OPTIMISATION OF NUT-CRACKING WITH NATURAL HAMMERS BY WILD CHIMPANZEES

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(VVith 3 Figures)

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Introduction

Studies on wild chimpanzees, particularly on their tool-use behaviour, revealed that chimpanzees are capable of solving practical problems which involve manufacture of tools, precise selection of material and transports of tools (MCGREW, 1974; MCGREW *et al.*, 1979; TELEKI, 1974; VAN LAWICK-GOODALL, 1968). The choice of tools in a habitat where the availability of material is not a limiting factor is documented for termite-fishing (MCGREW *et al.*, 1979), which shows the chimpanzees' capacities to adapt their actions to a technical problem. In tool behaviour they also demonstrate their abilities to anticipate some of their actions, *e.g.* by transporting a tool for termite-fishing, even when out of sight of any termite mound.

The study presented in this paper deals with the pounding of nuts with natural hammers on anvils. One observation of a chimpanzee cracking palm-seeds on a rock anvil, using a stone hammer, has been made by

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BEATTY (1951) in Liberia. STRUHSAKER & HUNKELER (1971), RAHM (1971) and BOESCH (1978) have made some observations on nutcracking places in the Tai forest, Ivory Coast. They provide evidence that the chimpanzees use stones and clubs to crack different species of nuts on root and rock anvils. Recent studies in Guinea by SUGIYAMA & KOMAN (1979) and SUGIYAMA (1981) report that the chimpanzees crack palm-seeds using stone hammers and stone anvils. The main questions treated in this paper are: How do chimpanzees solve the technical problem and how do they adapt their solution to the different properties of the 5 nut species they crack? The paper presents the first results obtained during 20 months of a three-year project which started in July 1979.

Study area

The wild chimpanzees *{Pan troglodytes verus)* on which this study was done live in the Tai National Park, Ivory Coast. Its 3500 sqkm are the largest remaining area of tropical rain forest of West Africa. The forest is of the *Eremospatha macrocarpa* and *Diospyros manu* type and harbors, among the large mammals, the pygmy hippo *(Choeropsis liberiensis)*, the forest elephant *(Loxodonta africana)*, the buffalo *(Syncerus differ nanus)*, the bongo *(Boocercus euryceros)*, two species of wild pigs *{Polamochoerus porcus* and *Hylochoerus meinertzhageni)*, the gold cat *(Felis aurata)* and the leopard *(Panlhera pardus)*. Ten species of monkeys live in the park: 2 prosimians, Bosnian's potto *(Perodwticus potto)* and the Dwarf galago *(Galagoides demidovii)*, and 8 species of simians: *Cercopithecus petaunsta, nictitans, diana, campbelli; Colobus badius, polykomos, verus* and *Cercocebus atys*. The area is predominantly flat. The numerous small streams are bordered by a specific flora, whereas the rest of the forest is quite homogeneous. The climate is characterized by two rainy seasons (March-June and September-October) and two dry seasons (July-August and November-February) with approx. f800 mm rainfall per year. The temperature varies between 24-28°. Our study site is located in the western part of the reserve, 20 km east of the nearest village, Tai, and the Liberian border. In this region the park is at the present time efficiently protected against the logging companies. Human predation is low, exept on elephants; the native tribes, the Gueres and Oubis, do not eat the meat of chimpanzees.

General methods

In order to keep human influence low, we did not supply artificial provisioning and simply tried to follow the chimpanzees by their vocalisations, making visual contact whenever possible. In order to avoid scaring them, we never pursued fleeing chimpanzees; we tried to be seen as often as possible in a passive resting position, and we observed either singly or at most in twos. At the time these data were collected, the chimpanzees had not habituated to us, due mainly to the very poor visibility in the forest. Any visual contact can usually be made only at a distance of less than 30 m, which is far too close for an unhabituated chimpanzee. At the nut-cracking places, we recorded data on the nut-shells, the anvil and the presence or absence of a hammer. The cracking places ("ateliers") and all nut trees known to us were entered on a map. In order to experience the technical problems faced by the chimpanzees when they crack nuts, we tried to open many of each species ourselves, using all types of available hammers. Specific data programs are described in the respective sections.

