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Tool Use and Tool Making in Wild Chimpanzees

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Abstract. Reported incidences of tool use and tool making for three wild chimpanzee populations increase from Mahale (12 and 3 types of use and making, respectively), Gombe (16 and 3) to Tai (19 and 6). Sticks are commonly used and prepared at all three sites. However, Tai chimpanzees seem to perform more modifications on the material before using it. They are also the only chimpanzees seen to pound objects with tools and to combine two different tool uses to get access to one food item. Tool making is the rule for abundant material (grass, twigs), but appears to be rarer for scarce, hard material (clubs, stones). Factors involved in the acquisition and the benefit of tool use are discussed along with factors affecting the frequency and complexity of tool making in chimpanzees.

Introduction

The last decades have provided us with a wealth of observations from wild animals using tools in many different contexts [1,2]. To be classified as a tool, an object must be held in the hand, foot or mouth and used so as to enable the operator to attain an immediate goal [2]. This definition excludes certain activities considered as tool use by other authors, for example nest making by chimpanzees [3]. Some primates use tools in a very flexible way, but in the wild only chimpanzees have been observed to make tools.

Assessing the complete technological repertoire of one speciesand the variability existing between populations helps us to understand the uniqueness of tool use and making within this species, as well as the factors affecting the emergence of such behaviours within a zoological order (i.e. animals with similar physical constraints). However, comparisons of the same species between study sites or between different species are difficult, as observation conditions vary greatly in the duration of study (from weeks to decades), in the observation methods (viewing from a hide to active following of individuals) and in the living conditions of the animals (from captive to free-living). A comparison of tool use within a single species would limit the impact of phylogenetic influences. The chimpanzee *(Pan troglodytes)* is the best candidate for such an approach. Data from three long-term studies on wild populations in East and West Africa now permit for the first time an analysis of the impact of natural environmental influences on tool use and making.

The present paper has three aims: (1) Reporting our observations on tool use and making in a chimpanzee population living in an evergreen tropical rain forest in the Tai National Park, Ivory Coast. (2) Comparing them with observations made on wild chimpanzees in the Mahale Mountains National Park [3-6] and in the Gombe Stream National Park [2, 7-13]. These latter two sites are located in a savanna/woodland region. (3) Trying to understand some of the factors affecting tool use and tool making by wild chimpanzees.

Methods

The wild chimpanzees of the Tai National Park, Ivory Coast, have been studied since September 1979. At the time of writing, the community we are studying includes 80 individuals living in a 27 km^2 home range in the western part of the park. The area is predominantly flat with numerous small streams bordered with a specific flora. The climate is characterized by two rainy seasons (March-June and September-October) with approximately 1,800 mm rainfall per year.

Tool-use behaviours were only recorded by the two of us during the 9-year period on an opportunistic basis, whenever they were observed, apart from the nut-cracking. Our presence was not constant in the field but reached an average duration of 9 months per year distributed so as to cover all seasons. However, we tried to spend every year the September-March period in the field so as to collect data for our priority projects; the nut-cracking [14-17] and the hunting behaviours [18]. Habituation to human observers was a slow process and only after 5 years were we able to follow by sight some of the males. We did not carry out artificial provisioning, but tried to follow the chimpanzees by their vocalisations, making visual contact whenever possible. It is at present still difficult to follow some timid females.

Knowing that females seem to be the keenest tool users [2, 4], it is not surprising that it took us years to have a fair idea of the variety of their tool uses. For instance, females practise ant dipping mostly at the rear of a party and always interrupted it when we approached. We saw this behaviour for the first time in autumn 1987, i.e. 8 years after observations started. Similarly, in 45 months of initial observation, Goodall [7] saw ant dipping only once, although it is common in Gombe. This is the primary reason why we restrict comparisons in this article to observations made on chimpanzee populations habituated to human observers and studied for many years.

