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## **Possible Causes of Sex Differences in the Use of Natural Hammers by Wild Chimpanzees**

The wild chimpanzees of the Tai National Park, Ivory Coast, present an important sex difference in nut-cracking behavior: Adult females more frequently perform the two most difficult techniques, coula cracking in the tree and panda cracking. Adult females are more efficient than males in all the three nut-cracking techniques for one or the other measure of efficiency (number of hits/nut and number of nuts opened/min). The analysis of 5 hypotheses which may explain these differences, stresses the role of the difference of sociability and sexual dimorphism between the sexes, both negatively affecting the nut-cracking techniques and performance of the adult males. We shall discuss the role of these factors on the evolution of the division of labor and food-sharing in the chimpanzee and in early hominids.

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### **1. Introduction**

Division of labor in man is defined by different activities carried out by different classes, based on age and sex, that contribute to the total food supply (Isaac, 1978; Lenski & Lenski, 1974). Generally, males do the hunting and females the gathering. The resulting food sharing developed a system of reciprocal social obligations based on reciprocal altruism (Isaac, 1980; Trivers, 1971). This sexual division of labor is suspected to have evolved quite early in the hominid line. Many authors (Isaac, 1978, 1980; Leakey, 1981; Leakey & Lewin, 1977; Pilbeam, 1980) stress its importance for the appearance of early hominids.

Among subhuman primates, sexual specialization which we considered as a possible preadaptation for true division of labor, was only observed in a few cases: in the Gilgil baboons in Kenya, only adult males hunt (Harding, 1975); in chimpanzees, hunting is also predominantly a male activity, although females have been seen taking part in all phases of the hunt. Females usually obtain parts of the meat through tolerated or active food sharing (van Lawick-Goodall, 1968, 1975; Teleki, 1973, 1975). Up to now, no particular female activity has been observed among primates that would constitute a reciprocal activity of which the males might eventually become dependent. The chimpanzees in Gombe present the beginnings of a sex difference in termite-fishing techniques, in that the females tend to fish more frequently than the males (McGrew, 1979). However, no food sharing occurs between the sexes. We can only speculate about the selective pressures that induced the sexes to specialize in different activities. The most considered hypothesis (Isaac, 1980; Leakey & Lewin, 1977; Zihlmann, 1981) is that females, due to the long dependency of their offspring, would be prevented from ranging as widely and would not be capable of putting forth a great impulse of energy in a sudden and short activity, two suspected requisites for hunting. In primate evolution, the length of the period during which the offspring is carried by its mother increases, and it is presumed, therefore, that the hominid females left the hunting to the males (Isaac, 1978, 1980; Johanson & Edey, 1981; Leakey, 1981; Zihlmann, 1981; Zihlmann & Tanner, 1976). However, the hunting behavior of chimpanzees shows that females with dependent infants can take part successfully in

hunting (van Lawick-Goodall, 1975, pers. comm.; Boesch, pers. obs.), as a dependent infant can be left for the time the hunt takes place, or it can follow its mother while she is hunting. Furthermore, monkey and antelope prey do not range widely within a chimpanzee's environment and the argument of females with offspring not being capable of moving over long distances applies only for the special case of hunting large, widely ranging prey. It seems that there could be other reasons that might have played a role in the appearance of the division of labor.

We present in this paper a case of sex difference in the use of hammers and anvils to crack nuts by wild chimpanzees in the tropical rain forest. The analysis is aimed at trying to understand the selective pressures and casual constraints or preadaptations that cause the observed sex difference and to find at what age it appears. The study is based on four years of field work.

## 2. Methods

The wild chimpanzees (*Pan troglodytes verus*), on which this study was done, live in the Tai National Park, Ivory Coast. The Tai forest measures 3500 km<sup>2</sup> and is the largest remaining area of primary tropical rain forest of West Africa (see Boesch & Boesch, 1983 for a more detailed description of the habitat). We estimate the number of chimpanzees in our community to be about 70. They live without significant human disturbance in a home range of 27 km<sup>2</sup>. The closest traditional plantations are situated 10 km from their home range limits. The native tribes, the Oubi and Guere, do not hunt chimpanzees for totemic reasons. We habituated the chimpanzees without artificial provisioning to tolerate our presence. The visibility in the forest is about 20 m, which is far too short a distance to be tolerated by a wild chimpanzee. Therefore, habituation was a slow process and only after two-and-a-half years, in January 1982, could we observe some nut-cracking chimpanzees that were aware of our presence. During the nut season of the fourth year, most adult and adolescent males tolerated us at visibility distance, i.e. 10–20 m. The females, particularly those with dependent offspring, remained shy towards us. They started to tolerate us during the nut season of the fourth year, i.e. one year later than the males. The fact that in four years 8000 field hours yielded only 440 hours of actual observation, reflects the difficult forest conditions. The time of direct observation represented 1% of the time spent in the field during the first two years, progressed to 5% during the third year and to 15% during the fourth year.

The chimpanzees in the Tai forest crack five species of nuts. We were able to collect enough data for two of them, *Coula edulis* and *Panda oleosa*. Nut cracking was recorded by focal-animal sampling (Altmann, 1974); the animals were originally distinguished by the distinct sound of their hammer. Their performance, i.e. number of hits needed to open a nut and number of nuts eaten per minute (hits/nut and nuts/min) could be recorded by hearing and their behavior by sight (for more details of the methods see Boesch & Boesch, 1981). A "cracking session" began when we discovered a particular cracker and ended only when he or she moved out of sight. During a session the chimpanzee could sometimes use more than one anvil. We never ended the session by moving ourselves. Age and sex was determined as soon as possible, by using morphological criteria, distinguishing between infants, juveniles, adolescents and adults (van Lawick-Goodall, 1968, 1975). We applied clear-cut limits between the classes: infants up to six years, juveniles from seven to nine years and adolescent males from 10–15 years, females from 10–13 years.

During the last three months of the fourth nut season, we carried additional nuts of the respective species to two natural nut-cracking places of coula and one of panda, and we cleared channels to these cracking places of the small vegetation. This was done in order to permit good photographs and movie films of the nut-cracking behavior. Only habituated individuals tolerated us with the cameras at these places, and no performance data were taken on these occasions. Specific data programs are described in the respective sections.

### 3. Results

#### A. Sex Differences in Nut Cracking

In two previous articles (Boesch & Boesch, 1981, 1983), we provided a description of the three techniques the chimpanzees use to crack coula and panda nuts: coula cracking on the ground, in the tree and panda cracking on the ground. In all three techniques, a hard surface is used as an anvil, e.g. a rock or a surface root, and a stone or a wooden club as a hammer. An anvil showing traces of wear, resulting from nut pounding, surrounded by nut shells is named an "atelier" (for description, choice and availability of these materials see Boesch & Boesch, 1983). Coula trees are very abundant and so are the root anvils and the clubs to open these nuts. Panda trees are rarer and their very hard nuts can only be opened with stones, which are rare in this forest. We never saw a chimpanzee open nuts without both a hammer and an anvil.

Table 1 presents all the nut-cracking sessions of which we could determine the age and sex of the cracker, recorded during the four nut seasons 1979–83. This table and Table 2 are similar to those published in our previous report (1981) but include a larger sample as well as new data on all subadult classes. The preliminary results are confirmed: The two more complicated of the three observed techniques, cracking coula in the tree and panda cracking, are used predominantly by females, although the complete data are less striking for panda than during the first two years (Boesch & Boesch, 1981).

**Table 1**

**Frequency of cracking sessions of each age–sex class seen cracking coula nuts on the ground and in the tree, and cracking Panda nuts. Panda observations are separated into (a) animals starting to crack before the arrival of the observer, and (b) animals starting in our presence, in order to show the bias due to habituation (see text for further explanations)**

	Coula		Total	Panda	
	on the ground	in the tree		(a) start not observed	(b) start observed
A ♀	336	68	404	89	3
Ad ♀	20	9	29	10	1
Juv ♀	35	17	52	4	—
Inf ♀	8	3	11	—	—
A ♂	255	6	261	19	18
Ad ♂	147	10	157	8	8
Juv ♂	4	8	12	—	—
Inf ♂	3	1	4	—	—
Total	808	122	930	130	30

Infants up to 6 years.

