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Hunting Behavior of Wild Chimpanzees in the Taï National Park

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ABSTRACT Hunting is often considered one of the major behaviors that shaped early hominids' evolution, along with the shift toward a drier and more open habitat. We suggest that a precise comparison of the hunting behavior of a species closely related to man might help us understand which aspects of hunting could be affected by environmental conditions. The hunting behavior of wild chimpanzees is discussed, and new observations on a population living in the tropical rain forest of the Taï National Park, Ivory Coast, are presented. Some of the forest chimpanzees' hunting performances are similar to those of savanna-woodlands populations; others are different. Forest chimpanzees have a more specialized prey image, intentionally search for more adult prey, and hunt in larger groups and with a more elaborate cooperative level than savanna-woodlands chimpanzees. In addition, forest chimpanzees tend to share meat more actively and more frequently. These findings are related to some theories on aspects of hunting behavior in early hominids and discussed in order to understand some factors influencing the hunting behavior of wild chimpanzees. Finally, the hunting behavior of primates is compared with that of social carnivores.

Hunting is generally described by paleoanthropologists as a central behavior in hominid evolution (Hill, 1982; Isaac, 1978, 1983; Isaac and Crader, 1981; Johanson and Edey, 1981, Leakey, 1981; Leaky and Lewin, 1978; Washburn, 1978), even though opinions still diverge about which adaptation was crucial for the making of mankind, i.e., tool making (Washburn, 1960, 1978), food sharing (Isaac, 1978, 1983), seed eating (Jolly, 1970), or division of labor (Hill, 1982; Zihlmann, 1981). Recently, Shipman (1986) cast doubt on the hunting proficiency of early hominids based on findings from bed I in Olduvai Gorge (2–1.7 million years old). Analyzing cut marks on bones, she concludes that hominids in that period relied on scavenging for their major meat procurement rather than on hunting, thus confirming the increasing importance according to scavenging in descriptions of early hominids' diet (Isaac and Crader, 1981; Potts, 1984). Similarly, new evidence coming from the field of primatology has cast doubt on the uniqueness of hunting in man. Recent observations on hunting of mammalian prey in nonhuman primates (for example, Badrian and Malenky, 1984; Butynski, 1982; Goodall, 1986; Kudo and Mitani, 1985), and the increase in complexity and frequency of hunting behavior among primates (comparison of baboon hunts with chimpanzee hunts—Strum, 1981; Goodall, 1986), cause us wonder whether hunting is really a characteristic of man and whether the shift toward an omnivorous diet did not occur early in primate evolution. The actual field data tend to show how hunting evolved, both in Carnivora (Ewer, 1973; Estes and Goddard, 1967; Kruuk, 1972, 1975; Mech, 1970, 1975; Peters and Mech, 1975; Schaller, 1972) and in Primates, among the latter mainly in the superfamilies of Cercopithecoidea and Hominoidea. This evidence suggests that it may be too simple to propose a unique evolution of hunting in early man; indeed, anthropologists favor the idea that a radical change in the habitat (a shift from the forest to a more open savanna/woodland environment east of the Rift Valley in East Africa) of early hominids forced them into a series of adaptations, of which the hunting of mammals would be

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a major one (Coppens, 1983; Johansen and Edey, 1981; Leakey, 1981 Leakey and Lewin, 1978; Pilbeam, 1980).

Data on predation on mammals in primates have been collected from a wide range of species, for example, blue monkey (Butynski, 1982), vervet monkey (Galat and Galat-Luong, 1977), macaque (Estrada and Estrada, 1977, 1978), mandrill (Kudo and Mitani, 1985), most savanna-dwelling baboons (Altmann and Altmann, 1970; Hamilton and Busse, 1982; Harding, 1975; Hausfater, 1976; Goodall, 1986; Kummer, 1968; Strum, 1981; Rhine et al., 1986), orangutan (Sugardjito and Nuhuda, 1981), pygmy chimpanzee (Badrian and Malenky, 1984), and the common chimpanzee (see references below). However, observations on all these species vary in length, living conditions of the animals, and recording procedure, so that comparisons done in order to understand the factors influencing hunting in primates are difficult. For such a purpose, studies on one behavior (hunting) and one species (chimpanzee), living in a natural environment, may permit a reliable comparison of such a complex behavior.

The chimpanzees are predators of at least 19 different mammalian species (Goodall, 1986; Nishida and al., 1983; Teleki, 1981). They tend to reach kill rates of the prey species comparable with those of some social carnivores, total meat intake apart, which is quite different. In Gombe Stream, chimpanzees kill an estimated 8–13% of the red colobus population (Busse, 1977). In the Ngorongoro crater, spotted hyenas kill 11% of the wildebeest population and 9% of the zebra population (Kruuk, 1972). In the Serengeti, lions kill 6% of the zebra population (Schaller, 1972). One community of chimpanzees in Gombe Stream was observed to hunt 33 prey per year during a 10-year period (Goodall, 1986). A comparison between chimpanzee populations should allow us to understand how hunting in a primate species may be influenced by different factors, such as the environment, prey availability, food availability and social aspects.

In addition, with the accumulation of observations on chimpanzees' hunting behavior, a behavioral comparison between Carnivores and Primates becomes feasible, allowing us to test the hypothesis proposed by some authors (Schaller and Lowther, 1969; Thompson, 1975, 1976) that carnivores' hunting behavior is closest to that of humans and that it should be studied as a possible model for human evolution. However, we also suggest that it is important to analyze differences in hunting behavior (and factors influencing them) between different primate species, with a view toward comparing such traits and abilities on the level of zoological orders.

The present paper has four aims:

1. To present the hunting data of a wild chimpanzee population living in a dense tropical rain forest, the Taï National Forest, Ivory Coast, an environment not studied so far for the hunting behavior of chimpanzees.
2. To compare the forest study with two studies made on wild chimpanzee populations living in a more open environment (savanna/woodland) in the Gombe Stream National Park and in the Mahale Mountains National Park, both in Tanzania, in order to acquire an impression of the variability chimpanzees can display within the same behavior, i.e., hunting.
3. To understand how some of the differences between these three populations appeared and how the environmental differences affected them.
4. To compare some aspects of the hunting behaviors of chimpanzees and the social carnivors.

METHODS

The wild chimpanzees (*Pan troglodytes*) of the Taï National Park, Ivory Coast, have been studied since September, 1979. At the time of writing, the community included 79 individuals, with 9 adult males and 26 adult females, living in a 27-km^2 home range in the western part of the park, about 20km from the village of Taï (for more details on the environment, see Boesch and Boesch, 1983). The closest traditional plantations are located about 6 km from their home range limits. The native tribes, the Oubi and the Guere, do not hunt them for meat or totemic reasons. The forest is the evergreen rain forest type, with an average rainfall of 1,800 mm per year and an average temperature of 24°C. Among the larger mammals present, many of them potential prey, we note: the forest elephant (*Loxodonta cyclotis*), the pygmy hippopotamus (*Cheoropsis liberiensis*), the bongo (Tragelaphus euryceros), the bushpig (*Potamochoerus porcus*), the giant forest hog (*Hylocheorus meinertzhageni*), six species of duikers (*Cephalophus jentinki, C. sylvicultur, C. ogilbyi, C. dorsalis, C. zebra and D. monticola*), the royal antelope (*Neo-*

tragus pygmaeus), one species of otter (*Lutra maculicollis*), the honey badger (*Mellivora capensis*), the long-nosed mongoose (*Mungos obscurus*) the African brush-tailed porcupine (*Panthera pardus*), and some carnivores—the leopard (*Panthera pardus*), the golden cat *Profelis aurata*), the pardine genet (*Genetta pardina*), and the civet cat (*Viverra civetta*). Besides the chimpanzees, ten species of primates live in the area: three colobus (*Colobus badius, C. polykomos, and C. verus*), four cercopithecoids (*Cercopithecus diana, C. petaurista, C. campbelli, and C. nictitans*), the sooty mangabey (*Cercocebus atys*), the dwarf galago (*Galago demidovii*), and the Bosman's potto (*Perodicticus potto*).