Results

Tool Use in Tai Chimpanzees

Table 1 provides a list of the forms of tool use performed by Tai chimpanzees: tools are used more frequently for feeding than in aggressive contexts. Branches, stones and twigs are the major raw materials, grass being absent in the Tai forest. We shall now analyse some of these tool uses:

Ant Dipping. Tai chimpanzees eat driver or safari ants from ground nests with the help of sticks. Although the ants belong to two different species *{Dorylus nigricans* and *Dorylus gerstaeckeri),* they behave in a very similar way by building their nests in the ground and commonly hiding the entrance with loose soil. Tai chimpanzees regularly eat the ant eggs, larvae and pupae by taking them directly with the hands from the nest (70 observations): they open the nest entrance by rapidly and vigourously raking out

Table 1. List of types of tool use in Taï chimpanzees observed during a 9-year period

Tool-use activity	Tool-use aim	Number of observations	Tool material	Tool size in cm: length (range) thickness (range)	Number of tools used (number of tools made)
(1) Insert	ant dipping	20	twigs; (n = 28)	23.9 cm (58–11) 5.7 mm (3–10)	35 (34)
	wood-boring bee killing	6	twigs; (n = 3)	29.0 cm (29) 7.3 mm (7–8)	11 (11)
	honey fishing	15	twigs; (n = 42)	28.1 cm (60–14) 7.8 mm (3–18)	45 (45)
	bone marrow extraction	33	leaf stem, twigs; (n = 24)	14.4 cm (5–35) 4.0 mm (2–7)	51 (50)
	brain eating	1	twigs		1 (1)
	eye eating	1	twigs		3 (3)
	nut emptying	93	twigs; (n = 91)	15.4 cm (4–80) 4.1 mm (2–9)	196 (172)
(2) Probe	wood boring bee nests	6	leaf stem, twigs; (n = 7)	14.8 cm (10–22) 4.8 mm (4–6)	11 (10)
	corpses	4	twigs		4 (0)
	wounds	1	twigs		1 (1)
	bark interstice	1	twigs		2 (2)
	other objects	3	twigs		3 (1)
(3) Clean	sponging	12	leaves		12 (12)
(4) Display	aimed throwing	6	branches		16 (2)
	throwing	3	branches		13 (1)
	dragging	7	branches		12 (0)
	hitting	4	branches		4 (0)
(5) Pound	nuts	932	clubs, stones; (n = 719)	clubs = 81% stones = 19%	1,037 (85)[1]

[1] Data on tool use and making by identified individuals only for the sample of 1983–1988.

handfuls of loose soil until they excavate a hole large enough to insert an arm up to the shoulder. They then withdraw one or two handfuls of grubs from the bottom. After struggling in a frenzied way to remove the ants biting them, they eat the spoils, often combined with leaves collected afterwards. Ant dipping with sticks has been observed 14 times: the chimpanzee holds the stick with one hand and dips it among the soldier ants guarding the nest entrance. When the ants have swarmed about 10 cm up the tool, the chimpanzee withdraws it, twists the hand holding it and directly sweeps off the ants with the lips. Tai chimpanzees use short sticks (average length = 23.9 cm, range = 50-11 cm: see table 1) and perform the dipping movement about 12 times per minute. Tests, in which we used the same sticks as the ones used by the chimpanzees immediately after they left the site to capture with the same technique the soldiers guarding the same ant nests, indicated that they take 15 ants per dipping movement.

Of the 14 cases of ant dipping, only two involved adult males and they gave up without any success. However, all the 9 adult males of our community regularly take handfuls of grubs from the nests (4.55 observations per individual), whereas only 8 of the 23 adult females were seen to do so (1.37 observations per individual). Thus, Tai chimpanzees normally eat handfuls of ant grubs, and sometimes they eat soldiers by dipping for them with tools. A sexual difference is observed when we compare both techniques: females use tools sucessfully to eat ants more often than males (2 X 2 contingency table, $x^2 = 6.90$, $p < 0.01$).

The picture is further complicated by the fact that the chimpanzees eat two species of driver ants in the Tai forest. We observed the larger ant species *(D. nigricans)*, the grubs of which constitute the bulk of the chimpanzees' ant intake, to be captured with tools only briefly by one young adolescent female. For the smaller species *(D. gerstaeckeri)*, the chimpanzees were observed to use both techniques, dipping as well as eating with the hands. Comparison of the behaviour of the chimpanzees feeding on the two species and the authors' personal experience indicate that the bites of the smaller species are more painful, but that they move less rapidly up the stick.