Juveniles from 7–9 years.

Two biases influence these results because of the greater degree of habituation of the males from the third year onward, the period during which most observations were made. Both may cause an overrepresentation of males. (1) Double counts: For the following reasons no such bias is to be expected for coula. Most coula cracking happens in groups of moving chimpanzees. Coula trees and wooden hammers being abundant, the shy animals, disturbed by us, will simply go farther away to another anvil where they might be recorded again, just as the more tolerant individuals do as they move along. Thus, our presence mainly caused females' sessions to end sooner than males' sessions. So, if a shy animal does not move over a longer distance when disturbed than a tolerant one, the number of recorded sessions is not affected. For panda, the rarity of trees and stones does not allow a disturbed animal to crack farther away. (2) Start of a session: We rarely observe the beginning of a cracking session for coula, since for the same reasons of abundance of materials, chimpanzees do not have to wait their turn at an anvil or for a hammer. In contrast, for panda cracking, due to the rarity of trees and stones, an animal that wants to crack nuts must wait its turn until the available stone is free. If we are present in such a situation, only the habituated individuals, i.e. so far mostly males, will wait and begin to crack in spite of our presence. Females will immediately leave the cracking site. Thus, the bias due to habituation favouring males plays an important role for panda. For this reason, we have differentiated between animals starting to crack *before our arrival* and those starting *in our presence* in Table 1, and we consider only the former data for the statistical tests.

Obviously, the results of the frequency of each sex cracking a given nut species have to be compared to the age-sex composition of the community. Due to the difference of habituation, it is still difficult to be positive about the number of the females. We identified 13 adult males and 23 adult females, and for the last three months, we did not encounter any new adult member.

Comparing Table 1 with the adult composition of the community, the sex difference for panda, using only animals whose beginning of the cracking session was not observed, is significant in favor of adult females ( $2 \times 2$  contingency table  $\chi^2 = 4.34$ , d.f. = 1,  $P < 0.05$ ). For the coula technique on the ground, the statistical test is not significant ( $2 \times 2$  contingency table  $\chi^2 = 0.42$ , d.f. = 1, n.s.). Both sexes may use it with equal frequency. The difference between the coula technique in the tree and on the ground is significant

**Table 2** Overall means of the two efficiency measures (a) hits/nut and (b) nuts/min, of each age-sex class for Coula and Panda

	Coula						Panda		
	No. of sessions	on the ground		No. of sessions	in the tree		No. of sessions	(a)	(b)
		(a)	(b)		(a)	(b)			
A ♀	217	6.26	2.26	53	7.55	2.02	70	17.28	0.52
Ad ♀	12	8.42	2.00	9	10.54	1.33	9	44.85	0.32
Juv ♀	25	18.26	1.15	16	15.20	0.96	5	72.00	0.10*
Inf ♀	8	45.81	0.32	2	46.12	0.58	—	—	—
A ♂	183	7.02	1.91	5	8.69	1.50	36	22.31	0.48
Ad ♂	138	6.71	2.00	10	10.85	1.45	13	22.71	0.61
Juv ♂	3	8.58	1.21	8	9.28	1.14	—	—	—
Inf ♂	4	94.25	0.39	—	—	—	—	—	—

\* Only one older juvenile succeeded in opening a Panda nut.

(2 × 2 contingency table  $\chi^2 = 32.40$ , d.f. = 1,  $P < 0.001$ ) in favor of the adult females cracking in the tree.

Comparing for the adolescents and adults of the same sex, the difference between the two coula techniques is not significant (2 × 2 contingency table  $\chi^2 = 2.82$ , d.f. = 1, n.s. for males and  $\chi^2 = 3.37$ , d.f. = 1, n.s. for females). But the difference between the adolescent males and females is in favor of the adolescent females who more frequently crack in the trees (2 × 2 contingency table  $\chi^2 = 13.65$ , d.f. = 1,  $P < 0.001$ ). The difference between the juveniles of both sexes for both coula techniques is not significant.

Table 2 presents the overall means of the two efficiency measures (hits/nut and nuts/min) of each age–sex class, collected for coula and panda. The small sample of adolescent females compared to adult or juvenile females could be due either to a small number of animals of this age class or to the fact that some juvenile females were more habituated to us than adolescent females, which was the case at least for one orphan juvenile female. Mean values of efficiency measures were first calculated for each session, and these were used for all the statistical tests (Mann–Whitney *U*-test, Siegel, 1956). Due to the high

Figure 1. Distribution of mean efficiency measures, (a) hits/nut and (b) nuts/min, of all adult males (—) and females (---) recorded during four years.

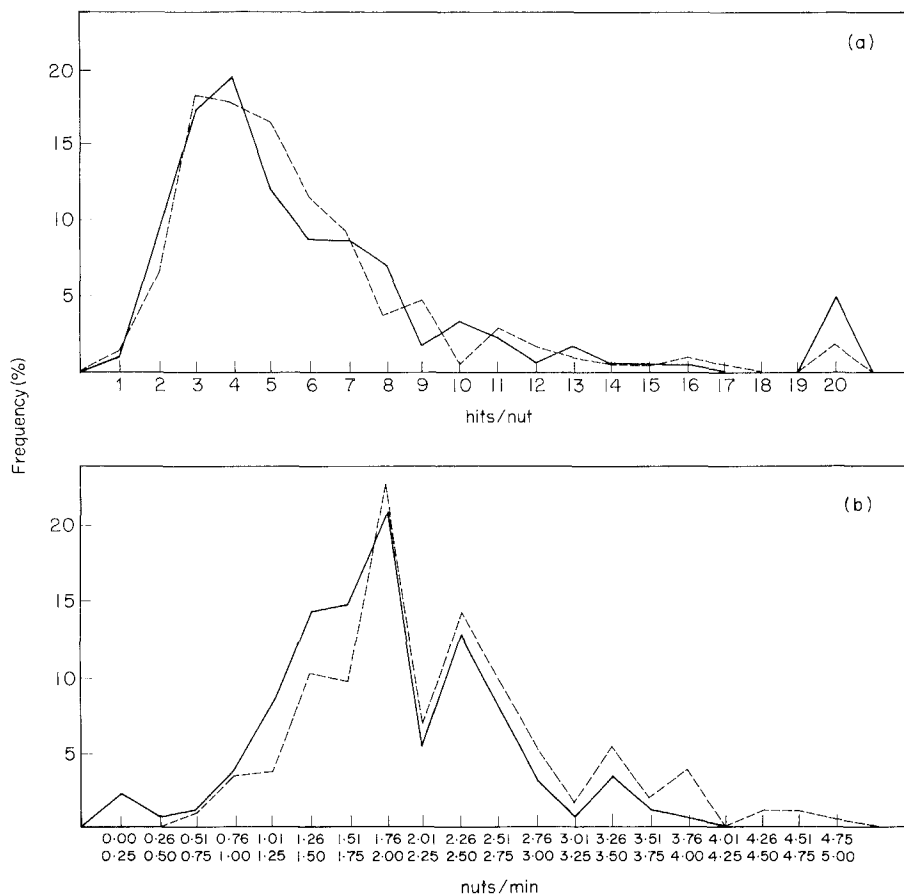


Table 3  
 Statistical comparisons of the session mean-efficiency measures for the two coula techniques (hits/nut and nuts/min) of all the different age-sex classes. The diagonal squares contain comparisons amongst the same age-sex classes between ground and tree techniques. The lower half represents comparisons of the technique in the tree, the upper half comparisons of the technique on the ground. All comparisons are made using the Mann-Whitney *U*-test. Each square contains the results of the test (in favor of . . . or n.s.)