We habituated the chimpanzees to our presence without artificial provisioning, and we followed them only by their drummings, and vocalizations, and, more recently, by sight. Due to the very limited visibility in this dense forest (at most 20 m on the ground) and the shy character of the chimpanzees, habituation was a slow process; only after 2 1/2 years could we observe some chimpanzees that were aware of our presence. From March, 1984 onwards, we could follow all the males by sight and remain within their group while they were hunting. For this reason, *we considered only the huntings observed during the last 2 years for the detailed analysis* (between March, 1984 to May, 1986). The main focus of our study was the nut-cracking behavior of the chimpanzees (Boesch and Boesch, 1981, 1983, 1984a,b), and our interest in hunting grew slowly with the increasing evidence of differences from the known behavior of other chimpanzee populations. During the nut seasons we mainly followed the females, who hunt less frequently than males (see below), and a certain amount of hunts were, therefore, missed. However, we gained the impression that hunting mostly occurs when Coula nuts are out of season and that we missed few hunts performed by the central animals. In order to keep the human disturbance at the lowest level, not only for the hunters but also for the prey, usually monkeys, we trained ourselves to move on the ground under groups of arboreal monkeys without being noticed by them, particularly not until the chimpanzees were noticed.

Comparisons of hunting behavior at different study sites are difficult, and data-recording procedures have to be compared. In Taï, all hunting behavior data were recorded by one observer (C.B.), and all aspects of the meat-eating episodes were recorded mostly by the two of us, regularly controlling agreement of observations. In Gombe Stream and Mahale Mountains, hunting and meat eating were recorded by a number of observers, who changed regularly over the years. Intercompatibility of the observations may, therefore, be lower in these two sites than in Taï, but the quantity of observations is probably more important in those sites. We shall base our comparisons on published materials. For Gombe, we shall use Busse (1977, 1978), Goodall (1968, 1975, and especially 1986), Teleki (1973, 1975, 1981), and Wrangham (1975). Whenever possible, we shall give preference to the data of the 10-year span from 1972 to 1981 (Goodall, 1986), when banana provisioning was kept very low. For Mahale, the three published papers on hunting behavior will be used (Kawanaka [1982], Nishida and al. [1983], and Takahata et al. [1984]).

Comparing behaviors of different animal populations living in different sites and studied by different observers may be, in the strictest sense, impossible, as one can hardly ever control all variables. We shall, nevertheless, attempt such a comparison, and we consider that small differences should be attributed to the different observational conditions and methods, whereas large, and clear-cut differences should reflect a reality. When methods differ strikingly, we shall make no comparison.

DEFINITIONS OF HUNTING AND FOOD SHARING

Another aspect that makes comparisons difficult is the many different meanings of certain terms. In an attempt to clarify the issue, we shall present our definitions of common terms that cannot be avoided when speaking of hunting behavior. They prove to be useful for describing the Taï chimpanzees' hunting behavior but may be more difficult to use with predators living in very different environments or using different hunting techniques.

Bystander

Any animal present in the group in which a hunt is taking place, not playing any active role. It may look intently at what is happening and even follow the movement of the hunt. During the same hunt, an individual can change from the role of bystander to that of hunter, according to its actions. For example, a bystander, interested in participating actively in a hunt, can do so when the situation stimulates it, such as when a prey falls to the ground.

Hunter

Any animal that shows by its physical movements its intention to play an active part in a hunt: In Taï, the distinction between bystanders and hunters is simple since the hunts take place mostly up in the trees. Once a bystander climbs up to the height in the canopy where the prey live, looking and orienting itself toward them, it becomes a hunter. For hunts taking place on the ground, the rush toward the prey is used to differentiate between the two states.

Hunt

Any situation during which at least one animal, due to its behavior, can be classified as a hunter.

Group hunt

Any hunt in which more than one hunter acts at the same time against the same prey or group of prey. If only one hunter is hunting at a time, within or outside a group of bystanders, or if many hunters are acting each against another group of prey (with different hunting directions), we classify such hunts as solitary.

Some hunters may test the physical abilities of a prey by rushing toward it for only some meters (hyenas, lions or wolves). Classifying such a rush as a hunt can be questionable. Schaller (1972) uses a clear criterion of a minimal approach toward the prey of 60 m to classify a hunt. In Gombe, it seems that it is often difficult to distinguish between bystanders and hunters. Busse (1978) describes "group hunts" in which only one hunter acts at a time but within a group of bystanders. Similarly, Teleki (1973) describes a "cooperative hunt" (May 14, p. 68), in which only one individual acts; the second one is sitting and merely watching the action.

Cooperation

This word has acquired two different meanings, which need to be clarified. In the hunting context, cooperation has generally been attributed to the behavior of two or more individuals acting together to achieve a common goal (see, for example, definitions in Busse, 1978; Goodall, 1986; Kruuk, 1972; Schaller, 1972). In the analysis of the individual behavior, Hamilton (1964) has defined cooperation more strictly: an animal acts cooperatively only if it does things that benefit the fitness (in terms of survival and reproduction) of both itself and the recipient of its actions (Axelrod and Hamilton, 1981; Wrangham, 1982), even at the expense of its own fitness (Krebs and Davies, 1987; Maynard Smith, 1982, 1983). However, this more strict definition of cooperation can lead to the paradox that the same group behavior could be considered cooperative or not only according to its outcome. For example, an elaborate collaborative group hunt performed by one population could increase its hunting success

TABLE 1. Operational definition of cooperation for group hunts: four levels of growing complexity of organization between hunters

Category	Definition	Variation
Similarity	All hunters concentrate similar actions on the same prey, but without any spatial or time relation between them; however, at least two hunters always act simultaneously	Similar actions are varying elements of pursuing a prey, i.e., stalk, chase . . .
Synchrony	Each hunter concentrates similar actions on the same prey and tries to relate *in time* to each other's actions	Hunters may begin at the same time or adjust their speed to remain in time
Coordination	Each hunter concentrates similar actions on the same prey and tries to relate *in time and space* to each other's actions	Hunters may begin from different directions or adjust their position and speed to remain coordinated
Collaboration	Hunters perform different *complementary* actions, all directed toward the same prey	Examples are driving, blocking escape way, and encirclement

and would, accordingly, be classified as cooperative, whereas the same collaborative group hunt in another population could fail to increase their hunting success and would then not be considered cooperative (see also Busse, 1978). To avoid such a paradox, we proposed to use cooperation in the hunting context according to the first definition and refer to "cooperation sensu Hamilton" when it fulfils the additional criteria of increasing the outcome, compared with similar actions performed by a single individual.