Killing of Wood-Boring Bees and Nest Inspection. Some large bees *(Xylocopa* sp.) make nests in dead branches on the ground or in a tree. A chimpanzee, in order to get access to the grubs and the honey, first tests for the presence of adults by probing the nest entrance with a stick. If present, adult bees block the entrance with their abdomens, ready to sting. The chimpanzee then disables them with the stick to make them fall out and eats them rapidly. Afterwards, the chimpanzee opens the branch with its teeth to obtain the grubs and the honey.

Honey Fishing. Honey of four bee species is eaten by chimpanzees: the honey bee *(Apis* sp.) and three species of stingless bees *(Trigona* sp.). Groups of chimpanzees fish with sticks for the honey after having tried to take out what they can with their hands. They usually extract with their hands honeycombs from undisturbed hives of honey bees and run away from the bees to quietly eat their catch. By contrast, hives that have already been disturbed, either through the falling of the tree or because of the intervention of other predators, are cleaned of the remaining honey with fishing tools. *Trigona* bee nests, which are either on tree branches or on the ground, are exposed with the teeth and

Fig. 1. An adult female is cracking a hard Panda nut with an 8-kg hammerstone while her 3-year-old daughter is intently watching a large adult male using a small stick to extract kernel remains from a piece of nut opened and partly eaten by the female.

hands by chimpanzees, which use tools once the hole is too deep or too narrow to reach the honey directly with the hands.

Eating of Bone Marrow, Brain and Cleaning of Eye Orbits. Ta'i chimpanzees regularly eat the marrow of long bones of colobus monkeys with the help of small sticks, after opening the ends with the teeth [18]. This behaviour is shown by subdominants at the end of meat-eating episodes. Once, a juvenile female ate small parts of the brain of an intact skull that she could not break open by inserting a small stick through the foramen magnum. On another occasion, an adult female used three sticks to clean the orbits of a colobus monkey skull after she had just eaten the eyes.

Emptying of Nuts. After opening nuts by pounding with a hammer, parts of the kernels may be too difficult to be reached with the teeth or fingernails and some individuals use sticks to remove these remains instead of pounding the nut further with the hammer as others do. However, in this context, most tools were used by individuals finishing the remains of another nutcracker (fig. 1). Only for one nut species *(Detarium senegalense)* is this the size of the nut makes it impossible for the chimpanzee's canine to reach all the embedded kernel and chimpanzees therefore commonly use sticks for this purpose if they do not succeed in pulling out the whole kernel intact.

Nut Cracking. We have described this behaviour precisely elsewhere for two nut species [14-17] and shall here present only new observations concerning another nut species *(D. senegalense). Detarium* nuts have a flat coin-like shell, about 5 cm in diameter. The shell is surrounded by rope-like fibres and the drupe. When the drupe is still intact, chimpanzees face serious difficulties in tearing apart the very strong fibres with their teeth and hands. When food is abundant, they neglect *Detarium* nuts at that stage of development. About a month later, the drupe has decayed and the fibres start to break when hit by a hammer. The nuts can at that time be opened even without a hammer, just by biting them open. Thus, *Detarium* nuts are eaten at different periods, either using a tool or not. The efficiency measures vary accordingly: for the same individuals cracking nuts at both stages, the efficiency increased when the drupe was decayed (nuts opened per minute; $n = 5$, 0.55-0.86 nuts/min, Wilcoxon signed rank test, $T = 15$, $p < 0.05$). Individuals not using a tool tend to choose their nuts more carefully, e.g. one female rejected 17 of 32 nuts after the first bite. However, decayed nuts were opened by a given female 2.4 times quicker with a hammer than with the teeth alone. Thus, tool use seems to be more efficient, although both the nuts and the hammer have to be transported to an anvil. Some individuals may use both techniques, but at the end of the *Detarium* season most of them eat nuts without the help of a tool.

Cross-Population Comparison of Tool Use

In table 2, we compare the tool use of Tai chimpanzees with that observed in the Gombe and Mahale Mountains: most tools used at the three sites are sticks and they are used with the 'inserting in hole' movement, be it a nest entrance, a nutshell cavity or an interstice between the bark and the trunk. We shall limit the comparison to forms of tool use for which the Tai data have brought new information.