Coula 1979-1983

grd tree	A ♀ h/h	A ♀ n/mn	Ad ♀ h/n	Ad ♀ n/mn	Juv ♀ h/n	Juv ♀ n/mn	Inf ♀ h/n	Inf ♀ n/mn	A ♂ h/n	A ♂ n/mn	Ad ♂ h/n	Ad ♂ n/mn	Juv ♂ h/n	Juv ♂ n/mn	Inf ♂ h/n	Inf ♂ n/mn
A ♀	grd ** z = 2.97	grd ** z = 2.36	n.s. z = 1.58	n.s. z = 1.26	A ♀ *** z = 5.09	A ♀ *** z = 6.14	A ♀ *** z = 4.76	A ♀ *** z = 4.80	A ♀ *** z = 0.04	A ♀ *** z = 3.93	A ♀ * z = 2.25	A ♀ ** z = 3.01	n.s. z = 0.81	A ♀ ** z = 2.40	A ♀ *** z = 3.36	A ♀ *** z = 3.40
Ad ♀	n.s. z = 1.03	A ♀ ** z = 2.37	n.s. z = 4.15	grd ** z = 2.1	Ad ♀ * z = 2.17	Ad ♀ *** z = 3.39	Ad ♀ *** z = 2	Ad ♀ *** z = 0	n.s. z = 1.47	n.s. z = 0.21	n.s. z = 0.77	n.s. z = 0.04	n.s. z = 16	A ♀ * z = 3.5	A ♀ ** z = 2	A ♀ *** z = 0
Juv ♀	A ♀ *** z = 4.19	A ♀ *** z = 5.67	n.s. z = 43	n.s. z = 42	n.s. z = 0.36	n.s. z = 0.69	Juv ♀ *** z = 3.15	Juv ♀ *** z = 3.44	A ♂ *** z = 4.78	A ♂ *** z = 5.11	Ad ♂ *** z = 4.47	Ad ♂ *** z = 5.45	n.s. z = 1.04	n.s. z = 0.48	Juv ♀ * z = 2.05	Juv ♀ * z = 2.30
Inf ♀	A ♀ ** z = 4.19	A ♀ ** z = 5.67	Ad ♀ * z = 0	n.s. z = 1.5	Juv ♀ ** z = 0	Juv ♀ * z = 2	n.s. z = 8	n.s. z = 3.5	A ♂ *** z = 4.63	A ♂ *** z = 4.57	Ad ♂ *** z = 4.72	Ad ♂ *** z = 4.68	Juv ♂ ** z = 0	Juv ♂ ** z = 0	n.s. z = 13	n.s. z = 12
A ♂	n.s. z = 0.06	A ♀ * z = 1.75	n.s. z = 19.5	n.s. z = 18	n.s. z = 19	A ♂ ** z = 5.5	A ♂ * z = 0	n.s. z = 0.71	n.s. z = 1.59	n.s. z = 2.01	A ♂ * z = 2.01	n.s. z = 0.79	n.s. z = 0.77	A ♂ * z = 1.96	A ♂ *** z = 3.23	A ♂ *** z = 3.32
Ad ♂	A ♀ * z = 1.69	A ♀ ** z = 2.44	n.s. z = 40	n.s. z = 36	Ad ♂ * z = 45	Ad ♂ ** z = 27	Ad ♂ * z = 0	n.s. z = 21	n.s. z = 24	grd ** z = 2.44	grd ** z = 2.45	grd ** z = 2.45	n.s. z = 0.63	Ad ♂ * z = 2.21	Ad ♂ *** z = 3.36	Ad ♂ *** z = 3.32
Juv ♂	n.s. z = 0.61	A ♀ *** z = 3.69	n.s. z = 34.5	n.s. z = 30	Juv ♂ * z = 34.5	n.s. z = 44.5	Juv ♂ * z = 0	n.s. z = 15.5	n.s. z = 9	Ad ♂ * z = 18	n.s. z = 33	Ad ♂ * z = 10.5	n.s. z = 11	n.s. z = 10.5	Juv ♂ * z = 0	Juv ♂ * z = 0
Inf ♂																
A ♀	n.s. z = 0.50	tree * z = 1.78	← Sequences over 10 min													

\* *P* < 0.05. \*\* *P* < 0.01. \*\*\* *P* < 0.001.

number of statistical tests made on Table 2 as well as the small sample of some age-sex classes, we will draw conclusions only from tests significant at the 1% level. The 5% ones will only be considered if they follow a general trend, i.e. constant progress in efficiency through the age classes, or when the result was predicted. Multivariate analysis will be done when more data on subadults are available. Figure 1 shows the distribution of efficiency measures of all adult males and females recorded in four years. Statistics of the coula comparisons are presented in Table 3. The following conclusions can be drawn:

(a) *Comparisons between the two coula techniques:* In terms of efficiency, cracking coula on the ground is acquired earlier than cracking in the tree by the animals of both sexes. At adolescence, they crack significantly more efficiently on the ground for one or both measures than in the tree. Adult females are better on the ground for both measures. In order to test our hypothesis that cracking nuts directly in the tree gives the advantage of saving time in collecting the nuts, we compare the performance of all females cracking for 10 min or more on the ground *versus* in the tree. In this time span, nuts must be collected at least once. In this comparison the difference for the first measure is not significant but, as expected, the second measure (nuts/min) is significant in favor of the tree technique. Thus, cracking in the tree is more efficient for the number of nuts eaten per minute.

(b) *Ontogeny of the techniques:* The few observations on subadults allow us to draw some careful preliminary conclusions on development within the same sex (Table 3). *For the ground technique* no chimpanzee younger than four years old has been seen to try to crack coula nuts, although they show interest in the opened nuts, the action of cracking and the tool used by their mothers. No chimpanzee younger than five years succeeded in opening a coula nut (five observations), although their trials were done by using the right materials and behavior. Infants between five to six years old succeeded in opening coula nuts, but much perseverance and practice is still required, and they progress until adolescence, males even until adulthood in the hits/nut measure. In the juvenile female class, the progress is quite rapid, as we noted a significant difference between young and old juvenile females for both measures, but old juvenile females still remain less efficient than adult females although the difference with adolescents is not significant. *The tree technique* is developed by infant females and juveniles of both sexes with the same efficiency as the ground technique. At adolescence, females reach their adult efficiency for the first measure (hits/nut) but continue to progress for the second until adult. The males reach their final efficiency for the tree technique at adolescence, but the comparison with the adult females raises the question of whether adult males ever acquire it as well. Thus, the technique continues to be improved into adolescence and partly into adulthood.

(c) *The sex difference:* The skill in both coula techniques seems to improve equally in both sexes until adolescence. The sex difference appears in both cases at adulthood, females being more efficient than males for the second measure (nuts/min). This result is not in total accord with our previous preliminary report (Boesch & Boesch, 1981), where adult females were superior to adult males for both measures (hits/nut and nuts/min) on the ground. The following explains this difference: usually coula nuts fall on the ground when they are completely ripe and decay within two weeks, which was the situation we met during the first two nut seasons. During the third and fourth season, the weather was extremely dry, without any rain at all, and dry coula nuts were preserved much longer (six weeks). A dry coula nut requires 22% less hitting impulse to open it. Furthermore, the dried almond, having shrunk a little, becomes detached from the surrounding husk and

may remain intact even when pounded with too-powerful hits. Thus, dry nuts require less precision to open them optimally. This difference in the physical properties of the nuts is also reflected in the performance of the adults of both sexes. When cracking *dry nuts*, males and females improve the second efficiency measure (nuts/min) (Mann–Whitney *U*-test: A♀  $z = 3.06$ ,  $P < 0.01$ ; A♂  $z = 3.49$ ,  $P < 0.01$ ), but only males need less hits per nut (Mann–Whitney *U*-test:  $z = 4.81$ ,  $P < 0.001$ ). Females were thus superior in performance for both efficiency measures in the case of the *fresh coula nuts* that made up the sample of the first two seasons, mastering the necessary supplement of strength and precision with the same number of hits/nut as for dry nuts.

This sex difference towards a slight physical difference in the nut has a secondary effect on the behavior of the sexes: Males seem to be aware of the fact that they have more difficulties in opening fresh coula nuts and they tend to crack them less often than females (Table 4). Towards the end of the season, when the nuts are dry, they seem to concentrate on feeding on coula nuts and crack them more frequently than females. This difference is significant ( $2 \times 2$  contingency table:  $\chi^2 = 11.02$ , d.f. = 1,  $P < 0.001$ ); thus males crack coula nuts more frequently than females when nuts are easier to open.

