the 11 cm (nonobligatory) shallow (Fisher exact test, $p < 0.05$) and the 16 cm (obligatory) deep condition ($p = 0.001$). Using the Freeman-Halton extension of the Fisher test [24], we found that the overall distribution of the three categories of responses (no tool, stick, and leaves) was significantly different from the null hypothesis (i.e., the two populations are identical in their techniques to access the honey; $p < 0.01$ and $p < 0.001$, respectively), providing statistical evidence that Kanyawara and Sonso chimpanzees responded in a group-specific manner. To assess the size of this difference, we calculated the Lambda value for predicting tool use (yes or no) and for predicting the response category (no tool, stick, leaves). The Lambda test is a nonparametric variable that gives the proportional reduction in error when group membership is used as a variable to predict behavior [25].

Table 1. Summary of the chimpanzees of the Sonso and Kanyawara communities engaging in the honey acquisition task

Community	ID	Age	Type	Mode	Use of Tool	Length of Direct Interaction	Total Time of Interaction	Latency to First Tool Use	Mean Latency to All Tool Use
Sonso	AN	adult	deep	M	no	30	30	n.a.	n.a.
Sonso	HL	juvenile	deep	H	no	98	98	n.a.	n.a.
Sonso	HT	adult	deep	H, L	yes	102	102	4	4
Sonso	HW	subadult	shallow	H	no	27 ^b	127	n.a.	n.a.
Sonso	HW	subadult	deep	H, L	yes	100	127	54	54
Sonso	HY	infant	deep	H	no	91	91	n.a.	n.a.
Sonso	KL	adult	shallow	H, M	no	60	60	n.a.	n.a.
Sonso	KM	subadult	shallow	H	no	4	4	n.a.	n.a.
Sonso	KN	subadult	shallow	H, M	no	14	14	n.a.	n.a.
Sonso	KS	juvenile	shallow	H	no	60	60	n.a.	n.a.
Sonso	KU	adult	shallow	H, M	no	105	105	n.a.	n.a.
Sonso	MN	juvenile	deep	H	no	45	45	n.a.	n.a.
Sonso	ML	adult	deep	H	no	45	45	n.a.	n.a.
Sonso	NB	adult	deep	H, M	no	478	478	n.a.	n.a.
Sonso	NR	subadult	shallow	H, M	no	108	170	n.a.	n.a.
Sonso	NR	subadult	deep	H, M	no	62	170	n.a.	n.a.
Sonso	NT	juvenile	deep	H	no	493	493	n.a.	n.a.
Sonso	PS	subadult	shallow	H, M, L	yes	106	106	***	***
Sonso	RE	subadult	shallow	H, M, L	yes	279	279	61	61
Sonso	SB	adult	deep	H	no	75	75	n.a.	n.a.
Sonso	ZG	subadult	shallow	H, M	no	30	30	n.a.	n.a.
Sonso	ZK	juvenile	shallow	H	no	50	50	n.a.	n.a.
Sonso	ZL	subadult	shallow	H	no	194	194	n.a.	n.a.
Sonso	ZM	adult	shallow	H, M	no	105	105	n.a.	n.a.
Kanyawara	AJ	adult	shallow	H	no	1307	1307	n.a.	n.a.
Kanyawara	AL	adult	deep	M, S	yes	10	10	4	4
Kanyawara	AT	juvenile	deep	H, M, S	yes	259	259	20	20
Kanyawara	BO ^a	juvenile	deep	H, M, S	yes	97	97	3	3
Kanyawara	ES	subadult	shallow	H, S	yes	1448	1734	0	0
Kanyawara	ES	subadult	deep	H, S	yes	286	1734	**	**
Kanyawara	EU	juvenile	shallow	H	no	112	958	n.a.	n.a.
Kanyawara	EU	juvenile	deep	H, S	yes	846	958	**	**
Kanyawara	KK	adult	shallow	H, M, S	yes	260	260	***	***
Kanyawara	LK	adult	shallow	H	no	114	114	n.a.	n.a.
Kanyawara	LR	adult	shallow	H, S	yes	446	446	***	***
Kanyawara	LR	adult	deep	H, S	yes	502	502	***	5
Kanyawara	NP	juvenile	deep	H, M, S	yes	2899	2899	40	27
Kanyawara	OG	juvenile	deep	H, M, S	yes	852	852	8	8
Kanyawara	OT	subadult	deep	H, M, S	yes	834	834	20	26
Kanyawara	PB	subadult	shallow	H, S	yes	296	296	88	88
Kanyawara	PG ^a	adult	shallow	H	no	5	11	n.a.	n.a.
Kanyawara	PG ^a	adult	deep	H	no	6	11	n.a.	n.a.
Kanyawara	QT	adult	shallow	H, M, S	yes	1515	8795	0	125
Kanyawara	QT	adult	deep	H, M, S	yes	7280	8795	***	7
Kanyawara	TJ	subadult	deep	M, S	yes	269	269	45	45
Kanyawara	WL	adult	shallow	H, M, S	yes	1540	1540	34	25