Ant Dipping. Gombe chimpanzees hold the stick with one hand among the soldier ants *(D. nigricans)* guarding the nest entrance. Once the ants have swarmed about halfway up the tool, the chimpanzee withdraws the stick and sweeps it through the closed fingers of the free hand. The mass of insects is then rapidly transferred to the mouth [9, 10]. Gombe tools are on average 66 cm long (range: 15-113 cm) and dipping is performed 2.6 times per minute. McGrew [10] calculated that 292 ants are taken per dipping movement. At Gombe, the Tai dipping movement has been observed only with 2 individuals, McGregor and Pom [9], and the direct removal of grubs from the nests with the hands only 3 times [9, 10].

Thus, two strategies of exploiting driver ants seem to be present in both populations; Tai chimpanzees rely mainly on a technique not involving tools, but may sometimes use tools, whereas Gombe chimpanzees rely almost exclusively on tools for their intake of driver ants. Tool use rewards seem to be higher in Gombe (760 ants/min) than in Tai' (180 ants/min), probably due to the differences in movement and in tool size. However, larvae and pupae are more nutritious than adult ants (4.5 more protein and 1.4 more fat [19]) and the Tai' males habit of

Table 2. Tool use activities of table 1 observed at three long-term study sites of wild chimpanzees, classified following the

Tool use activity (type	Tool use goal		
	Gombe	Mahale	Tai
(I) Insert (grass, stick, club)	(1) termites (lsp) (2) ants (lsp) (3) bees (lsp)	(1) termites (2 sp) (2) ants (4 sp) (3) honey	(1) ants (2 sp) (2) bees (1 sp) (3) honey (4 sp) (4) bone marrow (5) brain (6) eyes (7) nuts (4 sp)
(II) Probe (grass, stick, club)	(1) termite nests (2) tree holes (3) feared objects (4) other items	(1) ant nests (2) tree holes (3) feared objects	(1) bee nests (2) feared objects (3) wounds (4) under bark (5) other items
(III) Clean (stick, leaf)	(1) sponging (2) wounds (3) dirt (4) brushing (5) catching	(1) ants (2) dirt	(1) sponging
(IV) Display (club, stone)	(1) aimed throwing (2) throwing (3) dragging (4) hitting	(1) aimed throwing (2) throwing (3) dragging (4) hitting	(1) aimed throwing (2) throwing (3) dragging (4) hitting
(V) Pound (club, stone, fruit, termite mound)			(1) nuts (5 sp)
(VI) Combined (club, stone + stick)			(1) pound + insert

(Gombe data are from Goodall [2, 7, 9], McGrew [10] and Teleki [13]; Mahale data are from Nishida and Hiraiwa [3] and from Nishida and Uehara [5].)

focusing on ant grubs may be more rewarding than the use of tools for adult ants. A handful of grubs is taken within a minute and the volume taken represents a big mouthful, possibly more than 25 g (representing about 21 min of ant dipping at Gombe [10]).

Mahale chimpanzees have been observed to fish for arboreal ants with tools, but driver ants are not eaten at all even if present [3, 4].Termite Fishing. Chimpanzees seem to restrict their termite-fishing technique to

Table 3. Sizes of sticks used for four different tasks by Tai chimpanzees: nut emptying, eating of bone marrow, ant dipping and honey fishing (frequency in percent of the number of tools)

	Nut emptying %	Eating of bone marrow, %	Ant dipping >%	Honey fishing %
Length				
0-10 cm	36	36	7	0
11-20 cm	46	56	39	26
21-30 cm	14	4	36	36
31-40 cm	1	4	**3**	28
41-50 cm	0	0	11	5
+ 51 cm	2	0	3	5
Thickness				
0-2 mm	10	**8**	0	0
3-5 mm	78	83	53	36
6-8 mm	11	8	36	31
9-11 mm	1	0	11	21
12-14 mm	0	0	**0**	12
Number of tools	91	23	28	42

species *(Macrotermes subhyalinus)* [5, 9, 20], except for one observation on *Pseudacantho-termes spiniger* [6]. These species are restricted to the savanna area and are absent in the Tai' forest. Tai chimpanzees were never observed to fish for any termite species, although they feed on 5 species of termites without the help of tools *(Macrotermes ivo-rensis* are present but, with openings meters away, possess a very different structure of their underground mounds than *M. subhyalinus* and my own efforts to fish them were never successful).