Table 4

Frequency of adults seen cracking fresh vs dry coula nuts on the ground in all four nut seasons

	Fresh nuts	Dry nuts
A ♀	213	123
A ♂	126	129

Comparing the efficiency measures for panda is more difficult, because the greatly varying weight of the hammers affects these measures. Table 5 shows all efficiency measures of *adult females* for panda, classified according to the weight of the stone hammer used. The efficiency changes with the weight of the hammer. The function is continuous. However, in order to judge sex differences in efficiency, we chose five weight classes, 1–2 kg, 3–4 kg, 5 kg, 6 kg and 7 kg upwards. With this choice, efficiency measures differ significantly between these classes (Mann–Whitney *U*-test,  $P < 0.05$ ), but not within them.

Statistical comparisons are presented in Table 6 and the following conclusions can be drawn:

(a) *The sex differences*: One conclusion can be drawn with confidence: adult females are more skillful than adult males in the use of the heaviest hammers, but the time used for eating the opened nuts and for collecting new ones is obviously not different in the two sexes, so that the nuts/min measure is not affected. This sex difference does not seem to exist at adolescence.

(b) *The ontogenetic process*: The first successful attempt appears at a much later age for panda than for coula. Of 15 observed infants and juveniles, only one old juvenile (8–9 years old) succeeded in opening a panda nut. Most probably the strength needed to open these nuts greatly limits the learning process for the young chimpanzee. Later on, the progress seems quite rapid: Adolescent males are as efficient as adult males, whereas females still improve from adolescence to adulthood.

In conclusion, the three techniques show the following sex differences: coula cracking in the tree and panda cracking are predominantly female activities. Males crack dried coula



**Table 5** Overall mean-efficiency measures (hits/nut and nuts/min) of adult females for panda, according to the weight of the hammer. Below are shown the statistical results between efficiencies with each weight class and with combined weight classes. Weight classes presenting homogenous efficiency measures were pooled (Mann-Whitney *U*-test)

	1	2	3	4	5	6	7	9	10	11
kg	1.0-1.9 N = 5	2.0-2.9 N = 8	3.0-3.9 N = 5	4.0-4.9 N = 5	5.0-5.9 N = 27	6.0-6.9 N = 5	7.0-7.9 N = 7	9.0-9.9 N = 6	10.0-10.9 N = 1	11.0-11.9 N = 1
h/n	33.48	22.33	16.91	17.67	16.28	12.80	10.96	9.69	11.00	6.00
	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		***				*				
					n.s.				n.s.	
n/mn	0.65	0.85	0.58	0.43	0.51	0.36	0.59	0.61	0.37	0.50
	n.s.	**	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.
		***				**				
				*					n.s.	
									n.s.	

\*  $P < 0.05$ . \*\*  $P < 0.01$ . \*\*\*  $P < 0.001$ .

Table 6

Statistical comparisons for the panda technique, using the individual mean-efficiency measures (hits/nut and nuts/min) of the adult and adolescent males and females. Comparisons are made between animals using hammers of the same weight class (see Table 5). (Mann-Whitney *U*-test)

Weight class (kg)	A ♀ ↔ A ♂		Ad ♀ ↔ Ad ♂		A ♀ ↔ Ad ♀		A ♂ ↔ Ad ♂	
	Hits/nut	Nuts/min	Hits/nut	Nuts/min	Hits/nut	Nuts/min	Hits/nut	Nuts/min
1-2	n.s. <i>U</i> = 10	Δ♀* <i>U</i> = 8	n.s. <i>U</i> = 5	n.s. <i>U</i> = 8	A♀*** <i>U</i> = 6	Δ♀*** <i>U</i> = 4	n.s. <i>U</i> = 6	n.s. <i>U</i> = 9
3-4	n.s. <i>U</i> = 9.5	n.s. <i>U</i> = 8						
5	n.s. <i>z</i> = 1.52	n.s. <i>z</i> = 0.85	n.s. <i>U</i> = 2	n.s. <i>U</i> = 1	A♀*** <i>z</i> = 2.36	n.s. <i>z</i> = 1.36	n.s. <i>U</i> = 12	n.s. <i>U</i> = 10
6	n.s. <i>U</i> = 3	n.s. <i>U</i> = 8.5						
7-12	A♀*** <i>U</i> = 10	n.s. <i>U</i> = 59.5					n.s. <i>U</i> = 7	n.s. <i>U</i> = 10.5

\*  $P < 0.05$ . \*\*  $P < 0.01$ . \*\*\*  $P < 0.001$ .

nuts on the ground more frequently than females. The adult females are more efficient than the males in all the three techniques in one or the other measure of efficiency. All these differences seem to appear during the transition from adolescence to adulthood. Our aim is now to try to understand the causes of these observed sex differences.

### B. Causation of the Sex Differences

In order to explain the observed sex differences between adult males and females, we forward the following five hypotheses that might explain all or part of them (see Boesch & Boesch, 1981). Due to the described difference in habituation of the animals, the former hypotheses 5 and 6 concerning ontogenetic differences cannot be tested here and will be the object of future research.

- (1) Females are more dependent on the calorific and protein content of the nuts: males obtain more of it through hunted meat.
- (2) Males choose the presence in the group rather than nut cracking when both are not possible at the same time. Some more solitary techniques might thus be neglected by males.
- (3) The concentration of the males during the nut cracking is lower than that of females, and this affects their efficiency.
- (4) Males have more motor difficulties than females in nut cracking, which lowers their efficiency. We shall distinguish between two levels: (a) The tools, which may be part of the males' displays, are more emotionally loaded for males than for females, and this lowers their motor control of the technique. (b) Males have more motor difficulties than females for reasons bound to the physical control of the pounding movement.
- (5) Cognitive differences between the sexes exist in the adaptation to technical difficulties, such as in compensating a bad choice of materials or in planning the transport of material, which affects the males' efficiency.

*Hypothesis 1: dependency on nutritional content.* This hypothesis might be valid for the following reasons:

Lactating and pregnant human females need a supplement of 1000 kcal per day (Gunther, 1971 quoted by McGrew, 1979).

Female chimpanzees share part of their food with their offspring, which is not the case for males (McGrew, 1975; Silk, 1976).

Males obtain more calories and proteins through meat than females (Teleki, 1973, 1975; van Lawick-Goodall, 1968).

Nuts are very calorific (300–500 kcal/100 g) and rich in protein (5–18%), whereas fruit and leaves of the forest contain less than 5% protein (Boesch & Boesch, 1983; Hladik *et al.*, 1971).

First, we have to investigate whether the Tai chimpanzees might depend at all on nuts, which means on tool use, for their daily intake of food. Analyses of other tool techniques, such as termite fishing, ant dipping, and fishing for wood-boring ants put a doubt on the nutritional importance of this tool-acquired food (McGrew, 1979; Nishida & Hiraiwa, 1982). We estimated the daily intake of coula nuts by recording the duration of group cracking sessions and by ensuring that specific individuals did actually crack during this time, by recording them at least twice during this session. We then calculated the number of nuts eaten by multiplying the efficiency measure (nuts/min) of these individuals for that day by the time the group cracked nuts. This may be both, an under- or an overestimation; an underestimation because animals often crack nuts alone or in small groups and are then difficult to follow, and an overestimation because they might not crack nuts during the whole cracking session. We think that this measure more probably underrates nut consumption. We were able to calculate it in 49 cases both with male and female adults, obtaining a mean number of 167 nuts (i.e. 1 h 30 min of work) per day, which represents 735 g of coula almonds per individual. Such a mean intake per individual and per day represents 2616 kcal and 39 g of protein, which shows that the Tai chimpanzees *depend or at least rely heavily on tool use* for their survival during the four months of the coula season. The panda consumption results are certainly more underestimated, as in most cases the animal fled on noticing us. The mean number of nuts per session is 28, but undisturbed chimpanzees may crack up to 60 nuts. This provides 352 and 754 kcal, respectively, and 16 or 34 g of protein. Thus, panda nuts represent a lesser nutritional contribution than do coula, but the protein intake remains important.

The hypothesis assumes that females depend *more* than males on the nutritional value of the nuts. We are actually unable to test it seriously, as this would demand a complete study of the chimpanzees' diet during the whole year, aimed at evaluating the respective role of meat and nuts. The observational biases as yet make it impossible to estimate reliably how many more nuts females eat than males. The following observations should allow us to weigh this factor:

- (i) Chimpanzees do not crack nuts without interruption all day long, and there are always individuals of *both sexes* that either relax or eat other food at cracking places, while they could actually crack nuts. Chimpanzees that cracked nuts most often while others were resting, were, however, not adult females, as we would expect under the hypothesis, but adolescent males. Accordingly, the adult females seem not to have any difficulties in obtaining their necessary daily intake of nuts.