TABLE 1. Nutritional values for 4 of the 5 nut species per 100 g

	Panda	Coula	Parinari	Detarium	Egg yolk
Knergy (Cal)	407	356	539	274	355
Protein (g)	17.8	5.3	8.7	7.2	16.0
Ash(g)	2.0	1.1	1.8	1.1	—
Moisture (%)	41.6	39.3	24.5	43.9	50
Fat(g)	17.8	13.4	48.4	4.7	32.0
Fibre (g)	5.8	1.9	5.2	1.8	—
Sugar (g)	0.87	1.2	0.97	0.51	0.5

Values for egg yolk of domestic chicken added for comparison. The sample analysed for each species was 100 g of fresh nuts.

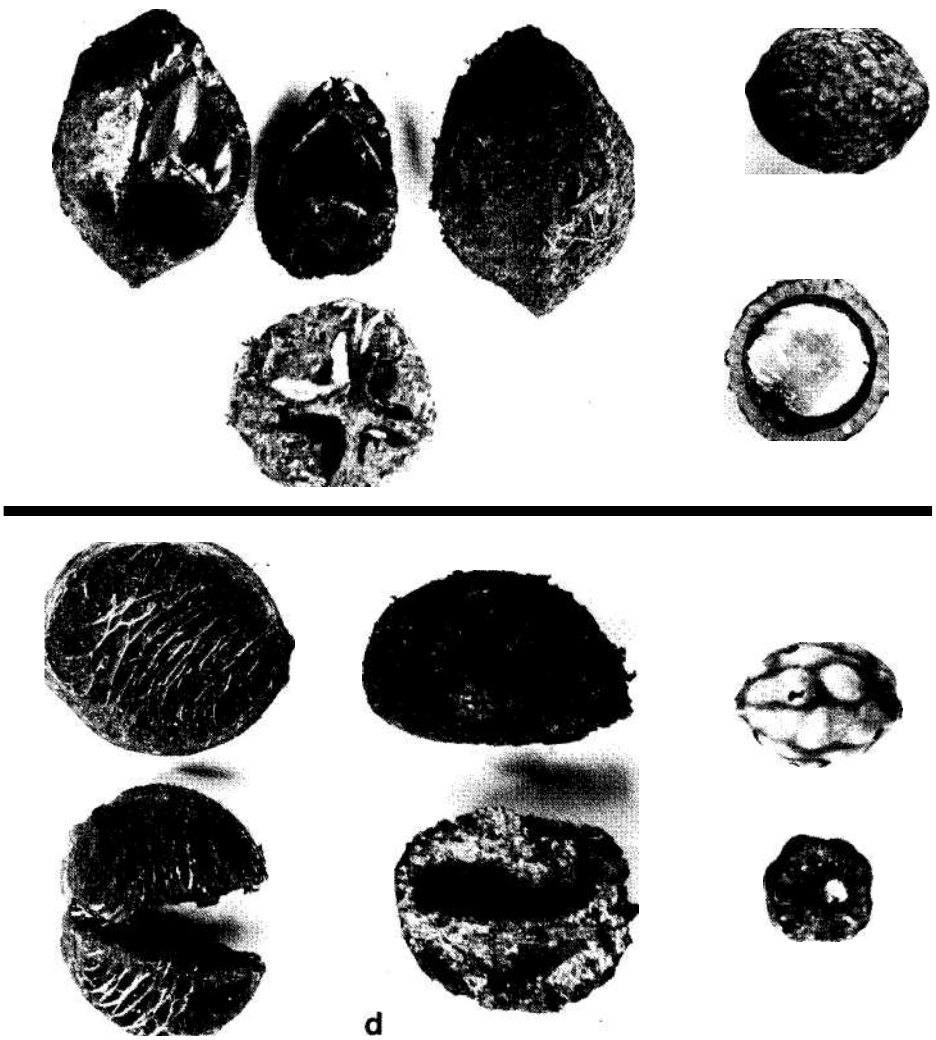
Description of the nuts

The chimpanzees pound 5 different species of nuts (Fig. 1). Fable 1 shows the nutritional value of the nuts. The calorific value is high for all of them, but the content of protein is especially high for Panda.

The nut of *Coula edulis (Olacaceae)* is spherical, 3-4 cm in diameter and contains a single kernel. It presents no dehiscence line which would facilitate opening. When the shell is cracked, the kernel is directly accessible. Coula trees are among the most abundant ones in the forest, growing on the slopes and the crests between the streams. Their production can vary from about 200-500 nuts per year. The nuts fall from the end of November to February. The chimpanzees eat them very frequently from November to March, with a peak in December when they seem to feed on Coula nuts almost throughout the day. They crack the nuts while they are still covered by a thin exocarp which detaches at the first hits. *Detarium senegalense (Caesalpinaceae)* has a flat, coin-like nut, 4-5 cm in diameter, containing a single kernel of the same shape. It has a clear radial dehiscence line and cracks open in two if hit on this line. Detarium are big, rather rare trees, with a nut production of over a thousand a year in December-January. Chimpanzees eat some of them at this period.