In the literature on hunting, the meaning of the word cooperation can change according to author (see, for example, Busse, 1978; Goodall, 1986; Kruuk, 1972; Schaller, 1972). In our opinion, this change of meaning occurs partly because groups of individuals may perform a large variety of actions representing different levels of cooperation, with increasing organization. In order to reflect this complexity within group-hunting techniques, we adopt an operational definition of cooperation based on the level of organization in the actions of the hunters (Table 1).

We want to emphasize that individual behavior within such a cooperative group may be classified by the four categories proposed by Hamilton (1964); altruistic, spiteful, selfish, and cooperative. If feasible, we shall proceed to such an analysis of hunting at the individual level. The definitions given in Table 1 represent different levels of organization of cooperative groups. They will be called "cooperative sensu Hamilton" only if an increase of success, compared with that of lone individuals, is subsequently proved.

Food transfer between two individuals can range from a mere stealing to the most giving. In order to keep track of this variability, we adopt an operational definition of food sharing, using six levels of increasing sharing intention of the food owner (Table 2).

RESULTS

Prey species

Table 3 presents the data on Taï chimpanzee hunts including all observations during the 7 years of the ongoing study. We considered only the observed hunts, including attempts and successes; our experience of collecting feces during 2 years showed that such a method is not reliable as it does not match with the visual observations. It is still worth mentioning that we could identify in 1 out of 381 feces the bones of a Latham's francolin (*Francolinus lathami*), confirming our impression that we are still unaware of some rarely hunted prey.

The main finding seen in Table 3 is that Taï chimpanzees chose monkeys, mostly colobus, for all but one hunt during this 7-year period. This specialization in *Colobus* monkeys is extreme: they are the prey in 95% of the hunts, and 81% of the hunted monkeys are red colobus. Three species of prey are new for chimpanzees, i.e., *Cercopithecus diana*, *Colobus verus*, and *Cercocebus atys*. Table 4 presents a comparative list of the major mammal prey of the three chimpanzee

TABLE 2. Operational definition of sharing: six levels of increasing sharing intention of the food owner

Category	Definition	Interpretation
S1—Theft	B forcefully takes part or all of A's food	Sharing takes place against A's will: A shows opposition
S2—Recovery	B takes part of the food that A has dropped on the ground or placed there	Sharing without intention of A and merely tolerance of B's proximity if close
S3—Passive sharing	B takes part of the food that A is holding. A makes *no movement to facilitate* nor to avoid B's action	A passively tolerates B's action but may accept that B holds the food pooled in common for some time
S4—Active-passive sharing	B takes part of the food that A is holding. A makes *a movement to facilitate* B's action	A actively tolerates B's action and expresses it by withdrawing its hand or by bringing the food toward B
S5—Active sharing	A *gives* part of its food to B either cutting off a piece or by holding a piece toward B	A makes an explicit action showing its intention to B
S6—Gift	A *gives* a part at least three times larger than its own remaining piece to B	A's generosity seems to show a greater sharing intention than the category above

TABLE 3. All observations of hunting attempts and successes observed during a 7-year period from September, 1979 to May, 1986 in Taï, classified according to prey species hunted and captured

	Hunts		Captures	
	No.	%	No.	%
Colobus badius	110	81	63	77
Colobus polykomos	16	12	11	14
Cercopithecus diana	3	2	3	4
Colobus verus	2	1.7	2	2.5
Cercocebus atys	2	1.7	1	1.2
Perodicticus potto	1	0.7	1	1.2
Rat (sp.?)	1	0.7	0	
Total	135		81	

TABLE 4. Major mammal prey species observed to be eaten by chimpanzees in Taï, Gombe, and Mahale[1]

	Tai		Gombe		Mahale	
	No.	%	No.	%	No.	%
Colobus badius	63	77	203	64	9	13
Colobus polykomos	11	14	—	—	—	—
Papio anubis	—	—	8	3	†	—
Cercopithecus ascanius	—	—	5	2	11	16
Pan troglodytes	†	—	5	2	2	3
Other primates	7	9	—	—	4	6
Bushpig	†	—	51	16	6	8
Bushbuck	—	—	39	12	13	19
Blue duiker	†	—	—	—	19	27
Others	—	—	4	1	5	7

[1] Taï and Mahale data include all observed hunts, whereas Gombe data include only the 10-year period from 1972 to 1981 (Goodall, 1986). Prey species hunted by chimpanzees in one site that are present but not hunted in another site are marked for that site with a single dagger (†).

populations and the frequency with which they were observed to be caught and/or eaten. Taï chimpanzees are the most specialized hunters among chimpanzees; only six mammalian species have yet been seen to be eaten out of 27 available prey species (we counted as available species all mammals present in an area except the Carnivora, the Tubulidentata and the Proboscidea), whereas Gombe chimpanzees eat 9 species out of 16 available, and Mahale chimpanzees eat 13 out of 23 available (no data are available on the presence of small mammals).

As can be seen from Table 4, the proportion of monkeys in mammal prey decreases from Taï to Mahale, as does the proportion of red colobus which remains, nevertheless, the major prey in Gombe. Infant chimpanzees have been observed to be killed and eaten by adult chimpanzees in Gombe and Mahale when males of a community encountered a lone stranger female with an infant. In the consecutive fights, the infants were often snatched away from their mothers, killed, and in part eaten (Goodall, 1986; Goodall and al., 1979; Nishida and Hiraiwa-Hasegawa, 1985; Nishida and al., 1983). Cases of cannibalism within a community are rarer; an adult female killed and ate new-born infants of her own community (Goodall, 1986), and twice males ate new-born infants of females belonging to their community (Norikoshi, 1982; Takahata, 1985). In Taï, we never saw anything of that nature, and, since March, 1984, the period in which we could more constantly follow the males, we never saw them encounter any lone stranger chimpanzee. All encounters with strangers were made between groups, the males of both communities facing each other and the females with infants remaining at the rear. The possible lack of cannibalism in Taï might be explained by this seemingly lower rate of encounters with lone female strangers.

Availability of potential prey

The Taï chimpanzees' specialization in monkeys may reflect a simple difference in the availability of potential ungulate prey.

The major difference in Table 4 comes from the absence of hunting of bushpigs and duikers in the Taï forest, which are, however, fairly common there. We encounter small duikers (Blue, Bay, Zebra, and Ogilby) 2 to 3 times per day in the forest. Many close encounters between chimpanzees and duikers were witnessed (12 observations). The chimpanzees either ignored them or seemed scared when duikers rushed through one of their groups, and the duikers avoided them without giving any alarm calls. Descriptions from Gombe (Goodall, 1986 and personal communication) and from Mahale (Takahata and al., 1984) show that chimpanzees concentrate on small infants of blue duikers or bushbucks. In Taï, we have not even seen a small infant duiker in 7 years, which may mean that, in the forest, these animals hide their babies so well that they are difficult for the chimpanzees to find by chance. This factor may explain in part the lack of hunting for duikers. However, on the January 10, 1987, we made a most intriguing observation concerning the duiker-chimpanzee relation and generally perception of prey by them:

> The core group was cracking Coula nuts and moving in a hilly region. While watching some males, including the most keen and experienced hunter, we heard a blue duiker (*Cephalophus monticola*) screaming some 60 m away. They looked in the direction, then ignored it. I went there; the screams came from a thicket where infant chimpanzees were playing. When they moved out, I saw a 9-year-old male juvenile (Fitz) dragging along by one foot a very young blue duiker still alive, followed by three infants and their mothers, who seemed less concerned. The four youngsters played with the duiker for 15 minutes, Fitz repeatedly trying to place it on his back or his shoulder while walking, as if it was a young chimpanzee. For each rough movement, the duiker screamed loudly. By then they had reached another thicket where they were joined by more females and two adult males. The screaming stopped, but a 4-year-old infant came out with the duiker, followed by two other infants. They played for 8 minutes with the duiker, meanwhile dead. An adult female joined the play session, kicking the duiker with one hand and one foot. Several adult males passed nearby without showing any interest. The dead body was abandoned intact on the ground, 33 minutes after the capture. The corpse was found 20 minutes later by an adolescent female. She smelled it, threw it 3 m aside, and left. The examination of the body revealed no wound; only some fur was taken away on its side, probably by the infant biting it playfully.