- (ii) Competition by males for ateliers (anvils and hammers) is not an argument favoring hypothesis 1, since it is low, even when chimpanzees crack close together. We observed 24 cases of "stolen" ateliers out of 613 observed cases of group-cracking chimpanzees, during the last year. When tension is observed, the adult females tend to crack at the periphery of cracking groups rather than to give up.

In conclusion, even if this hypothesis may play a certain role for the females, it certainly does not explain why one sex should use an additional and special technique (coula in the tree) to obtain its daily intake of nuts, since they could nearly always use the simpler technique on the ground instead. For panda, the hypothesis could apply for the season when there are no coula nuts.

*Hypothesis 2: social interest.* The reasons why this hypothesis might play a role are the following:

The male hierarchy is more rigid than the female one (van Lawick-Goodall, 1968, 1975; Simpson, 1973), and males may depend on their presence in their group to maintain their status.

Males of the same community defend their territory co-operatively. Females are more independent and solitary (Goodall *et al.*, 1979; Pusey, 1979; Wrangham, 1979).

Hunting is mostly done by the group of males (van Lawick-Goodall, 1968; McGrew, 1979; Teleki, 1973, 1975), and their chance of obtaining meat might be better there.

Estrous females follow the group of males; reproductive possibilities will thus be better for a male who is also following the group (van Lawick-Goodall, 1975; Tutin, 1979; Wrangham, 1979).

There is difference in the size of coula- and panda-cracking groups that supports this hypothesis (Table 7).

Table 7

**Group size when cracking coula and panda nuts. Several animals cracking in the same group were recorded as one group when in visual or auditory contact with each other. The totals in this table and those of the following Tables 8 to 16 vary: due to the difficult visibility conditions, it was not possible in all cases to record all types of data on each animal**

	Number of solitary animals and dyads	Number of groups of three or more adults	Total
Coula nuts	65	348	413
Panda nuts	80	45	125

Animals were recorded as cracking alone or in pairs when no larger group was either seen or heard in this area 30 minutes before and after the observation. The difference is highly significant ( $\chi^2 = 111.08$ , d.f. = 1,  $P < 0.001$ ); coula cracking is mainly group activity. ( $\chi^2$  tests with d.f. = 1, made for Tables 7 to 16, are all  $2 \times 2$  contingency tables, see Siegel, 1956).

This hypothesis assumes that males may favor their presence in the group to the nut cracking if they have to choose. Table 8 shows the frequency of adolescent and adult males and females seen cracking coula nuts on the ground and in the tree and panda nuts; again,

**Table 8** Sociability of males and females seen cracking coula (ground and tree) and panda nuts

	(a) Alone or in pairs		(b) Auditory contact with the group		(c) Visual contact with the group	
	Coula	Panda	Coula	Panda	Coula	Panda
A ♂	3	3	40	9	191	26
Ad ♂	4	3	60	4	79	9
A ♀	40	64	103	20	153	8
Ad ♀	—	6	3	1	2	4

group size is defined by the number of adults. We differentiate between (a) animals cracking alone or in pairs with the group being, to our knowledge, absent; (b) animals cracking alone or in pairs but with auditory contact to the group; included are animals that began to crack within the group, but allowed it to move on, and (c) animals cracking in visual contact of two or more adult chimpanzees. Pairs were always two females, usually with their offspring, except for two cases of an adult male cracking together with an adult female.

- (i) Males crack both species of nuts more frequently in groups with auditory and visual contact than do females (coula:  $\chi^2 = 24.61$ , d.f. = 1,  $P < 0.001$ ; panda:  $\chi^2 = 38.52$ , d.f. = 1,  $P < 0.001$ ).
- (ii) Males cracking in groups do it more often for both nut species by conserving *visual* contact with the group members than do females (coula:  $\chi^2 = 29.65$ , d.f. = 1,  $P < 0.001$ ; panda:  $\chi^2 = 11.31$ , d.f. = 1,  $P < 0.001$ ).
- (iii) The differences between adolescent males and females in grouping tendencies for coula and panda cracking are not significant ( $P > 0.05$ ).
- (iv) The differences between adult and adolescent males cracking in visual as opposed to auditory contact with the group for coula is the only significant one in adult/adolescent comparisons ( $\chi^2 = 28.10$ , d.f. = 1,  $P < 0.001$ ). Adult males more often crack coula in visual contact with the group than adolescent males.
- (v) The position of adolescent males is an intermediate one between adult males and females for coula, as the difference between adolescent males and adult females regarding visual *versus* auditory contact with the group is not significant ( $\chi^2 = 0.20$ , d.f. = 1,  $P > 0.05$ ), but is significant regarding cracking in groups *versus* alone ( $\chi^2 = 11.10$ , d.f. = 1,  $P < 0.001$ ). Adolescent males more often crack in groups than females, but when in groups they are more often at its periphery with mere auditory contact than adult males.

In conclusion, adult males prefer to crack coula nuts in visual contact with other group members and were often seen to stop cracking in order to follow the movement of the group (40 observations out of 44 such situations). Adult females were observed to go on cracking more often than males when such a conflict occurred (43 observations out of 63 such situations). We think that these differences may explain why adult male crack panda nuts less often than females (Table 1). Panda trees are widely scattered and usually there is only one hammer at their anvil, which rarely presents an interest for more than one adult. Thus, when a group of chimpanzees arrives at a panda atelier, males will generally follow the

group movement, whereas females, less inclined to keep group contact, will stay behind alone to crack panda nuts. The comparisons of the four panda seasons confirm this interpretation. During the first two seasons, the groups did not frequent panda regions and only two solitary males were seen cracking panda nuts, compared with 35 females. During the last two seasons, groups did frequent some panda regions and 35 males were seen to crack panda nuts—all but one in visual or auditory contact with the group (Table 8). This is in contrast to 57 females, of which only 24 cracked in visual or auditory contact with the group. When several males were at a panda atelier, one would crack nuts while the others sat a few metres away, often waiting for their turn to use the hammer.

These results on grouping tendencies could explain in part why adult males crack panda nuts less often than adult females, but so far we have no explanation for the lower male efficiency (hits/nut) in panda cracking.

*Hypothesis 3: concentration.* To test this hypothesis, we use the side glances an animal casts around itself while cracking nuts. We defined as a side glance the movement of the head an animal makes to look away from the anvil (see Figure 2). Behaviors alien to nut cracking such as scratching and body inspection were also recorded. Table 9 shows the frequency of sessions in which the cracker looks around while pounding or eating nuts. Most chimpanzees that look around while eating do so with almost every nut of a session. Those not looking around generally never look around, so that a cracking chimpanzee is easily classed in one of these categories. All animals that look around while pounding do so also while eating. Excluded were side glances made by an animal only towards us or to search the ground around the anvils looking for nuts. Glances by a mother to her infant sharing nuts with her or playing around her (five observations) are not classified as side glances, as we want to analyse the interest of the nut cracker toward the other adult group members. To test this hypothesis, the side glances cast while eating the nut were considered as a measure of diversion due to social interest, whereas we interpreted the side glances made during the hitting of the nuts as an inverse measure of the chimpanzee's true concentration. At the present state of habituation it was not possible to determine precisely the two glancing rates, especially for the females.

**Table 9** Frequency of coula cracking sessions on the ground with and without side glances during the 1982 and 83 coula nut seasons. No chimpanzee was seen to cast side glances only while pounding

	Side glances while eating only	Side glances while pounding and while eating	No side glances	Total
A ♂	77	19	16	112
Ad ♂	47	6	36	89
A ♀	14	4	86	104

(i) Adult males look around them much more while eating the nuts than do adult females ( $\chi^2 = 98.52$ , d.f. = 1,  $P < 0.001$ ). Males look regularly at other adults during the consumption of the nuts, but they also look in the direction from where other animals might arrive.