Data points are sorted per individuals and community. Individuals are presented in alphabetical order, sorted per community. Several individual engaged with the holes in the two experiments. Time is given in seconds. For each individual, the community of origin (Sonso or Kanyawara) and age class are given (adult, subadult, or juvenile). Infants were not taken into account, because they merely played and did not try to acquire the honey. Measurements were taken as mode of contact with the hole by hand (H), mouth (M), or tool (S: stick; L: leaves), excluding visual information acquired by gaze. For each individual and setting (deep 16 cm hole; shallow 11 cm hole), tool use was scored (yes or no). Total time engaging with the hole is given for both settings separately and combined. Latency to tool use = time (s) from first engagement with the hole to first contact with a tool. All cases where individuals had a previous knowledge of the hole were excluded. *Individual manufactured tool but did not use it. **Delay in the onset of the automatic video camera did not allow exact time measures before taking a tool. ***Individuals with prior knowledge of the hole (either with a previous setting or a previous nontool engagement) excluded from the analysis.

^a Individuals missing a hand because of a snare.

^b Engagement with the combs only, not with the hole.

which was not the case. Because of all these reasons and the fact that chimpanzees in both communities selected tools quickly and in community-specific ways, it is more likely that their decisions were based on cultural knowledge in line with the evidence from captivity [17]. To our knowledge, this experiment is the first to compare two genetically indistinguishable populations of the same subspecies [23] with the same task, thereby controlling for both genetic and environmental factors [13]. Through the use of a standardized hole, filled with the

same type and amount of honey, under the same environmental conditions, any differences in observed behavior are most parsimoniously attributed to the individuals' prior learning histories or, more specifically, the differences in their cultural backgrounds [4, 5].

The behavioral results obtained with this experiment also reflect subtle differences in dietary habits between the two communities [26, 27]. The Kanyawara chimpanzees eat *Apis* honey about once per month and unsuccessfully try to obtain



Figure 2. Tools Used by the Chimpanzees during Honey Acquisition

(A) Wedges of leaves manufactured by chimpanzees at Budongo during experiment 1.

(B) A selection of sticks manufactured by chimpanzees at Kibale during experiment 1 and 2.

honey at a similar rate (Kibale Chimpanzee Project, unpublished data, 1991–2001). By comparison, honey consumption is rare in Sonso, but this has nothing to do with the antipredator behavior of the bees, which fiercely attack chimpanzees at both sites (T.G., unpublished data). In our experiment, Kanyawara individuals engaged longer with the hole, and they revisited the experimental spot regularly when feeding in the vicinity. At Sonso, honey consumption appeared to be much more opportunistic, coinciding with feeding at a nearby *Raphia farinifera* tree [28].

From a cognitive point of view, our results suggest that chimpanzees rely on their cultural knowledge to solve a novel foraging problem. Kanyawara chimpanzees occasionally attempt to acquire small amounts of honey (~1–5 mg) available in the nests of solitary carpenter bees (*Xylocopa* spp.). Such attempts always involve a probing stick used to obtain the waxy honey. They continued to use this technique when the food was encountered in the spatially and visually novel setting of our field experiment. In contrast, the Sonso chimpanzees do not use tools to access food and, consequently, their first approach to the problem was to use their fingers. The Sonso chimpanzees produce leaf sponges to retrieve water from hollows in trees, and some individuals applied this technique to the novel problem of the experimental situation. The fact that they consumed the combs beforehand, possibly perceived the smell of honey, and perceived the presence of bees, makes it improbable that they anticipated finding water in the artificial hole.