This observation tends to indicate that Taï chimpanzees have a highly *specialized "prey image"*. When they have the opportunity to capture an animal not belonging to this image, they tend to ignore it (see also the next section). Subadults were interested in the duiker but handled it as a toy rather than as an edible animal.

Close encounters between chimpanzees and bushpigs were witnessed (four observations); chimpanzees tended to ignore them, but they would flee or bark aggressively when an adult male bushpig tried to keep them at distance during food competition for Coula nuts (two cases). For bushpigs, another factor has to be taken into account. In Gombe, they live in small social groups; 93% include five or fever adult members and they seem to be mainly nocturnal (Goodall, personal communication). Taï bushpigs were always seen in groups larger than five individuals, and they seem to be very active during the daytime. The active defense of adults living in large groups could easily repel any chimpanzee; in Gombe, they defend themselves efficiently in small groups (Goodall, 1986). Interestingly, the giant forest hogs of the Taï forest live in much smaller groups then bushpigs, and twice we observed clear signs of hunting interest on the part of the chimpanzees who made detours toward the hogs after having heard them scream. Thus differences in group size and in breadth of prey image and difficulty in finding prey in the forest may partly explain the apparent disinterest of the Taï chimpanzees toward species that are commonly preyed upon in other regions. Other abundant species have been noted as prey in East Africa and seem to be neglected in Taï, i.e., squirrel and mongoose. Thus additional reasons must exist to account for the differences in prey selection; we shall discuss some of them later.

In Gombe, some authors tried to estimate the frequency of encounters between the prey and the chimpanzees. Busse (1977), using as a criterion for an encounter a distance of visible and/or auditory contact of 100 m between them, estimates that Gombe chimpanzees encounter red colobus once every 55 daylight hours. Wrangham and Bergmann-Riss (in press, cited in Goodall, 1986), using a criterion of 200 m distance between both species, estimate the encounter rate to be one every 12 hours. These estimations are surprisingly low, when one considers that red colobus are as abundant in Gombe as in Tai, with home ranges of 1 km^2 for groups of about 50 individuals (Gombe: Clutton-Brock, 1975; Taï: Galat, 1978; Galat-Luong, 1983; Galat and Galat-Luong, 1985). We estimate the encounter rate as three encounters every 4 hours, using an auditory and/or visible distance of 200–300 m (sample size: 265 hours, 45 minutes). Our different encounter rate could partly explain the difference in prey selection between the two populations.

Opportunism versus intentional hunting

Busse (1977) concludes that chimpanzee hunting in Gombe is mainly opportunistic; during a 2-year period, he observed chimpanzees encountering red colobus 85 times with hunts occurring 64 times (75%). All observers working in Gombe confirm the impression that hunting is, for the most part, opportunistic (Goodall, 1986; Teleki, 1981; Wrangham, 1975). The same behavior was observed in Mahale (Nishida et al., 1983; Takahata et al., 1984). In Taï, based only on our estimation of the encounter rate (7.5 encounters in a 10-hour day), 6.6% of encounters are followed by a hunt.

A more direct method of evaluating the opportunism of the chimpanzee hunts, however, would be to record the behavior of the hunters before a hunt begins and to determine the moment when a hunt is decided and according to what signal. In 78 hunts out of the 100 meat-eating episodes we observed during the last 2 years, we were with hunters before a hunt began (minimum one hour before). Each time we recorded all changes of direction and any behavior indicating an incipient hunt, based on the following behaviors: Taï chimpanzees tend to follow the same direction for hours; when changing it, they communicate by means of drumming and pant-hooting to any group members within auditory distance. Hence we defined "*detour for hunting*" as a clear change of direction made without any auditory signal directly following the sound produced by the possible prey. Visibility being at most 20 m in the forest, we have the impression that the detection of prey is mostly made by ear. We have defined "*search*" for prey as follows: the chimpanzees become totally silent, remain very close together, move one behind the other, and stop regularly to look up into the trees, alert to the sound of monkeys. Many silent changes of direction may occur. A chimpanzee might eat a fruit or leaf while passing by, but no general feeding of the group occurs during a search. These searches last on the average 16 minutes, 27 seconds (Sample = 39, range = 5–50 minutes). Unclear cases were classified as opportunistic (prey overhead, or found in the way of the initial direction).

In Taï, 31% (24 out of 78) of the hunts must be classified as opportunistic, whereas in half of the hunts we could observe clear signs of hunting intention before any prey was seen or heard (searches only). As the observation of January 10, 1987 stressed, Taï chimpanzees have a specialized prey image and therefore begin a hunt by selecting a prey. Since monkeys can be detected by the rustle of the foliage in which they jump, it has happened that searching hunters have arrived under such a group before seeing them. In 13% of the searches, they then looked for another prey. This always happened with *C. diana*, which are very agile and much quicker than colobus; they are hunted only when very low in the canopy. Hence this image of the prey is also influenced by the context: duikers would be rejected in any case, whereas diana monkeys would be rejected except if they forage unalerted in the lower canopy.

We can conclude that Taï chimpanzees hunt more often by deliberately seeking out a prey than do Gombe chimpanzees, but this behavior does not exclude an opportunistic component when the Taï chimpanzees have found a specific potential prey.

Prey size

There is a difficulty in determining the prey size because of low visibility, which makes it impossible for us to identify the prey before the capture (and often the division) is made. This is in sharp contrast with Gombe, where the prey is normally identified before its capture (Goodall, personal communication). Therefore we shall limit ourselves to comparing the capture frequency of adult versus infant/juvenile prey and not discuss the sex. Table 5 presents data from Taï, Gombe, and Mahale on size of prey.

Taï chimpanzees tend to hunt proportionally more adult prey than chimpanzees in Gombe and Mahale, but the prey species may affect the prey size, as can be seen from the Gombe and Mahale data when comparing primate with ungulate prey. If we compare *only* red colobus data, Taï chimpanzees hunt

TABLE 5. Age of prey captured by chimpanzees from Taï, Gombe, and Mahale, classified as adults (A) and infant/juvenile (I+J)[1]

	Tai		Gombe		Mahale	
Prey	A	I+J	A	I+J	A	I+J
Colobus badius	27	31	29	101	2	4
Other primates	6	2	—	50	2	6
Ungulates	—	—	0	90	5	23
All prey	33	33	29	241	9	33

[1] For Gombe no data is published for ungulates, but Goodall (1986) says no adult bushpigs nor bushbucks were killed.