(ii) Adult males also look around them more while eating the nuts than do adolescent males ( $\chi^2 = 16.36$ , d.f. = 1,  $P < 0.001$ ). The difference is also significant between adult

Figure 2. Typical side glance cast by Ulysse, an adult male, while eating a coula nut.



females and adolescent males in favor of the latter ( $\chi^2 = 35.0$ , d.f. = 1,  $P < 0.001$ ), who again have an intermediate position between the adult males and females (see hypothesis 2).

The adult males demonstrate clearly that nut cracking is in conflict with another interest, presumably that in social companions. This might explain why the adult males rarely crack coula nuts in the tree. For a chimpanzee in a tree, the visibility to the ground is restricted at best to the area vertically beneath it and it cannot monitor either the presence or the activity of its companions. Only one male out of six seen cracking nuts in a tree was the sole occupant, but beneath him were more than 15 crackers on the ground. He continuously exchanged food-grunts with another adult male who was cracking at the foot of this tree until he descended to crack on the ground together with that male. These food-grunts are usually produced when the chimpanzees arrive at an abundant food source. We did not hear it again for coula, except a few times between adolescent males. The five other males seen cracking coula in the tree had a social motive, as they did it in the same tree and at the same time as an estrous female, with the group cracking on the ground near this tree. In one of these cases, the group on the ground moved on and the male in the tree immediately followed, while the estrous female continued to crack for 20 minutes. This is an impressive example of the males' preference for the group. The tendency of males to remain in groups also when in tree crowns is general: Table 10 shows the associations of adults seen in trees other than coula, i.e. outside the nut-collecting context. Adult males maintain group contact even when they are up in the trees more than adult females do ( $\chi^2 = 54.49$ , d.f. = 1,  $P < 0.001$ ).

Table 10

Grouping of adults seen in trees other than coula during four years

	Alone or in pairs	In groups of three or more adults	Total
A ♂	71	370	441
A ♀	171	274	445

The data of adolescent males in Table 1 confirm this. The eight observed cases of adolescent males cracking in a tree in 1982–83, are due to two animals only, Darwin and Clyde. Adolescent males have a precarious social position, trying to achieve a dominant rank over the adult females, with all the conflicts this implies (van Lawick-Goodall, 1968, 1975). It is perhaps relevant that both Darwin and Clyde are the only adolescents out of six that might have difficulties in reaching this goal: Darwin has a badly injured left foot, all the toes being torn off and only the heel remaining. Clyde, who is an orphan, has only the thumb of his right hand left. These injuries handicap the two adolescents in social challenges which include rapid pursuit or escape up the trees. Possibly, this leads them partly to abandon group contact and the attempt at rising in rank.

(iii) The difference for adults of both sexes that look or do not look around *while hitting* the nuts, which we chose as a measure of concentration, is significant ( $\chi^2 = 8.42$ , d.f. = 1,  $P < 0.01$ ) in favor of the males. When we compare the efficiency measures of adult males looking or not looking around while hitting a coula nut on the ground, the difference is significant for both measures (Mann–Whitney *U*-test: hits/nut,  $P < 0.001$ ; nuts/min,  $P < 0.01$ ) in favor of those not looking round while hitting the nuts. The same difference should appear for the females, but our sample is too small for testing. The conclusion that the males lack concentration, which makes them less efficient would be premature: From direct observations we know that the animal that looks around while hitting usually has a very bad hammer (see hypothesis 5) and therefore technical difficulties. This was true for three of the four females in Table 9 and for 13 of the 19 males. The poor hammers were either too light or of inappropriate shape. Qualitative impression suggests that the chimpanzees responded with a loss rather than a compensatory increase of concentration or attention. Others cracked while social excitement was present, such as a new group arriving or some males displaying nearby (five observations on one female and four males). Thus, beside the first explanation that males lack concentration, it might as well be that they concentrate as well as females and lose it, as females do, when facing technical difficulties or when social events occur. In hypothesis 5, we shall analyse further the possible causes of the seemingly higher frequency of males to choose bad hammers, which can lower their efficiency. At the present stage of the analysis, we cannot differentiate between these two explanations.

Data on behavior external to the nut cracking, such as scratching, are very rare and seem also to be provoked by technical difficulties.

These results on side glances might provide an explanation why the males so rarely crack coula nuts directly in the tree compared to the females, but so far a definitive explanation of efficiency differences is missing.

#### *Hypothesis 4: motor abilities.*

(a) The first level of this hypothesis concerns the fact that a tool could be emotionally loaded, as it has been observed that clubs and stones are sometimes part of the males'



displays (van Lawick-Goodall, 1968, 1970). It is true that males occasionally (three observations during the fourth year) use clubs in their displays and it is, in fact, possible that display emotions interfere with their nut-cracking use of the hammer. As no specific male behavior during nut cracking, sign of these emotions, were identified, we could not measure the effect on the efficiency. What can be rejected is the more elaborate hypothesis that an encountered technical difficulty causes exasperations and violent hammering due to these display emotions: So far, we have not observed any male showing signs of exasperation or tendency to hit the nuts violently, not even when more than 30 hits were needed to open a nut, or when they did not succeed in opening it at all. Yet, more subtle signs of emotionality in hammering males may have escaped us.

(b) The following motor differences are known:

Young female chimpanzees more often manipulate objects than young males. Furthermore, they manipulate their young siblings more often (van Lawick-Goodall, 1968; McGrew, 1979).

In humans, females are superior to males in certain manual dexterities from early childhood onwards (Garai & Scheinfeld, 1968; Ember, 1981).

In an attempt to reveal motor sex differences, we tried to analyse the movements of cracking animals. A chimpanzee hitting a *coula nut* moves its head and trunk. Small movements of head and shoulder are obligatory for this action. Big movements of the head and trunk, as it were an anticipation or amplification of the hitting movement, are easily distinguishable from the former. Table 11 presents the frequency of these two types of movements in adults and adolescents of either sex cracking *coula* nuts on the ground.

**Table 11**

**Frequency of sessions of adult animals cracking *coula* nuts that (a) are showing a marked movement of the head and trunk, or (b) are not moving while hitting the nuts. Data of the 1982 and 83 nut seasons**

	Marked movements while hitting	None or small movements	Total
$\Lambda \text{ } \sigma^{\circ}$	107	41	148
Ad $\sigma^{\circ}$	94	8	102
$\Lambda \text{ } \varphi$	14	108	122
Ad $\varphi$	2	9	11

Adult males more often make large movements while hitting the nuts than adult females ( $\chi^2 = 97.58$ , d.f. = 1,  $P < 0.001$ ). Similarly, adolescent males more often exhibit marked hitting movements than adolescent females ( $\chi^2 = 36.92$ , d.f. = 1,  $P < 0.001$ ). Adult males, however, make these movements less often than adolescent males ( $\chi^2 = 13.87$ , d.f. = 1,  $P < 0.001$ ).

These same movements, even amplified, are also typical and occur consistently in infants and juveniles. Whereas they disappear in adult females, they persist in males and are somewhat reduced only in adults.

A more detailed analysis of the hitting movement reveals another difference between males and females. The nut cracking animal normally sits close to the anvil, sometimes even with the head vertically above it, and it hits the nut by bending the elbow, the whole pounding movement being concentrated in the forearm (Figure 3). In other cases, the animal sits farther away from the anvil and hits the nut by keeping the arm more or less

Figure 3. Coula cracking by Ulysse, an adult male, showing a typical elbow-flexion movement. See text for further explanations.



stretched out with the elbow joint remaining in a rigid position; the chimpanzee accompanies the movement with a forward flexion of the trunk. A given animal in a given session uses only one of these two motor patterns and there is no intermediate form. The difference shown in Table 12 between the adults is highly significant ( $\chi^2 = 75.12$ , d.f. = 1,  $P < 0.001$ ) in favor of males.

What could explain this intriguing difference? Anatomical variations in the locomotor apparatus are not sexually specific and cannot cause such a difference, but muscular power is much larger in males than in females (Short, 1979). As we observed not only adult males but also infants and juveniles cracking with an amplified movement and rigid, stretched out arms, we wonder whether *the control of strength* might be an explanation; too little strength in infants and juveniles, too much in adult males. The former would amplify it with wide movements. The adult males would try to control their excess of strength by keeping the arm stretched out, the rotation being made partly by the shoulder and partly by the trunk. Such a movement may seem to us ineffective for the purpose, but some data on males seem to support it. If this movement is really correlated with the control of strength, we should find a decrease in its use when hitting with one arm, which should exert less excessive strength, than when hitting with both arms. Indeed, out of 32 males making an elbow-flexible movement (Table 12), 30 used only one arm for hitting, in contrast with 40 that used one arm out of 85 with rigid arm movement.