Body Care. Gombe and Mahale chimpanzees seem rather fastidious and body cleaning seems to be common: intriguing is the observation that males regularly wipe semen from their penis after copulation [9], a behaviour never observed at Tai.

We can conclude that chimpanzees possess a large diversity of tool use. At Mahale 12, at Gombe 16 and at Tai 19 different kinds were identified. At all sites, chimpanzees use tools to introduce into holes (inserting and probing tools), to clean or to throw. However, only Tai' chimpanzees were seen to pound objects with tools and to combine two different tool uses to get access to a single food item.

Tool Making by Tai Chimpanzees Tool making is common among Tai' chimpanzees; it has been observed in 30% of all cases of tool use observed (table 1). This tendency to fashion the tool before using it depends in part on the raw material: only 1.6% of the stone hammers and 6.5% of the wooden hammers were fashioned for a total of 1,037 hammer uses, whereas sticks were made in 91 % of the observations (n = 363). Hammers are made of hard material and the low availability of these materials in the forest [16] makes it more economical to search for a tool in a nut-cracking area rather than to search for the adequate raw material with which to produce an adequate tool. By contrast, sticks are of a material easily to modify and, with such a material, chimpanzees usually make their tools at arm's reach, rarely searching further.

The sizes of sticks made for four types of tool use may be compared to test the hypothesis that chimpanzees fashion tools specifically for a determined task. For example, holes to reach ants or honey are larger and deeper than holes to extract marrow from bones or kernel remains from nutshells. Therefore, the latter tools should be finer and shorter than the former. Table 3

Table 4. Tool making observed with Tai chimpanzees over a 9-year period

Type of tool making	Raw material	Tool	Number of observations
(a) Detaching from substrates with teeth or hands	leafy twig branch	stick + club	5
(b) a + cutting to a specific length with teeth or hands	leafy twig	stick	18
(c) b + removing leaves or bark with teeth or hands	leafy twig	stick	293
(d) c + sharpening the end with teeth	leafy twig	stick	13
(e) c + modify length with teeth or hands	stick	stick	23
(f) Breaking in two by hitting on hard surface	branch stone	hammer hammer	55 17
(g) Breaking in two by pulling while standing on the branch	branch	hammer	6

presents data on the lengths and the thicknesses of tools used for these four tasks. Sticks for bone marrow and emptying of nuts are shorter (x^2 = 48.96, d.f. = 6, p < 0.001) and finer (x^2 = 46.99, d.f. = 3, p = < 0.001) than those made for ant dipping and honey fishing. In fact, at Tai, chimpanzees make sticks of two different sizes; the smallest for bone marrow and nuts, longer and thicker ones for ant dipping and honey fishing. It is relevant that in almost all the cases the chimpanzees prepare an adequate tool with all the necessary modifications beforehand, and modifications after first use occur for only 6.5% of the sticks used. Tai chimpanzees hence seem to show an advanced understanding of the relations between objects, allowing them to make specific tools for a determined task.

Tai chimpanzees' tool making is presented in table 4: under tool making we include all alterations actively accomplished on a object to modify its shape. The complexity of the fashioning of sticks increases from (a) to (d), in which a twig may undergo four successive modifications before being used by the chimpanzee. This is mainly the case for cleaning kernel remains from Panda shells (n = 11). Some of these twigs undergo a fifth modification when the chimpanzees modify the length during use (n = 2). In most cases (83%), the twigs undergo 3 modifications before being used.

Hammers are produced according to three methods, the easiest being when a hammer happens to break while being used to open a nut (n = 44 wooden and 17 stone hammers). In 37 of these 61 cases, one of the two pieces was subsequently used as a hammer (n = 31 wooden and 6 stone hammers). On the other hand, a nutcracker may intentionally set out to break a branch by hitting it powerfully on a root *without* any nut under it, until it breaks in two (n = 11). The third method consists of a chimpanzee standing with one or both feet on a branch and breaking it in two by pulling forcefully upwards with its hands (n = 6).