TABLE 6. Duration of all Taï hunts (in minutes) in which we could see the beginning and the capture observed during the 2-year period March, 1984 to May, 1986

	< 10	10–20	20–30	> 30	Total
Number	27	30	11	14	82
%	33	37	13	17	

[1] Mean time of all hunts: 18.19 minutes; range: 1–120 minutes.

more adult monkeys than do those from Gombe ($X^2 = 10.14$, : $P< 0.001$). Qualitative observations also confirm that this difference is a major one. Gombe hunters aim their actions toward infants and, frequently snatch them away from their mothers' bellies, leaving the mothers unharmed (Goodall, 1986). This behavior was never observed in Taï, where small infants seemed to be caught incidentally, the objective being the mother. In addition, the capture of only a large infant seemed to be a disappointment, and the hunt usually continued afterward (13 observations out of 19 single infant captures).

Hunting frequency

During the 22 months we were in the field from March, 1984 to May, 1986, we observed 100 hunts (attempts or successes). From these data,we calculated two hunting frequencies:

1. One hundred hunts observed in 22 months = *4.5 hunts per month.* We should correct estimation 1 by the number of days we effectively followed (minimum auditory contact) the core male group for a minimum of 1 hour per day. The other days we either saw no chimpanzees at all or only a solitary individual for a short time. Therefore estimation 2 is still an underestimation unless one excludes unobserved hunts.

2. One hundred hunts observed in 299 group days = *10 hunts per month.*

In Taï, according to estimation 2, chimpanzees hunt about 120 times per year, i.e., almost once every 3 days. In Mahale, the highest rate of hunting was 54 episodes for the M group during a 33-month period (Takahata et al., 1984), giving a hunting frequency of 1.63 hunts per month. This figure represents a third of estimation 1 for Taï, and, despite differences in recording methods (i.e., in Mahale six observers made the sample—no indication of number of days spent in the field could be found), it tends to indicate a smaller hunting frequency in Mahale than in Taï.

In Gombe, during the last 10 years (1972–1981), 315 hunts were observed by the Tanzanian field assistants, who are permanently in the field. This figures gives a hunting frequency of 2.62 hunts per month and means that chimpanzees in Gombe hunt more than in Mahale but less than in Taï (estimation 1). New estimations in Gombe, including solitary hunts, give a rate of 150 red colobus killed in 5 years (Wrangham and Bergmann, in press, cited in Goodall, 1986), which gives, when corrected by taking into account hunting success and the proportion of other prey hunted (Goodall, 1986), an estimation of 103 hunts per year. This figure is slightly smaller than our estimation 2 ($P > 0.05$), which does not include solitary hunts (see Methods). We may conclude that forest chimpanzees hunt at least as frequently as chimpanzees living in a more open environment.

Hunting duration

In 82 cases out of the 100 hunts or meat-eating episodes we saw during the last 2 years, we were within the group of hunters just before the onset of hunting and could thus measures its duration, ending with the capture of the prey. Table 6 presents these results.

TABLE 7. Hunting success observed in Taï from March, 1984 to April, 1986

	March 1984–1985		April 1985–1986		Total	
	No.	Success rate (%)	No.	Success rate (%)	No.	Success rate (%)
Colobus badius	44	38	39	72	83	54
Colobus polykomos	5	20	7	86	12	58
Cercopithecus diana	2	100	1	100	3	100
Colobus verus	0	—	2	100	2	100
Total	51	39	49	75	100	57

Published data on duration of colobus hunts are available from Gombe (Busse, 1977), where chimpanzees tend to be successful or give up hunting within the first 7 minutes in 53% of observations (out of 64 hunts, 34 lasted less than 7-minutes). When compared with the Taï colobus hunts using the same 7 minutes criterion (out of 82 hunts, 23 lasted less than 7 minutes), hunts in Taï lasted significantly longer than in Gombe (X^2 = 8.47, $P < 0.01$).

Hunting success

An attempt to evaluate hunting success should take into account all hunts that failed. From Gombe we know that chimpanzees may remain silent before and during a hunt, the screaming following only the capture, so that observers may easily miss a hunt when following a chimpanzee not involved in it. Only an increase in the number of observers following different individuals increases the probability of recording all attempts. This was done in Gombe and to some extend in Mahale, whereas in Taï, in order not to slow down the difficult process of habituation we did not use this method. Taï males hunt almost permanently in groups (see Table 9), and we were present before a hunt began 82 times out of 100 predatory episodes; thus we probably had a fair chance to witness almost all hunts while following the male core group. Table 7 presents our data on hunts, both attempts and successes, classified according to the prey species.

No important differences in hunting success for the two major prey, the red and black and white colobus, are apparent. The overall success rate in Taï is slightly larger than in Gombe but not significantly (Gombe success rate for 10 years of red colobus hunts = 41.4%; X^2 = 0.85, $P > 0.05$). No comparable data exist from Mahale.

Similar results between Taï and Gombe were obtained for multiple kill rates; during a hunt chimpanzees regularly succeed in capturing several prey, either at the same time or one after the other. Goodall (1986) presents a sample of 9 years for 116 colobus hunts in which chimpanzees made 44 multiple kills (mean number of kills = 2.29 colobus). The proportion of multiple kills is the same in Taï, i.e., 14 out of 55 successful hunts (mean number of kills = 2.14, X^2 = 2.06, $P > 0.05$).

We divided the Taï data into two periods, the second one beginning in June 19, 1985, when suddenly the success rate increased to 100% during 6 consecutive months. The change between the two periods could not be attributed to any change in the observation, procedure, which remained constant for the 2-year period; the same observer was also used. The only change we could find was that of the behavior of one of the hunters: Snoopy, who was always ready to participate in a hunt, became in this interval an adult male and had visibly gained in strength and confidence when facing an adult colobus. He developed an exceptional persistency, continuing the hunt on and on until capture was achieved. The other hunters were also aware of his behavioral change and waited for Snoopy to reactivate the hunt. A subsequent decline in success was because of the sudden noninvolvement of this young male during the month of February, 1986. If we excluded this month from the computations of the second period, the rate of success would be 89% for 37 hunts.

Prey reactions

We considered four different types of prey reaction when faced with the hunters: 1) freezing reaction; 2) flight reaction; 3) attack of a single prey against the hunter(s); and 4) mobbing reaction of many prey together against the hunters.

In colobus monkeys, the first two reactions were always combined, depending on the hunter's movements. As long as they were unnoticed by the hunters, they would freeze.

TABLE 8. Comparison of red colobus reactions when hunted by chimpanzees in Gombe and Taï[1]

	Number of hunts	Flight + freeze	Attack by a single colobus	Mobbing	Success of attack + mobbing
Taï	68	61	1	10	2
Gombe	64	—	15	3	13

[1] See text for further explanations. Success is defined as a resultant stop of the hunt. Data on Gombe come from Busse (1977). A group of prey may react in several ways, so the sum of reactions exceeds the number of hunts observed.

If the hunters approached, they would flee farther away and freeze again. Thus we shall analyze these two reactions together. Table 8 presents observable red colobus reactions when being hunted and compares responses in Gombe and Taï.

We never observed a single adult colobus chasing away an adult chimpanzee. (The only observation of this nature in Table 8 was against a subadult female.) Even mobbing, which includes at least four adult colobus at one time, was never successful against an experienced hunter, who may even capture one of the mobbers (two observations). Four mobbings were successful inasmuch as they were directed toward young adults momentarily alone that retreated to the ground; the hunt continue however. Two were successful in that the hunt stopped as a result of the mobbing.