Table 12

**Frequency of arm movements (Figure 2) observed in adults of both sexes cracking coula nuts on the ground. Data of the 1982 and 83 nut seasons**

	Hitting by keeping the elbow in a rigid position	Hitting with a substantial elbow movement	Total
A ♂	85	32	117
A ♀	10	80	90

Concerning the adolescent males, the following question arises: why do they still use this amplified movement although they have certainly acquired enough strength to open a coula nut without it and they do not yet have the excess of strength of adult males? Adolescent females seem to have already acquired a movement comparable to that of adult females. The only suggestion we can forward is that the estrous swelling might impose upon the females the learning of a different movement. At maximum swelling, the females crack nuts by either placing their swelling beside a prominent root, or by standing bipedally. To crack in this position with the same movement as juveniles, i.e. the arm stretched out, would either oblige them to stand back farther from the anvil (arm-plus trunk-length distance), which means loss in precision, or stay close to the anvil, which would mean adopting an unusual upright position. Juveniles do sometimes with difficulties try such solutions. But all the observed females in estrous (13 cases) that cracked in a bipedal posture, did so with the trunk in a horizontal position, sometimes even with the head above the anvil. They performed the hitting movement entirely by elbow flexion and not in the shoulder joint as do juveniles and males. Thus, the elbow flexion movement may appear with the first big swelling and young adolescent females should not have acquired it. We do not yet have enough data to test this.

In conclusion, the change in the movement of hitting that occurs in the females between juvenile and adolescent stage may be a rapid adaptation to the indirect influence of the swelling appearing with the estrous cycles. Males, for reasons not yet understood, maintain a juvenile-type movement into adulthood. There are some exceptions: e.g. one prime male, Wotan, is a very efficient cracker. He is the only adult male we saw crack nuts with an elbow movement like adult females when using a very small club.

Sex differences in the hitting movements occur also in *panda cracking*. Opening a panda nut requires powerful hits at the beginning. To free the next two or three separately embedded almonds, subtle and precise hits are needed. A powerful hit, whatever the weight of the hammer, is given at least from the height of the animal's chest (high hits). A subtle, well controlled hit should be given from a height below the animal's chest. Improbable as it seems, it is easy to discriminate two distinct classes of sessions here as certain animals use only high hits throughout an entire session. Table 13 shows that they are mostly males ( $\chi^2 = 23.23$ , d.f. = 1,  $P < 0.001$ ); they seem to control their strength less through subtle hits to get access to the embedded almonds of the nut.

The panda data confirm those for coula: males seem to have difficulties in controlling their strength; at least, they vary their movements less than females to carry out subtle hits. According to the present hypothesis, this should affect their efficiency. Proving this for coula is impossible, as males cracking coula with an elbow movement, did it with a heavy club or stone, and it is hazardous to try to sort out the respective influence of these two

Table 13

**Frequency of sessions of adults cracking either with well controlled hits or with little or no control, when pounding panda nuts during the four panda seasons**

	Marked control of hits: high and low	Little or no control of hits: only high	Total
A ♂	9	21	30
A ♀	25	1	26

factors. For panda, the males' sample is too small for comparing efficiencies of both movement types for all hammer weight classes, except for two classes: in the 7 kg class, the difference is not significant; in the 5 kg class, males using only high pounding movements are better for the second efficiency measure (Mann-Whitney *U*-test: nuts/min:  $P < 0.05$ ). To conclude that males not varying their pounding amplitude are more efficient than those doing it would be premature: direct observations show that the former try much less carefully to open all the almonds of the nut. Thus, they eat nuts quicker but leave more almond remains than the others. The comparison is thus inconclusive and we can only infer, from the analysis of Table 6, that the poorer performance of males when using heavy hammers might be a sign of their greater difficulties in controlling the strength required for the manipulation of these hammers.

In conclusion, the sexual dimorphism in the muscular strength appears to imply difficulties for the males in acquiring the same hitting movement as the females. How this difference affects the efficiency measures remains difficult to measure.

*Hypothesis 5: cognitive abilities.* Sex differences in solving particular technical problems in nut cracking might exist for the following reasons:

Studies on captive primates in acquisition and learning of various tests, such as delayed response, matching to sample or reversal learning, found either no differences between males and females, or reported that females were superior to males. Such differences in favor of females were found in the rhesus monkey, the Japanese macaque, the olive baboon and the chimpanzee (reviewed by Mitchell, 1979).

In humans, cross-cultural differences appear not only in the cognitive development of infants, but also between adults of either different cultures or different sexes (Dasen & Heron, 1981; Ember, 1981; van Leeuwen, 1978).

Chimpanzees that crack nuts may choose hammers which lead to difficulties in opening the nuts (more than 10 hits per nut). If the hammer is too small or thin (<20 cm long or <5 cm in diameter), it requires more strength to open the nuts or it has to be grasped with the extremity of the fingers. Hammers of an irregular shape require a very specific pounding angle, and those of poor soft quality or about to decay, are of little use. Table 14 presents the reactions of adults in such situations: (a) adapting their sitting posture and location, the grip of the hammer, or changing the hammer with an immediate success in improving the efficiency (less than 10 hits per nut), (b) adapting in such a way, but without improving, the efficiency to less than 10 hits per nut; after a variable number of eaten nuts, the animal finally gives up and leaves the last nut intact on the anvil, and (c) no adaptations, but the animal continues, requiring more than 10 hits to open the nuts.

Adult males choose more often a bad hammer than adult females do (total Table 14 *versus* total Table 1 minus Table 14 for coula on the ground:  $\chi^2 = 8.95$ , d.f. = 1,  $P < 0.01$ ).

Table 14

**Adult animals that made a bad choice of a hammer (raw total) and were (a) successfully adapting themselves to the problem, (b) adapting without success or (c) not adapting themselves at all. Data are collected for coula cracking on the ground during the 1982 and 83 nut seasons**

	Bad choice of a hammer Total	Attempt of adaptation with success (a)	Attempt of adaptation without success (b)	Continues without adaptation (c)
A ♂	30	8	16	6
A ♀	16	12	1	3

As exposed above (see hypothesis 3), two reasons, either a lack of concentration due to social diversion or cognitive differences, may explain this difference. The fact that both sexes equally often realize when a tool is bad (columns a + b in Table 14) argues against the lack of concentration. Also from direct observations, we notice that it is the technical difficulties due to the bad hammer that entail a change in the chimpanzee's behavior: When after many hits the nut remains intact, the cracker will look around, rest for a short time and attempt to adapt to the technical problem. These behaviors are not present at the beginning of the session and after many nuts with a good hammer.

The sexes do not differ in their attempting to adapt to a bad choice (a + b *vs* c:  $\chi^2 = 0.08$ , d.f. = 1, n.s.), both sexes realizing when a tool is bad. However, females are significantly more often successful in their adaptation, whereas males more often give up after an unsuccessful attempt (a *vs* b:  $\chi^2 = 9.55$ , d.f. = 1,  $P < 0.01$ ). This might have a negative side-effect on the males' coula performance, as hypothesis 5 requires, in that because of their bad hammers they reach lower efficiency. Yet, Figure 1 shows that efficiencies of 10 hits/nut or more do not differ conclusively between the sexes and does not explain the observed sex difference for the second efficiency measure (nuts/min).

Differences between the sexes appear also in the hammer transports. Hammers are normally transported from one anvil to another. We found only a few hammers that had been dropped somewhere, instead of being carried to an operative atelier. We saw 11 adult males, but no females, to thus abandon a hammer they were carrying. This might be a sign of inconsistency in their planning of action. The observations of stone transports by males and females between distant panda trees (more than 40 m) support this idea. Table 15 lists the adults we saw cracking panda nuts after having carried the stone and those who cracked at an anvil that already had a stone before they arrived. We never saw the transport itself and inferred it when we were certain that there had been no stone at the tree

Table 15

**Adults observed to crack panda nuts after having transported the stone, or cracking at an anvil that had a stone already, in four years (see text for further explanations)**

	Cracking after having transported the stone	Cracking without transporting the stone	Total
A ♂	0	38	38
A ♀	12	72	84

the day before the observation, and that no chimpanzee had cracked at this tree in the meantime, which can be ascertained by the freshness of the nut shells remaining on the anvil.