As argued before, the fact that all the chimpanzees reacted in a community-specific way supports a culturally based rather than an individual acquisition of the behavior. We define culture as a community-specific set of behaviors that an individual is exposed to and can socially learn from. According to this view, the Sonso chimpanzees do not use sticks during feeding because they have never seen another chimpanzee using sticks in this context, but once someone invents the technique, it may spread through the community through socially aided processes [21, 29]. Our experiment does not show how individuals originally acquired their set of foraging behaviors, only how individuals apply their knowledge when confronted with novel problems. As a final point, our study highlights the fact that the “exclusion method,” commonly used to identify cultural differences among populations [10], may not always be suitable to identify all cultural variants. As mentioned, both chimpanzee populations have been observed

to use leaf sponges, but only the Sonso individuals applied this technique to the experimental condition, suggesting that the complexity of a behavior and its contextual use should be taken into account when comparing cultural differences between populations [30].

From a methodological point of view, we have demonstrated that, by using simple cognitive tests to which there are several solutions, the disparate influences that affect behavior can be studied systematically in the wild. We were able to control for the genetic, environmental, and task-related influences, leaving cultural differences as the most plausible explanation. Field experiments of this kind, when combined with the necessary observational studies and supported by more controlled studies in the laboratory, can provide a robust test to systematically compare cultural differences in wild animals.

Experimental Procedures

Subjects and Study Sites

The Sonso community (01°43'N, 31°32'E) has been studied in the Budongo Forest since 1990 and has been fully habituated to human observers since 1994. At the time of the study, the community consisted of 69 individuals. The Kanyawara community (00°33'N, 30°21'E) has been continuously studied in Kibale National Park since 1987 and has been fully habituated since 1994. At the time of the study, the community consisted of 46 individuals. The distance between the two sites is about 180 km.

Procedure

Natural honey was acquired from local bee farmers of the Masindi District, Uganda, whose bees of the genus *Apis* forage freely in Budongo Forest. At both sites, the experimental holes were drilled in dead logs with a manual drill. At Budongo, the holes were drilled into a *Cleistopholis patens* tree that had fallen recently (see Supplemental Data). At Kibale, the holes were drilled into a *Strychnos mitis* tree that had also fallen recently. At both sites, the tree fall had generated a relatively open area of about 25 m², surrounded by thick vegetation. Twigs, climbers, and leaves were available as potential raw material for tools in large quantities at both sites. At Budongo, the log was located next to a *Raphia farinifera* tree where chimpanzees often came to feed [28]. The site was usually visited by small subgroups that also used the place as a resting area. At Kibale, the log was located 30 m from a fruiting *Aningeria altissima* tree, in a cleared area where chimpanzees usually came for grooming and resting after feeding. Both situations were similar in that there were no particularly interesting objects in the vicinity that might have prevented them from exploring the environment.

Every morning, honey was poured in the hole by the experimenter (TG). The 11 cm (nonobligatory) shallow hole was filled with 90 ml of honey up to 6 cm beneath the surface. The 16 cm (obligatory) deep hole was filled up to 10 cm beneath the surface. Additionally, honeycombs were provided around the 11 cm hole or covering the 16 cm hole (Figures 1A and 1B) to provide a conspicuous visual cue and to attract the chimpanzees. The change in the arrangement of the combs was made to better protect the liquid honey from wild bees, which had started to forage into the hole at the time the second experiment started.

A motion-sensitive video camera PixController DVREye was positioned to survey the hole and the immediate area (20 m²). All experiments were set up in the absence of any chimpanzees. Access to the honey spot was unrestricted, and no additional means were used to attract individuals to the hole or to encourage them to engage with it. The experimenter then left the area, only to come back while following a group of chimpanzees on their daily ranging. Additional video recordings were made by the experimenter with a Canon FS100 handy video camera. No interaction happened between the experimenter and any of the animals. Experiments at Budongo took place between February 20 and March 25, 2009 and at Kibale between April 2 and 22, 2009.

All statistical tests were calculated with SPSS v. 16.0 except for the Freeman-Halton extension of the Fisher Test, which was calculated via the Vassar College method (<http://faculty.vassar.edu/lowry/VassarStats.html>). Fisher exact tests give a measurement of the difference between populations but no indication of effect strength. To estimate the size of the effect (i.e., how different the two populations were), we calculated Goodman and Kruskal's λ , a measure of proportional reduction in error. It indicates the

extent to which the modal categories and frequencies for each value of the independent variable differ from the overall modal category and frequency, i.e., for all values of the independent variable together. Values for λ range from zero (no association between independent and dependent variables) to one (perfect association between the two). λ is calculated with the equation

$$\lambda = (\varepsilon_1 - \varepsilon_2) / \varepsilon_1$$

where ε_1 is the overall nonmodal frequency and ε_2 the sum of the nonmodal frequencies for each value of the independent variable.

Supplemental Data

Supplemental Data include two figures and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01774-6](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01774-6).

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