In Gombe and in Mahale, adult colobus monkeys can successfully chase away single adult male chimpanzees and even groups of them (see Goodall, 1986). Busse (1977) gives some details on the prey's response when hunted by chimpanzees.

Red colobus react aggressively in both Taï and Gombe with the same frequency ($X^2 = 2.09$, $P > 0.05$). In Taï, the mobbing reaction is more frequent than in Gombe ($X^2 = 12.36$, $P < 0.001$) but the success of the colobus reaction is lower in Taï than in Gombe ($X^2 = 5.96$, $P < 0.05$). Goodall (1986), analyzing a different period, reported an even higher rate of success than does Busse: chimpanzees ran away in 16 out of 19 colobus attacks. This comparison tends to indicate that Taï chimpanzees are less impressed by the colobus attacks than Gombe chimpanzees. Taï colobus rely mainly on mobbing when they respond aggressively to being hunted, although their success rate is low. Descriptions provided by Goodall (1986) of Gombe chimpanzees fleeing from colobus sound incredible to someone acquainted with the chimpanzee-colobus interactions in Taï.

Size of the hunting groups

According to the definitions we proposed at the beginning of this paper, we always differentiate between bystanders, i.e., group members watching the hunt passively, and hunters. Of the 100 predatory episodes observed during the 2-year period, we recorded the number of hunters acting at the same time during 80 of these hunts, using only identified individuals. The number of hunters varies during each hunt, and there is a tendency for some hunters to wait and look for the reaction of the prey when they are driven by some of the chimpanzees before taking part in the hunt. For Table 9, we considered only the maximum number of

TABLE 9. Size of hunting groups and other parameters among the Taï chimpanzees for the 2-year period (only for collaboration, the highest organizational level of group hunt, was the sample size large enough for each class)

Number of hunters	Number of hunts		Rate of success		Duration of hunts >7 minutes		Collaboration	
	No.	%	No.	%	No.	%	No.	%
1	6	7.5	1	16	1	16	0	0
2	11	13.7	1	9	7	63	3	27
3	14	17.5	6	42	9	64	6	42
4	15	18.7	10	66	11	73	10	71[1]
5	19	23.7	9	47	15	78	16	84
6	8	10.0	4	50	8	100	7	100[1]
+6	7	8.7	6	85	7	100	7	100

[1] We could not determine if collaboration was used by the hunters for one of the hunts.

TABLE 10. Comparison of group hunting tendencies in Taï, Gombe, and Mahale chimpanzees

	Solitary hunts		Group hunts		
	No.	%	No.	%	Total
Tai	6	7	74	93	80
Gombe	55	64	31	36	86
Mahale	26	76	8	24	34

hunters in each of these hunts, recording only adult animals.

Table 9 shows that Taï chimpanzees *hunt as a rule in groups*: 92/5% of all hunts include at least two hunters acting together against the same prey. This result, combined with the fact that the majority of the hunts seem to be decided before any prey is visible to the hunters, gives us some clues as to how Taï chimpanzees hunt. The critical factor in initiating a hunt seems to be the presence of other group members ready to hunt. The choice of a prey is restricted to the animals that can regularly be found within a time span of 10–20 minutes (for searching time see opportunism verses intentional hunting above) from the moment the chimpanzees begin to search for prey. In the Taï forest, diurnal social monkeys have a density fluctuating from 15 to 66 individuals per km^2 (Galat and Galat-Luong, 1985) and are the most commonly encountered animals. The red and the black and white colobus, with densities of 66 and 23 ind/km^2 respectively, and weights at least double that of the *Cercopithecus* species, seem to be the optimal prey for hunters that can easily climb trees. Hence the specialization in colobus monkeys of the Taï chimpanzees can be understood as the result of a hunting strategy at an early time of decision-making for hunting.

Published data on East African chimpanzees allow us to compare solitary and group hunts (Table 10), including all observed hunts for Taï and Mahale. For Gombe, only data on baboon (Teleki, 1973) and red colobus (Busse, 1978) hunts are available. They account for 67% of all hunts (from 1972 to 1981 in Goodall, 1986); the rest often involve bushbuck. Typically, hunts of bushbuck infants in Gombe seem to be seizures of frozen prey by solitary individuals, so Teleki's and Busse's data may somehow overestimate the group hunting tendency.

The frequency of group hunts is similar in Gombe and Mahale ($X^2 = 1.21, P > 0.05$). Gombe as well as Mahale chimpanzees hunt in groups significantly less than do Taï chimpanzees (Taï versus Gombe: $X^2 = 54.42, P < 0.001$; Taï versus Mahale: $X^2 = 52.84, P < 0.001$). The difference is more extreme for hunts involving *only* red colobus (Taï group hunting tendency = 94%, Gombe = 31.2%). Furthermore, when hunting in groups, each Gombe chimpanzee often tends to hunt in a different direction toward different prey (Goodall, personal communication), which would be classified as solitary hunts in Taï.

Some questions arise concerning the reasons why chimpanzees show such a strong tendency to hunt in groups in Taï. Is there a real need to hunt in groups? Is the hunting success related to the hunting group size? Table 9 presents Taï data on these aspects as well as on the duration of hunts and frequency of collaboration.

Hunting success varies according to the number of hunters remaining very low for one (16%) or two (9%) hunters and increasing sharply for larger hunting groups (one and two hunters versus three or more hunters: $X^2 = 8.64, P < 0.01$). Taï chimpanzees seem to be aware of this difference, and the first lone hunter behaves so as to attract more hunters rather than trying to catch the prey on his own. He will follow the prey slowly, making them produce alarm calls. Sometimes his behavior may even look *deceitful*, in that he gives "hunting barks," although he is never in the situation that normally elicits such a call, i.e., rapidly pursuing or about to capture a prey. If no chimpanzees join the hunt, he will normally stop (see below for hunt durations in relation to group size). The only capture by a lone hunter we observed was made on an adult colobus that fell into the lower canopy as a result of struggles with other colobus. They seemed not to be aware of the chimpanzee's presence underneath the tree. Groups of two hunters may persevere for longer periods of time, but, independently of their skills, the presence of a third hunter is necessary to make a capture more certain. Indeed, when a third joins the hunt, the speed of all movements increases sharply.

TABLE 11. Group hunts for chimpanzees from Taï, Gombe, and Mahale classified according to cooperation level[1]

	No. of group hunts	Similarity		Synchrony		Coordination		Collaboration	
		No.	%	No.	%	No.	%	No.	%
Taï	72	5	7	9	12	9	12	49	68
Gombe	31	←		25	81		→	6	19
Mahale	8	←		8	100		→	0	0

[1] For each hunt, we recorded only the highest level of organization reached by the hunters. Taï and Mahale data include all observed hunts. Gombe data include 2 years of red colobus hunts (Busse, 1978) and 1 year of baboon hunts (Teleki, 1973).