Only females are suspected to transport stones for panda ( $\chi^2 = 4.52$ , d.f. = 1,  $P < 0.05$ ). As these transports involve considerable cognitive capacities (Boesch & Boesch, 1984), this result indicates the possibility that females might have a better planning of their action than males. It might be that in a specific panda area the males do not know the different stone locations, which is essential for transporting them optimally to the different panda trees, e.g. taking the nearest one to a goal tree. The ignorance, or the failure to fetch a known hammer, might be caused by the attachment of males to a group, which should restrict individual forays (see hypothesis 2). We suppose that males would limit themselves to crack only at panda trees which have a stone to crack at the anvil *and* when other group members are within their sight. This behavior will greatly limit their panda-cracking activity and might, thus, reduce the males' efficiency through less practice than the females. But, as the sex difference in efficiency for panda concerns only the heavy hammers, it is hard to see why less practice should affect the efficiency only for the heavy weights.

In conclusion, females seem to adapt themselves better to technical problems and seem to plan or make hammer transports more persistently than males. Thus, the sex difference postulated by the hypothesis does exist but seems not to explain the observed sex difference in nut-cracking efficiency.

#### 4. Discussion

The ontogenesis of nut cracking is a longer-lasting process than that of the other tool techniques used by chimpanzees. For these techniques, the first attempts are about two years earlier than the nut cracking, and at four years are already practiced; the infants possess the basic adult technique and use the tools in the correct context. Successful termite fishing is acquired at five-and-a-half years by young juveniles (van Lawick-Goodall, 1968, 1970), the driver- and wood-boring ants dipping techniques are acquired by old juveniles (McGrew, 1977; Nishida & Hiraiwa, 1982). However, their efficiency performance was not measured. Our preliminary results show that coula cracking on the ground is completely acquired at adolescence by females and at adulthood by males in terms of hits/nut. Coula cracking in the tree and panda cracking is completely acquired at adulthood by females; males acquire it at adolescence but remain less efficient than females at adulthood.

The data of all the four years confirm our previous results (Boesch & Boesch, 1981) indicating that nut cracking is the first non-human primate example of tool behavior showing an important sex difference in favor of females for both, frequency of the technique used and the efficiency reached (Beck, 1980; van Lawick-Goodall, 1970; Warren, 1975). The Tai chimpanzee males appear to neglect the two most difficult techniques, coula cracking in the tree and panda cracking, in order to keep close contact with other group members, mainly the group of adult males. Adult females and adolescent males, which often crack out of visual contact of the group, do not thereby lose the group contact completely, but need some time to join it, and that seems to be the crucial point. Males apparently want to be present in the group right when important events take place. We can think of two types of situations of importance to the males: first, status conflicts, which in chimpanzees always involve alliances, supportative behavior and opportunistic possibilities (Bygott, 1979; van Lawick-Goodall, 1968; de Waal, 1982). Second, and this

may be more important, situations that are not predictable and which need the co-operative action of the males. One is hunting behavior, which can be very silent and to be successful in the tropical rain forest demands at least three or four co-operating chimpanzees (pers. obs.). Fights against potential predators and territorial fights are even more crucial. In a forest habitat, the leopard density is known to be high compared with the savanna, one per square mile versus one per 10 square miles (Myers, 1976) and male chimpanzees chase them away co-operatively (one pers. obs. in Tai). Territorial encounters with neighboring communities are common (six encounters observed during eight months in Tai) and are very aggressive, involving tremendous charges by the co-operating males. Again these situations are not foreseeable, as the foreign community may appear without a sound or be well inside the home range when the encounter happens (Goodall *et al.*, 1979, Boesch, pers. obs.).

The motor difficulties encountered by the males seem to stem from their excess of strength. The chimpanzee has to control the action of its strength on a nut as exerted not by his hand, but by an insensitive tool. Guillaume & Meyerson (1930, 1931, 1934, 1937) studied the use of tools in baboons (*Papio* sp.) and chimpanzees. Their results show that the baboon is expert in continuously controlling the motor impulse in its own body. When acting on tools, the motor impulse is explosive and unconcerned with its immediate effect, only attentive to the final result. When the baboons reach with their hands to take a fruit outside the cage, they have no difficulties. Whereas, when they must use a stick to do so, they have difficulties in relating the stick to the fruit and they hit the fruit confusedly and do not succeed in bringing it nearer. "The inferior monkey fights against the tool; the ape submits to the tool. At the same time, it exploits the tool . . ." (1937, pp. 445, our transl.). For these authors, the use of a tool means subordinating the motor impulse to the new effects produced by the tool on a goal object. The feedback from these effects on the handling of the tool is a continuous correction. At the same time it represents an invention of new responses to new anatomical and instrumental techniques. This sophisticated process might still be difficult for the chimpanzees, especially when the motor control has to be applied to great strength. This complex control, made difficult because the feedback from the tool to the hand has different sensory characters than would that from the object, increases with the sophistication of the technique and was a long process to acquire during evolution. Female hominids being less strong than males (Short, 1979) had to deal with a smaller amount of motor impulse and might well have taken advantage of that during evolution and become experts in tool use. Males, in contrast, would be phylogenetically retarded in this respect.

The chimpanzees face the dilemma of evolving co-operative and powerful individuals for hunting and protection against predators and neighboring chimpanzees, and less co-operative and less powerful individuals to practice the more sophisticated tool use. The chimpanzees appear to have adopted a specialization in which males, the more powerful sex, became socially more co-operative than females. The females became less co-operative and concentrated on tool use. Thus, the specialization which already appears in baboons with the higher tendency of males to hunt, takes a further step in the chimpanzees with a female specific activity and a bigger specialization of the males.

Meat sharing between adult chimpanzees appears with the evolution of that sex specialization, as it was not observed in baboons (Harding, 1975). Males normally own the meat, but may share a part of it with the females. This sharing can take many forms: (a)

Crumbs or discarded pieces can be retrieved by a chimpanzee with hardly any sharing intention of the owner. (b) Pieces can be taken from the food held by the owner without reaction of the latter; this can be called passive food sharing. Isaac (1978) called it tolerated scrounging and maintained that there is no active sharing in chimpanzees. (c) Contrary to this, the owner may actively hold out a piece to another individual, which is active food sharing. (d) The owner may permit others to take food from his store for up to half an hour. All these types of one-way food sharing were seen in meat eating (van Lawick-Goodall, 1968; Teleki, 1973; Boesch & Boesch, pers. obs.) and in eating of the very big fruit, *Treculia africana*, in Tai. In all these variants, males mostly share with females. No reciprocal food sharing due to a specific female foraging activity was observed in Gombe and, moreover, no food obtained through tool use was ever observed to be shared between individuals, not even between mother and infant. The major nutritional role of a food in the animal's diet might be a condition for the evolution of food sharing. The Tai chimpanzees are the first chimpanzee population observed to heavily rely or even depend on tool-acquired food during four months of the year, and they often do share this food. Mothers always share nuts which they have cracked with their infants and juveniles (42 observations) whenever they beg for them instead of trying to open the nuts themselves. The same was observed among presumed siblings (six observations). It might be that the habit of sharing nuts in the mother-offspring bond or between offspring predisposes them to share food when adult. Indeed, one observation in Tai at least demonstrates the reciprocal component to male meat sharing toward a true division of labor with two-way food sharing between a male and a female. The nut cracker, an adult female, passively shared the panda nut she had opened with an adult male.

In conclusion, the Tai chimpanzees present a sex difference in tool use for mainly two reasons, difference of sociability and motor pattern. The higher frequency and in some measures, the higher efficiency with which females crack nuts with tools is a counterpiece to the higher frequency and skill of hunting in males. These two sex specific skills are raw materials from which a sexual division of labor of basic hominid type could have evolved. If chimpanzees survived, these might eventually lead to division of labor and food sharing.

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