Pannan excelsa (Rosaceae) and *Sacoglottis gabonensis (Huminaceae)* produce oval nuts, 4-5 and 3-4 cm long, respectively. Each contains two elongated almonds, of which usually only one develops fully. In spite of the relative-abundance of these trees, we found nutcracking places only near 20 Parinari and 4 Sacoglottis. Parinari nuts are cracked from June to October. Pounding of Sacoglottis was heard only once in October.

Panda oleosa {Pandaceae) has an egg-shaped nut of 5-6 cm length, containing 3 or 4 boat-shaped almonds, circularly arranged. Each almond is separately hemmed in the thick and hard shell. There is a dehiscence line for each almond. In order to free the almonds without smashing them, the nut must be hit between two of these lines. Strength has to be well controlled, as strong hits are needed at the beginning and gentle, precise



ones afterwards. For each almond, the nut has to be repositioned, but it is almost impossible to extract the last one intact. Panda trees are of medium size and are typically dispersed along the rivers. The nut production varies from 3 to about 50 nuts, although some may occasionally produce hundreds. The nuts fall from December to January and the chimpanzees eat them from January to October, with a peak between February and April, and occasionally even throughout the year.

We noticed that the correct positioning of the nut is important for all species, except for Coula. It is particularly difficult for Panda nuts, which is also by far the hardest nut to crack (Table 2), requiring a 10 kg stone to fall from a height of about 120 cm. For Coula, a 20 cm drop of the same weight is sufficient. Preliminary results suggest that the Panda nuts may be tougher than any nut exploited as food by hunter-gatherers in eastern or southern Africa (Ch. PETERS, personal communication).

Table 2 gives the impulses necessary to open the 5 nut species. We used the same materials as the chimpanzees, *i.e.* their wooden and stone anvils and wooden and stone hammers, weighing from 1 to 12 kg. By letting a hammer fall from various heights, we determined the minimal height necessary to cracks nuts of each species. A new nut was used for each fall. The results in Table 2 are means obtained with hammers of various weights. We tested about 80 Coula and 80 Panda nuts and about 10 of each of the 3 other species. As Table 2 shows, cracking a nut with a wooden hammer requires greater impulse than cracking it with a stone hammer. To crack a Panda nut a 10 kg wooden hammer has to fall from a height of 400 cm compared to 120 cm with a stone hammer of the same weight. For the softer Coula nuts, the relative difference is much smaller, namely 25 cm instead of 20 cm. Parallel but smaller differences are found for the two anvil types, stone and wood: Coula requires 5% and Panda 44% less energy when opened on a stone anvil rather than on a root.

Description of techniques

Three techniques of nut-pounding are distinguished in the following: Cracking Coula nuts on a ground anvil, on a branch anvil in the nut tree, and cracking Panda nuts on a ground anvil.

Feeding on nuts requires to bring together the anvil, the hammer and the nuts. They are hardly ever naturally found at the same spot in the forest. As the animals were not habituated to us, we had to reconstruct the sequential order of the techniques from short and incomplete observations. Since we contacted mostly animals that were already cracking nuts, the beginning of the process was rarely observed.

TABLE 2. Impulses necessary for cracking the 5 nut species using the different natural materials available in the forest ($I = m\sqrt{2gh}$). Club hammers were rarely found on granite anvils, the combination is not included

	Club-hammer on root-anvil	Granite-hammer on root-anvil	Granite-hammer on granite-anvil
Panda oleosa	102.76	59.51	33.34
Pannan exceha	56.28	46.22	-
Sacoglottis gabonensis	25.97	13.66	—
Coula edulis	17.34	12.17	11.50
Detanum senegalense	22.97	11.16	—