TABLE 12. Age/sex classes and roles of the Taï chimpanzees

Age and sex	Bystander	Hunter	Captor
Adult males	132	221	27
Adolescent males	24	60	4
Adult females	87	33	7
Adolescent females	31	17	–
Total	274	331	38

A correlation between number of hunters with hunting success is found (Spearman rank correlation coefficient: $rs = 0.86$, $P < 0.05$), as well as with hunting duration (Spearman rank correlation coefficient: $rs = 0.96$, $P < 0.01$). Hunters persevere longer as their number increases, and this may explain their greater success. Hunting in groups implies waiting for others before hunting and accepting that a larger proportion of the capture will be shared (see Meat sharing, below). These costs seem to be compensated for by an important increase in hunting success with three or more hunters. The decrease in success observed in groups of four or five hunters may reflect difficulties encountered by the hunters in organizing themselves when hunting, but such difficulties are seemingly resolved when six or more hunters participate (Table 9).

The available data from Gombe show no increase in hunting success according to the number of hunters. Apparently solitary hunts in Gombe are more successful than in Taï. (Busse, 1978; Goodall, 1986; Teleki, 1973). The pressure existing in Taï for group hunting may not exist in Gombe.

The hunting groups in Taï must be considered as cooperative sensu Hamilton (1964) since hunting success increases with the number of hunters; such evidence is missing for hunting groups in Gombe and Mahale.

The proportion of cooperation by collaborations is directly related to the size of the hunting groups (Spearman rank correlation coefficient: $rs = 0.99$, $P < 0.01$), as well as to hunting success ($rs = 0.83$. $P < 0.05$) (Table 9). However, a comparison of the three factors using a Kendall partial rank correlation coefficient (Siegel, 1956) shows that the level of cooperation is related to the number of hunters, whereas hunting success depends on both the number of hunters and the cooperative level used ($rxy.z = 0.96$). The data are not large enough to estimate the relative contribution to the hunting success of each cooperative level.

Cooperation

In Table 11, we present all the hunts in which we could determine the group hunting techniques used, evaluated by recording each individual's actions (see definitions in Table 1). As can be seen, Taï chimpanzees *hunt as a rule by collaboration* (68%).

Table 11 also compares the data on collaborative hunting from Gombe and Mahale with those of Taï. Taï chimpanzees collaborate significantly more often than do Gombe and Mahale chimpanzees ($X^2 = 18.74$ and $X^2 = 11.32$ respectively, both $P < 0.001$). If the same comparison is made between Taï and Gombe *only* for red colobus hunts, the difference is even larger (Taï collaborative level = 69.8%, Gombe = 10%). The differences in collaborative hunts between Gombe, Mahale, and Taï are clear-cut.

Age/sex of the hunter

Table 12 presents the age/sex classes of all observed hunters. Juveniles and even infants show some interest in hunting but rarely go further than some intentional movements toward the prey. One exception is a young juvenile male who permanently associates with the alpha male and who has developed an unusual interest in hunting. He even succeeded in capturing an infant red colobus when he was only 6 years old.

To be confident of the identity of the captor, we have to observe the capture, as a prey can be stolen within the first few minutes. Therefore captors were less often identified than other roles. Adolescents of both sexes actively take an important part in hunts, and we observed that they willingly take up the driving role. Some differences appear when we compare the adults classes:

1. Significantly fewer females are present at hunts than males (community composition; 9 adult males and 26 adult females, comparison between community composition versus bystanders + hunters: $X^2 = 35.72$, $P < 0.001$). Females tend to appear at the hunting site once the capture has been made but do not rush to join an audible hunt, a behavior in strong opposition to that of the males.
2. Females, when present during a hunt, are less active than males (comparison of bystanders versus hunters: $X^2 = 42.99$, $P < 0.001$). When present, females follow the hunt from the ground, remaining close to the action so as to reach the capture site rapidly. This is necessary if they are to claim a share of the meat before division occurs, when ownership is not yet clearly marked and begging is not yet necessary. However, some females, with or without an infant to carry, do actively hunt (13% of the adult hunters are females) (Table 12).
3. When hunting, females have a capture rate similar to males ($X^2 = 0.88$, $P > 0.05$). Females are apparently physically capable of capturing a prey such as an adult colobus.

The sexes differ in their general sociability inasmuch as females tend to forage away from the main core group more frequently than males. Therefore the number of females hunting, when no males are present, is underestimated, as we generally followed the main male core group. Recent observations of groups of three females (three observations) indeed revealed that females may hunt successfully even for heavy prey, such as adult black and white colobus.

For Gombe, Goodall (1986, p. 307) presents some data on the sexes involved in the hunts. When present during a hunt, females tend to hunt with the same frequency in Gombe as in Taï ($X^2 = 0.54$, $P > 0.05$). Over a 7-year period, females in Gombe made 23% of the kills, whereas in Taï during a 2-year period the proportion was 18%. Thus the hunting participation of the females might be similar at both sites. The female capture rate from Mahale seems to be comparable to that of Taï as well; Takahata et al. (1984) attribute 29% of the kills to females (Taï versus Mahale, $X^2 = 0.29$, $P > 0.05$).

Killing techniques

Because of poor visibility in the dense forest, we can rarely observe the killing of the prey precisely. Some tendencies were, nevertheless, apparent:

1. Infant/juvenile colobus are always immediately bitten in the head and then transported in their captor's mouth. Death immediately follows the first bite.
2. Adult colobus are rarely killed by their captor immediately. The chimpanzees begin to eat them while they are still alive, usually by biting open the belly and pulling out the viscera. Death generally follows such a disembowelling, occurring ~ 2–4 minutes after the capture (11 observations). On three occasions an adult colobus was seen to be dead while still intact, and large quarrels occurred between males over ownership, indicating that the prey can be killed properly when strong competition over ownership occurs. On one occasion the alpha male chimpanzee killed an adult colobus by neck bite just after the capture.

Descriptions from Gombe are fairly similar for infant prey, but important differences are observed for larger prey. Adult colobus may be killed by methods *never* observed in Taï, such as flailing the body so that the head is smashed against the branches, rocks, or the ground. Of 19 adult colobus captured in Gombe (Goodall, 1986 p. 291), only 6 were quickly dispatched, partially by disembowelling. All the others took more than 10 minutes to die (more than 40-minute struggles are reported), and disembowelling, if at all, happened only late in the consumption process. These difficulties in killing an adult prey were attributed by Teleki (1981) to the poor biting capacities of Gombe chimpanzees, but our observations differ. In Taï, division of the prey is the rule for an adult prey, and death always occurs within the first 4 minutes.

Division of the prey

The capture is generally followed by an outburst of screams that signals the success of the hunt and attracts chimpanzees within

TABLE 13. Outcome of contests for possession of the prey following capture, according to size of prey

Size of prey	Respect	Theft	Transfer	Division	Total
Infant/juvenile	22	3	1	2	28
Adult	3	1	4	25	33
Total	25	4	5	27	61

auditory distance. In Taï, some hunts are totally silent, and sometimes we knew that they had happened only from the sound of cracking bones. When an outburst of screams occurs, a period of social excitement follows, during which the captor of the prey is challenged by many adult males who are all interested in gaining access to a large portion of the meat. The outcome of these contests are not easy to follow, as many individuals join in what may look like a "mad rush" to get a piece of meat. Much aggression is also seen between participating individuals. This period of high excitement ends when ownership of meat portions is generally accepted and the meat consumption can begin. In Table 13, we present the general outcome of these contests for ownership from the point of view of the captor. We use the following four categories: *respect* indicates that the owner was able to keep the whole prey; *theft* indicates that the owner lost the whole prey to another chimpanzee; *transfer* occurred if the owner released the whole prey on his own initiative, normally during a social display and usually to a third party; and *division* occurred when the prey was cut in two pieces, generally between the ribcage and the rump.