Table 5. Comparison of tool making between the 3 chimpanzee populations

Type of tool Gombe making		Mahale	Tai
(I) *Cutting* to correct length (grass, twig, stick, stone)	(1) breaking with the hands (2) cutting with the teeth (3) pulling while standing on it (4) hitting against a hard surface	(1) breaking with the hands (2) cutting with the teeth	(1) breaking with the hands (2) cutting with the teeth
(II) *Shaping* (twigs, sticks)	(1) removing leaves or bark (2) sharpening ends with the teeth	(1) removing leaves or bark	(1) removing leaves or bark

Conclusively, Tai chimpanzees were observed to make tools with 6 different methods (table 5).

Cross-Population Comparisons of Tool Making

Overall, wild chimpanzees have been observed to make tools with six differents methods, three of them being common to all populations (table 5). The other three have been observed only in Tai chimpanzees, two of them being related to nut-cracking behaviour.

As in Tai chimpanzees, Mahale chimpanzees tend to make tools systematically before feeding upon wood-boring ants (4 species of *Camponotus* sp.). 76% of the raw materials are modified twice and 5.8% three times before being used as a tool (see table 3 in [3]). In Tai, the proportions are reversed, 5.1% of the raw materials are modified twice and 93.4% three times (table 4). These tools are not made for exactly the same purposes at the two sites, but all of them are made to be inserted in holes and thus have to conform to similar physical requirements of straight-ness, limited length, and thickness. Qualitative descriptions from Mahale indicate that, when making a tool, the chimpanzees tend to modify it progressively, i.e. testing the tool after each modification until it becomes adequate [3]. Thus, the standardization of the tools in Mahale chimpanzees seems to be only the result of the successive improvements made on the tool during use. In contrast, as mentioned above, Tai chimpanzees proceed to all modifications *before* using the tool. Hence, tool making in Tai chimpanzees seems to require a precise idea of the form an object must have to be considered a tool, as well as of all the technical steps necessary to perform on it to conform to this predefined idea.

Qualitative descriptions from Gombe confirm the results from Mahale and Tai. Gombe chimpanzees seem to regularly make small sticks for activities such as termite or ant fishing [7, 9, 10].

Discussion

From the above analysis it appears that Tai chimpanzees possess the largest diversity of tool using and making among the three chimpanzee populations studied. This raises the question as to the factors that favour this diversity in tool behaviour of Tai chimpanzees and we shall discuss some relevant points.

Acquisition and Propagation of Tool Use

Goodall [9] notes that the patterns necessary for the development of nut-cracking skills are already present in the Gombe chimpanzees, as they regularly pound *Strych-nos* fruits against hard surfaces to break them, and an infant was observed to hit an insect on the ground with a club and a stone. Thus, the absence of nut cracking in Gombe cannot be explained by the absence of the necessary skill, or by the absence of tools, as stones, supports (exposed roots) and hard-shelled fruits (oil palm nuts) are abundant in Gombe [9]. Observations made on Tai chimpanzees show that nut-cracking behaviour is not fully acquired before adulthood and that the first net benefits can be expected only after about 4 years of practice [14: unpubl. data]. Hence, such demanding tool use can develop only in a situation of rich nutritional rewards, in order to compensate for the energy and time invested over the years to acquire the technique. As subadults are more likely to test and acquire unknown habits [8, 21], the food they may acquire through their mother may contribute to such nutritional wealth, i.e. food sharing in the family may allow acquisition by youngsters of a difficult form of tool use. The more prominent role of food sharing during meat-eating episodes observed in Tai chimpanzees compared to Gombe and Mahale chimpanzees [18] may, if this hypothesis is true, have played a role in the acquisition of nut cracking in West African forest chimpanzees. For a demanding technique, food sharing may be a prerequisite of acquisition and propagation of tool use.

Benefits of Tool Use

Tools are thought to facilitate access to food that is hard to process [22-24]. As is apparent from the observations on tool use of Tai chimpanzees for eating driver ants and *Detarium* nuts, difficulty of access may change over time. Thus, it may be difficult to estimate the advantage of using tools in a specific situation. In addition, as for ant feeding, the reward obtained with a tool may be smaller than that reached without one (adult males obtain more per minute with their hands than with a tool). Sometimes, it may be optimal for individuals to wait for conditions to change rather than to develop tool use: in 1985, Tai chimpanzees neglected the many *Detarium* nuts that had fallen on the ground for up to 2 months before eventually eating them without the help of tools in March. Thus, the absence of tool use at one site may be related to different optimal foraging strategies rather than to an incapacity to use tools.