In all techniques, the chimpanzees collect as many nuts as they can carry in the mouth (30 observations), in one hand (10), in the mouth and one hand (12), or in the mouth and both hands (1). The load is then carried to an anvil. In all the 30 cases where the chimp's arrival was observed, a hammer was already lying on or besides the chosen anvil, and the chimp brought no hammer along. We never saw what happened when the chimpanzees brought the nuts to an anvil which had no hammer, *i.e.* whether the nuts were carried along on the search for a hammer or whether they were left on the anvil. When cracking Coula in a tree, the chimpanzees always picked up a hammer before climbing up and carried it along while collecting the nuts (34 observations). Panda nuts are mostly cracked by single animals and the beginning of the cracking sequence was only observed twice. Once we saw a chimpanzee carry the Panda nuts to an anvil which had a stone. The second time we saw an individual carry a stone hammer to an anvil before collecting the Panda nuts. The latter was never observed before a Coula cracking session. Hammers of wood and stone were carried in one hand (25 observations) or in the mouth (1). The most common sequence on the ground, regardless of the nut species, presumably consists in collecting the nuts and then carrying them to an anvil where a hammer is already present. The nuts are then cracked and each one is immediately eaten. Usually, nuts are collected several times during one feeding session. Before cracking a new nut, the chimpanzee cleans the hole on the anvil of broken shells by brushing it with one hand.

An "atelier" was defined as an anvil plus the remaining shells ol cracked nuts. The presence of a hammer was not included as a criterion. A "one-species atelier" is one with shells from only a single nut species:

TABLE 3. Distribution of anvil and hammer materials in "one-species ateliers" found from September 1979 to August 1980

	Total number of ateliers	*Anvils* roots	rocks	*Hammers* sticks	stones
Panda	468	441	27	8	70
Parinari	79	77	2	19	12
Sacoglotth	14	14	0	2	0
Coula	748	735	13	513	44
Detanum	125	124	1	44	7

91.5% of the ateliers were "one-species". Table 3 presents the composition of all the "one-species ateliers" found within a range of about 13 sqkm during the first year of our study. For Coula, the most abundant nut tree, we avoided double records of the same ateliers by daily entering on a map all the encountered ateliers and the area that had been searched. When walking through the same area again, no additional records were taken. For the other species, the nut trees with ateliers nearby were individually identified and marked on the map.

The anvils: The chimpanzees use 3 types of anvils to open nuts; surface roots about 10 cm in diameter (Fig. 2), rock outcrops, and branches in a Coula tree. The common characteristic of all types is that their surface is almost horizontal.

97% of the anvils are *surface roots* (Table 3). They are generally of larger diameter for the big Panda nuts. We recorded a root as an anvil only if it was obviously worn by pounding. Usually the bark is dislodged over a large surface of the root, and one or several impressions in the wood have been made by the nuts being hit. Fig. 2 shows examples of root anvils. The anvil wear is not always as species-specific as in the photographs. We never saw a chimpanzee making a hole except by hitting the nuts repeatedly on the same spot. Once a hole is worn too deeply it becomes useless, and the chimpanzees begin producing a new one by either using a spot adjacent to the old hole or by shifting to another root nearby. For Panda, another probable factor limiting the use of a hole is the great quantity of slowly perishable shells which eventually cover the root (Fig. 2c). They could be brushed away, but for unknown reasons the chimpanzees seem to prefer changing to new spots nearby.

The *rocks* chosen as anvils are usually situated near the nut tree and consist either of granite or of blocks of laterite. They, loo, show erosions resulting from nut-pounding, but much shallower ones than the wooden anvils.

Fig. 2a. Atelier of Coula nuts. The anvil, a surface root, presents one distinct depression (arrow) and is surrounded by nut shells. A wooden hammer is present.

Fig. 2c. Atelier of Panda nuts with a huge amount of shells, a granite hammer of 6.6 kg and a surface root as an anvil, presenting one big depression (arrow).

We calculated the availability of these two types of potential ground anvils in the forest by recording their occurrence along a transect 6.5 km long and 4 m wide, previously plotted on the map; the transect was chosen such as to sample all major types of vegetation in the forest. The resulting figures are: 22'638 roots (99.7%) and 79 rocks (0.3%) per sqkm. Table 3 thus shows that actual Panda and Coula anvils are biased in favor of rocks.

An anvil on a *branch* in a tree is chosen exclusively for feeding on Coula nuts and presents no other characteristics than being about horizontal, at least 5 cm in diameter and close to the nutbearing branches.

The hammers: Fig. 3 illustrates different types of hammers. They are either wooden clubs or stones and were recorded as hammers only if they presented clear abrasion and/or traces of hits.

A random sample of 210 *wooden hammers* in a Coula area was examined for size, shape and weight. 90.7% of these hammers were oblong pieces of branches (Fig. 3a); they show variable wear, but the majority (87.5%) were worn near the center of gravity, *i.e.* about halfway along the club. We observed that the chimpanzees hold the hammer above its center of gravity; by trying the technique ourselves, we noticed that this prevents the nut from bouncing out of the anvil after a hit. When we used a man-made hammer with a handle, rebounds could only be avoided by exact dosage of impulse. Clubs longer than 120 cm showed the traces of wear at one end. When using such a hammer, the chimpanzee lifts one end and pounds the nut with it while the other end is rested on the ground. Typical club hammers for Coula nuts were 20-80 cm long (75%) with a diameter of 4-10 cm (89%). They weighed less than 2 kg in 77% and 2-4 kg in 15.5% of the cases. Very small clubs of less than 20 cm long (4% or 8 hammers) seemed to be hand protectors rather than useful hammers. A fairly large proportion (14.5%) of club hammers were produced when large hammers were worn out at the center of gravity and broke into two pieces. Each half could be used again. Some of the hammers were of poor, soft quality of wood and presumably decayed between two nut seasons (9.5%). The annual turnover ot wooden hammers can be estimated roughly by the number of decayed and worn-out hammers (24% or 50 out of 210). Several fragments suggested that the chimpanzees occasionally made some hammers by breaking a fallen branch, a branch in a tree or a root of a fallen tree to convenient length. This was the only indication of tool-shaping found during the study period.

The *stone hammers* consist of granite, laterite or quartzite. a) Granite stones (Fig. 3b) are very hard and are a rarity in this forest. We never found one loose and of convenient size at the lew granite outcrops, and we saw only 4 out of 150 lying somewhere in the forest rather than beside an atelier. The weight of these stones varies from less than 1 kg to 24 276 kg. One of 42 kg, found at an atelier and showing traces of use as a hammer, was an exceptional curiosity. One might presume that it was rather used as an anvil, but its irregular, round shape would not provide the necessary stability. The depressions produced by pounding can be surprisingly deep. Of the sample of 150, 3 granite stones that were last used on Panda nuts, have circular, nut-sized depressions up to 1.8 cm deep (Fig. 3b 1), showing that the chimpanzees consistently use the same spots on the stone to hit the nuts. These artefacts indicate that nut-cracking has a long history in the Tai forest. It is not surprising that only a few ol the hammers are worn to that degree, since stones must regularly be lost in streams, under fallen trees or by breaking. We do not presently know whether chimpanzees replace lost stone hammers by breaking big boulders into blocks of convenient size. We so far saw no signs of such manufacture.

b) Laterite stones consist of a conglomeration of laterite soil, which is very crumbly and heterogeneous. 41 out ol a sample of 43 weigh less than 3 kg, the largest one 10 kg.

c) Quartzite stones are the rarest stone hammers; we found only 15 in 20 months.

The availability of potential hammers in the forest was determined as for the anvils and gives the following results: 7323 (97%) wooden clubs, 197 (2.5%) laterite stones and 40 (0.5%) granite stones/sqkm.

Choice of material

Wood is far more abundant in the forest than stone. If the chimpanzees chose by availability, one would except them to use almost exclusively wooden material for all nut species. The impulse measures (Table 2) show that it would be energetically adaptive to select the material in

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Fig. 3a. Wooden hammers used for pounding Coula nuts, showing traces of wear at the center of gravity (arrow).

Fig. 3b.. Granite hammers of different weights showing various degrees of wear (arrows), resulting from pounding Panda nuts. 1) 2.2 kg; 2) 4.2 kg; *3)* 11,6 kg.

b1

dependence of the hardness of nuts: The energy gain of cracking with stone rather than wooden tools is likely to outweigh the greater cost of searching a stone. We tested this expectation by examining the contingencies between a) species of nuts and material of anvils and b) species of nuts and material of hammers on the data of Table 3. The data on Sacoglottis were not used because the sample was small.

a) The species of nuts is significantly related to the material of anvils (X^2 = 18.35, df = 3, p<0.001); harder nuts are more often pounded on stone anvils. Proximity seems to affect the choice: Qualitative observa tions showed that all nut species were cracked on rock anvils if one was available within 10 m from the tree. Whereas 16 rock anvils for Panda were out of sight of any Panda tree, *i.e.* more than 30 m away, no such case was recorded for Coula. The upper limit of such nut transports is unknown, since we could not determine from which Panda tree the nuts had been carried.

b) The second relation, species of nuts and material of hammers, is also highly significant (x^2 = 312.61, df=3, p<0.001) for the four nut species. The chimpanzees choose stone hammers for harder nuts. The profit of choosing the right anvil material is smaller than that of choosing a convenient hammer (Table 2). Furthermore, a hammer has to be car ried to the anvil only once per session, whereas nuts have to be carried several times to an anvil. These two facts may explain why the chim panzees act more against the availability of the material in the case of the hammers than of the anvils. The 8 wooden hammers found on Panda ateliers might have been due to errors by subadult animals.