An additional benefit of tool use may be defence. The wood-boring bee stings are extremely painful. Inspection of the nests, by using sticks as a weapon in order to kill or incapacitate the adult bees blocking the nest entrance, prevents the chimpanzees from being stung. Similarly, defence by driver ants, once alerted, may be very active [9, 10]. The sight of a chimpanzee opening an ant nest immediately attracts other group members that will try to use the same hole. But rarely more than two succeed in doing so, due to the mass of alerted ants. Further exploitation of the same nest requires the use of a tool to protect the chimpanzee. Gombe chimpanzees may be more susceptible to the bite of the ants than Tai chimpanzees and thus immediately use tools when finding a new driver ant nest instead of trying first with the hands. In the hunting context as well, Gombe chimpanzees seem to be more vulnerable to colobus monkey bites than Tai chimpanzees [18]. Thus, defence may play a role in the development of tool use.

Choice of Material for Tool Making

In the Tai forest, twigs are more commonly available than stones and the chimpanzees fashion sticks much more frequently than stones. Thus, Tai chimpanzees have apparently developed high faculties in representation of space for finding the rare stones at previous nut-cracking sites [17] rather than developing sophisticated techniques to make tools of hard material: raw material being rare, it is more economic to search for tools rather than to search for raw material and then make the tools. Tool making in chimpanzees seems to be inversely proportional to the availability of material. Similarly, the ease to modify a material decreases from a stick to a large branch and a stone, and accordingly decreases the tendency of Tai chimpanzees to modify them.

The 'stone cache' interpretation of early hominid sites [25, 26] would follow the same pattern: the model propose that, by keeping stones in a constant place for habitats poor in such material, early hominids reduced the cost of searching for tools and invested in searching for food instead. Tool making might have been more common for tools made of abundant material and the early stone artefacts from Olduvai Gorge or Omo Valley might not be so primitive as previously thought [26-28]. *Australopithecus* could have been a regular user of tools of wooden material [see also 29 for a similar conclusion from anatomical evidence].

Tool making by chimpanzees demonstrates that various modifications can be applied to very simple objects and that these modifications may allow the individual to be less selective in choosing the raw material. Descriptions of the choice of raw materials for tools for fishing wood-boring ants [3] give the impression that Mahale chimpanzees are more selective than Tai chimpanzees, where twigs are rarely sought further than within arm's reach. Thus, an increase in the sophistication of tool making may permit less selectivity for the raw material and individuals become less dependent on the environment.

Culture and Tools

Forest chimpanzees (Tai) use and make more different types of tools than savanna chimpanzees (Gombe and Mahale). Ecological factors may obviously explain part of these differences, e.g. termite, ant and bee species are not the same in different habitats. Other differences may more indirectly relate to ecological factors, e.g. nuts and hammer stones being present in Tai and Gombe, our observations seem to make the acquisition of the nut-cracking behaviour dependent upon the richness of the nutritional context (including food sharing).

However, some tool uses seem to be independent of ecological conditions, e.g. why do only Tai chimpanzees eat the bone marrow of their colobus monkey prey with tools, or why do Mahale chimpanzees neglect driver ants or water in holes while Gome and Tai chimpanzees do not? Why do Tai chimpanzees not clean themselves of dirt or semen as do Gombe and Mahale chimpanzees? Many differences can be found in tool behaviour for which neither genetic nor ecological explanations are suitable. The question of attributing culture to chimpanzees therefore arises as evidence of traditional differences between chimpanzee populations are accumulating for hunting behaviour [18], and for plant-feeding habits [30], as well as tool use and tool making.

Summary

A comparison of 3 long-term studies of habituated wild chimpanzees revealed the following aspects: (1) The variety of tool use and tool making increases from Mahale and Gombe to Tai. (2) Tai chimpanzees seem to perform more modifications on the material before using it as a tool than do Mahale chimpanzees. (3) Tool making is frequent with common and easily modified material but rare with scarce and hard material. (4) Nut-cracking behaviour seems to be dependent not only on the presence of the raw material and nuts, but also on the abundant nutritional surroundings allowing the long-lasting acquisition process of this difficult technique. (5) Factors influencing the evolution of tool use and tool making are tested with these observations.

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