We now compare the petrographic material (Table 4) and the weight of the stone hammers (Table 5) used for Coula and Panda nuts, respectively, the samples for the other nut species being too small. The tables include all the hammers which we found at all ateliers during 20 months. The results of these tables show that the chimpanzees take account of both variables: They select harder stone hammers for Panda than for Coula (x^2 = 11-76, df = 2, p<0.01), and Panda stone hammers are heavier than those used for Coula (x^2 = 10.25, df = 3, p<0.02).

Transport of materials

The anvil not being transportable, the chimpanzees can transport the nuts, the hammers, or both. We restrict the analysis to Coula and Panda for which enough data are available.

TABLE 4. Material of stone hammers used to crack 4 species of nuts in two years. The degree of hardness is highest for granite stones, followed by quartzite and laterite

	Granite	Quartzite	Laterite
Panda	73	10	16
Pannan	4	1	1
Coula	33	4	25
Delarium	4	—	1

TABLE 5. Weight of stone hammers used to crack 4 species of nuts in two years

	Less 1.0 kg	1-2.9 kg	3-8.9 kg	9 kg and more
Panda	19	23	42	15
Pannan	0	2	3	1
Coula	21	21	16	4
Detanum	1	3	1	—
Total	41	49	62	20

a) *Transport of nuts.*

Coula nuts are eaten as early as possible, when they are still in the tree and not completely mature, but tasty. At the beginning of the season, around November-December, the chimpanzees collect the nuts in the tree and then either open them directly on a branch in the tree (distance of transport 0-5 m) or carry them to an anvil on the ground (distance about 20 in). Later on, from December to January, the nuts start falling and can also be collected on the ground. Fallen nuts decay in about 10 days. By collecting them directly in the tree, the chimpanzees not only ensure good quality but also gain almost two months of harvest time at the beginning of the season.

Panda nuts are not collected in the tree; we saw only one exception. Usually, they remain on the ground for about one month before the chimpanzees start pounding them. Nuts are collected about 5 m from the anvil. During the season of 1980, 37% of the anvils to which nuts were transported were chosen outside the area covered by the Panda tree, implying transports up to 15 m. 31 further ateliers of Table 3 are even oui of sight of any Panda tree, the distance of transport being at least 30 m

TABLE 6. Number and material of anvils to which Panda nuts were transported over a) more than 30 m and b) less than 30 m

	Rock-anvils	Root-anvils
a) More than 30 m	16	15
b) Less than 30 m	11	426
Total	27	441

(Table 6). The proportion of rock anvils is significantly higher (2 x 2 contingency table, x^2 = 128.34, df= 1, p<0.001) as soon as the chimpanzees transport nuts for more than 30 m. Thus, longer transports seem to be aimed at better anvils.

For *Detarium, Parinan* and *Sacoglottis nuts,* all the ateliers were within the area covered by these big trees. Transports did not exceed 10 m. To summarize, nuts are mostly carried to an anvil which is in sight of the collecting point.

b) *Transport of hammers.*

The hammers missing on many ateliers of Table 3 must have been carried off by the chimpanzees to different ateliers. We recorded these transports within a sample area of about 450 ha which the chimpanzees use very frequently for Coula and Panda cracking.

The numerous wooden hammers used on *Coula* ateliers (about 250) were not individually marked by us; too much time would have been necessary to check the numerous ateliers to which they could have been transported. We recorded a transport of these wooden hammers only when we recognized them by their shape and made certain that they were no longer at their previous location. Of 14 transports we knew both the starting and the end point and we measured the straight transport distance, using a 20 m rope. The stone hammers were individually marked with black dots and their transports were recorded more completely. To these we added the stone or club transports made by animals which we saw crack nuts in a tree. The height of the tree was considered as the minimal transport distance. As a consequence of these sampling errors, the number of hammer transports for Coula were underestimated, and probably more so for clubs than for stones.

For *Panda,* all the known nut trees were numbered and all the stone hammers were weighed and individually marked, except those less than 1

TABLE 7. Transport frequencies of different hammer types for Panda and Coula in 2 years

Hammers carried to ateliers of	Clubs	Granite	Laterite	Total
Panda nuts	1	214	32	247
Coula nuts	101	77	21	199

kg, which were mostly fragments; therefore, almost all transports made within the sample area were recorded; it contained 92 Panda trees, 330 ateliers and 40 stone hammers heavier than 1 kg. Club transports were recorded as for Coula.

Table 7 gives the summary of all these transports for both nut species. The enormous difference ($x^2 = 161.54$, df = 2, $p< 0.001$) of wooden versus stone hammer transports to Coula versus Panda ateliers confirms the interpretation of Table 3. Whether the proportion of laterite and granite hammer transports differs between nut species is uncertain (2 x 2 contingency table, $x^2 = 3.81$, df= 1, p = 0.05). The result that stone hammers are more often transported to ateliers for harder nuts cannot be caused by our incomplete records of the hammer transports for Coula. If our data contained the complete number of these transports, the tendency in favour of wooden clubs for Coula would even be more pronounced.

Table 8 compares the transport frequencies for stone hammers of different weights, regardless of material. The chimpanzees transport heavier stones for Panda nuts ($x^2 = 64.45$, df = 3, $p< 0.001$); the frequency of transports thus emphasizes the results of Table 5.

Are the distances of transports also related to the nut species? The data of Table 8 demonstrate the relationship. For the statistics, the two highest distance classes, 200-500 m and more than 500 m, were pooled in order to increase sample size. The chimpanzees transport stones over longer distances for the harder Panda nuts ($x^2 = 31.95$, df = 4, $p< 0.001$). Since the heavier stones used for Panda are as abundant as the lighter ones used for Coula (Table 5), this pattern cannot be caused by differential availability of the appropriate hammers. However, the difference could also be explained by the fact that Coula trees are growing mainly in sight of each other so that transport distances between anvils are small. In contrast, Panda trees are widely scattered and transports between anvils of different trees are therefore longer. More recent data will permit us to analyse which parameters, such as distance and weight, the chimpanzees take into account when transporting a stone for Panda cracking.

TABLE 8. Transport distances versus weight of granite, laterite and wooden hammers for Panda (Pa) and Coula (Co) in 2 years

Hammer-type	Pa 0-5 m	Co 0-5 m	Pa 5-20 m	Co 5-20 m	Pa 20-50 m	Co 20-50 m	Pa 50-200 m	Co 50-200 m	Pa 200-500 m	Co 200-500 m	Pa 500-more	Co 500-more	Pa total	Co total
Granite														
0-0.9 kg	1	—	4	1	—	—	1	—	—	—	—	—	6	1
1-2.9 kg	7	10	3	7	5	9	2	9	1	—	1	2	19	37
3-8.9 kg	22	2	16	6	8	4	19	—	8	—	—	—	73	12
9-more kg	11	—	8	—	1	—	2	—	—	—	—	—	22	—
Laterite														
0-0.9 kg	2	—	—	12	—	2	—	—	—	—	—	—	2	14
1-2.9 kg	1	—	—	1	2	—	—	—	1	—	—	—	4	1
3-8.9 kg	—	—	—	—	3	—	2	—	—	—	—	—	5	—
9-more kg	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wood	2	11	—	36	—	—	—	—	—	—	—	—	2	47
Total	46	23	31	63	19	15	26	9	10	—	1	2	133	112

Discussion

In answer to the main question treated in this paper, we conclude that the chimpanzees choose their pounding tools in adaptation to the hardness of the different nuts. In the best documented technique on tool-use so far, the termite-fishing (MCGREW *et al.*, 1979; VAN LAWICK-GOODALL, 1968) the chimpanzees choose their material at close range, since suitable material is not limited. In contrast, stones are rare in the Tai forest, yet chimpanzees use them frequently. In termite-fishing, the characteristics of a tool, *i.e.* length, diameter, flexibility and resilience, can be assessed by sight and touch. The shape, size and weight of a hammer can also be assessed by the senses, but its brittleness is not directly perceivable. It must be related to color, shape and weight of the tool. This assessment must often be made out of sight of the nuts, before the tool is transported.

Our results on optimal choice of materials confirm those of SUGIYAMA on chimpanzees at Bossou, Guinea. The Bossou chimps crack oil palm nuts *(Elaeis guineensis),* using stone hammers and stone anvils (SUGIYAMA, 1981; SUGIYAMA & KOMAN, 1979). We have measured the impulse necessary to open these palm nuts with the same method as for Table 2, using a root anvil and a granite stone (I = 7.2) and a root anvil and a club hammer (I = 17.5). It results that oil palm nuts are soiter than Coula and could be opened with clubs, which was never observed in the Bossou chimpanzees. However, they crack nuts only at the trees with stones available; 70 mature trees without stones around them were neglected. Of the 39 trees with cracking sites, 37 had stones nearby besides those used for cracking (SUGIYAMA, 1981). Thus, just as would the Tai chimpanzees, the ones at Bossou prefer stones when they are available. It is not clear, however, why they do not crack nuts at the trees without stones, using clubs, which should be available in their forest habitat. In the Tai forest, Elaeis does occur, but our chimpanzees were never seen to crack or eat Elaeis nuts. Might there be a traditional difference between our two populations, separated by 200 km?

Another difference between the two populations is that the Bossou chimpanzees use only loose stones as anvils, which we never observed in the Tai forest. It might be explained by the fact that palm trees do not have roots suitable as anvils. It would be interesting to know if they adapt their choice to the absence of suitable roots or to the abundance of stone material.

In contrast to the Bossou chimpanzees, Tai chimps frequently transport the nuts as well as the tools, and the transport distance for the rare stone tools can be as long as 500 m. These transports underline the fact that the same tools are reused often and over long periods of time. The deep depression on some stone hammers used for Panda nuts confirms this longevity of tools, a fact which has not be been documented for other tool-using techniques in animals.

One of the most common theories about the origin of tool-use in animals is that it was an adaptation for feeding on embedded food sources (see BECK, 1980; PARKER & GIBSON, 1977). We can add two relevant observations on the Tai chimpanzees.

a) Dental capacity: We never saw a chimpanzee open a Coula nut with its teeth, but we observed that *Cercocebus atys* often succeeded in doing so. The bone structure of the jaw and its muscular attachments indicate that chimpanzees have biting strength at least as great as that of *Cercocebus.* Furthermore, the enamel layer of the teeth for both species has about the same thickness (J. BIEGERT, personal communication). Thus, tool-use for consuming Coula nuts cannot be explained by the poor dental capacities of chimpanzees. However, qualitative observations on *Cercocebus atys* showed that cracking Coula nuts with the teeth seems to imply much muscular effort. The daily consumption of up to 200 nuts during 4 months might wear the chimpanzees' teeth excessively. Thus, tool-use in this case can be looked at as a precultural adaptation of chim panzees towards eating hard nuts, whereas *Ramapithecus* seems to have used a phylogenetical adaptation by thickening the enamel layer of the teeth in order to adapt them to the consumption of hard fruits and nuts (KAY, 1981; PILBEAM, 1980).

b) The size of the nuts: The fruit o{ *Strychnos aculeata* is opened by the chimpanzees of Gombe and Tai by just holding it in their hands and banging it against a hard surface (VAN LAWICK-GOODALL, 1968). Even though the fruits of Strychnos are harder than *Coula edulis,* we found no evidence that Tai chimpanzees use tools to open them. Measured with a granite stone on a root anvil, the impulse needed to open Strychnos is of 36.9. Because of their size (diameter 10-15 cm) they can conveniently be held in the hand, which is not the case for a small nut, such as Coula or Panda. Small size of an embedded food source may thus be another factor promoting tool-use.

The use of tools by chimpanzees for pounding nuts confirms the impression, obtained in other regions, that tool-use in primates originated in gathering activities and not in hunting (MCGREVV, 1979), even when the tool is a stone which might be considered an efficient weapon. An un-fashioned stone may serve as a perfect hammer to open nuts, but it may make a poor weapon against a mammal so large that it could not be safely killed with teeth and strength alone. The pebble tool which was found in association with *Ramapithecus* and proposed to have been used in hunting (LEAKEY & LEWIN, 1977) could just as well have been used in a gathering activity such as pounding hard food, comparable to Panda nuts. It seems to show the short of wear at only one spot which we see on the stone hammers used by the Tai chimpanzees (Fig. 3b).

Summary

The chimpanzees of the Tai National Park, Ivory Coast, use sticks and stones to open 5 different species of nuts. In spite of an unfavourable availability of the material in the forest, the animals choose their tools adaptively. For cracking harder nuts, they use harder and heavier tools and transport tools more often and from farther away. Some aspects of the evolution of tool-use in primates are discussed.

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Resume.

Les chimpanzes du Pare National de Tai, Cote d'lvoire, utiliscnt des batons et des cail-loux pour ouvrir 5 differentes especes de noix. Malgre une disponibihte defavorable des materiaux dans la foret, les animaux choisissent leurs outils de facon adaptive. Pour ouvrir les noix les plus dures, ils utilisent des outils plus durs et plus lourds et transportent les outils plus souvent et sur de plus grandes distances. Certains aspects de revolution de l'utilisation d'outils chez les primates sont disputes.