Division, which normally occurs between two individuals, does not exclude respect. Out of the 19 divisions in which we knew captor, he initiated 10 divisions and kept half of the prey; in five situations he was allowed by the more dominant animals to cut himself a piece of meat before they proceeded to the division among themselves; and in the last four cases, the captor was left empty-handed, although he later received some meat through sharing. In these four cases, division must also be considered as theft and added to that category in Table 13. Theft is slightly higher for large than for small prey (15% and 10%, respectively). Captors of all prey were respected in 86% of the captures. This partly reflects the fact that captors dominant individuals and consequently respected by the others. The Gombe stealing rate of whole prey is similar to that found in Taï (Gombe; 16 stealings out of 199 kills: $X^2 = 1.14$, $P > 0.05$; Goodall, 1986).

In Taï, small prey are usually kept wholly by their captor, while large prey are divided among two or three chimpanzees (Table 13) ($X^2 = 26.19$, $P < 0.001$).

The captor is one of the participants in the division if he is a high-ranking male. The second individual allowed by the group to take part in the division must also be high-ranking. Analysis of who was allowed to take part in such a division revealed a clear *change in the dominance rank order* of some individuals. Dominance in wild chimpanzees is difficult to determine in a straightforward way, as an individual's status depends in part on the presence in his group of some potential allies. As the composition of such a group fluctuates all day long, we may say that the individual's status may to some extent vary accordingly. This applies to dominance order in a social context as well as in the context of prey division. In the last context, our sample size is too small to allow a precise analysis of the dominance changes for all individuals. However, some dominance order could be found in both contexts and was clear for the four highest ranks. Two spectacular changes were observed, as shown in Table 14.

Schubert, the beta male in social context, dropped to the fourth rank in the division context, and he needed a complete 11 months to generalize his social rank to the division context. Ondine, the alpha female, rose to the third rank among the males in the division context, supplanting all males except Brutus, the alpha male, and Falstaff, the oldest one. She was able to face the combined aggressions of up to five males to get her place in the center of the division process.

No such long-lasting changes in the hierarchy according to the context were described in Gombe. Females were regularly dominated by males, although they could sometimes manage to conserve their captures against adult males. Out of 19 captures made by females in mixed groups, 12 were kept by female captors (Goodall, 1986). In Taï, we observed seven such situations. In six of them the female succeeded in keeping their prey, and an adult prey (three cases)

TABLE 14. Dominance order in 1984–1985 for all adult males and the dominant female of the Taï community in two different contexts, social and prey division

Chimpanzee	Sex	Social rank order	Division rank order
Brutus	M	1	1
Schubert	M	2	4
Falstaff	M	3	2
Macho	M	4	5
Ulysse	M	5[1]	6[1]
Rousseau	M	6[1]	7[1]
Kendo	M	7[1]	8[1]
Darwin	M	8[1]	9[1]
Snoopy	M	9[1]	10[1]
Ondine	F	10[2]	3

[1] The rank order between these young males was far from being so clear-cut, but we present this order based on the subsequent variation in their order observed in 1986.

[2] Ondine was probably the highest ranking female and as such could dominate young adult males in some social contests. In relaxed situations, she showed submissive behavior (pant-grunts) to some of them, i.e., Macho and Ulysse.

was pooled between two or three of them; together they resisted the males' attacks, the ownership shifting between the three of them.

Meat consumption and piece preferences

Table 15 presents the sequential order in which prey are eaten by Taï chimpanzees. Infant colobus are eaten head first and then downward through the vertical axis, the prey being held in the hands like an ice cream cone. Adults are disembowelled first, and then the limbs are eaten, with the head last. Taï owners of large portions of meat (the performers of division) normally keep either the ribcage or the rump until last, nibbling at them until they are clean.

Teleki (1973) found that in Gombe the prey were in general consumed in the following order; first the viscera, the chest, the ribcage, and the limbs, and finally the head. This sounds similar to Taï adult prey consumption, except for the late limb consumption. Some techniques of meat eating described in Gombe have *never* been observed thus far in Taï: first, twisting a limb round and round until it detached; second, biting into the prey's face in order to suck up and drink the blood; and third, consumption of the fecal content of the large intestine. Goodall (1986) and Teleki (1973) note that for Gombe chimpanzees the brain is a favorite item rarely shared, and if division occurs the owner retains the head's end for himself. In Taï, as in Gombe, if the skull is easy to open (infant prey), the brain is never shared. For adult prey, however, the skull was shared in 84% of the 25 cases in which we observed the consumption of the brain. Often the skull was shared many times, the brain being eaten only by the third or fourth owner. In the only episode in which the chimpanzees did not eat all the prey, they left uneaten both hindlegs, part of the ribcage, some bones, and the complete skull. So it seems that in Gombe the brain is much more prized than in Taï.

TABLE 15. Sequential order of consumption of the different parts of a colobus prey according to its size

Size	Order eaten	Body part
Infants (N = 23)	1st	87% head, 8% limbs, 4% throat
	2nd	82% ribcage, 8% viscera, 4% head or rump
	3rd	82% viscera, 13% rump, 4% limbs
	4th	74% limbs, 13% rump or ribcage
	5th	61% rump, 39% limb
Adults (N = 25)	1st	100% viscera
	2nd	100% limbs
	3rd	48% ribcage or rump, 4% head
	4th	48% ribcage or rump, 4% head
	5th	92% head, 4% ribcage or rump

Taï chimpanzees always opened the skull of adult colobus by breaking the bones at the back around the foramen magnum (ten observations). In Gombe, five out of seven skulls were broken through the top frontal part of the cranium, and the brain was eaten from there (Teleki, 1973); the others were opened as in Taï. Both in Taï and in Gombe, meat is commonly eaten by "wadging" with fresh green leaves (Goodall, 1986), but Gombe chimpanzees rarely swallow their wadges (Teleki, 1973), whereas Taï chimpanzees were always seen to do so.

On December 28, 1985, a small group of five chimpanzees, including four adult males, captured and ate an adult black and white colobus female as well as her infant (minimal estimated weight of both individuals 10 kg). This was the only case in which chimpanzees were seen not to eat all the prey, probably because of the small number of participants. The remains weighed 3 kg, so five chimpanzees were satiated with 7 kg of meat and bone, i.e., 1.4 kg per individual. Chimpanzees rarely have the opportunity to eat such an amount of meat. In Gombe, out of 39 captures, ten captors disappeared silently with their prey, thus avoiding having to share meat and the risk of the prey being stolen (Busse, 1978). In Taï, we observed this behavior only once out of 61 captures. Taï chimpanzees less often avoided conspecifics after the capture ($X^2 = 11.65, P < 0.001$). They seemed ready to share and did not avoid the risk of losing the prey to another individual (stealing rates are the same in both populations).

Taï chimpanzees feed for an average of 103 minutes on a prey (N = 39 eating episodes). Infants are eaten more quickly than adult prey (infant/juvenile: N = 16, average = 48 minutes, range = 17–140 minutes; adult: N = 23, average = 141 minutes, range = 80–220 minutes). In Gombe, Teleki (1973) observed 12 eating episodes with an average duration of 215 minutes (total time = 43 hours, range = 90–540 minutes). He states that the size of the prey affects the duration of the meat consumption less than the number of individuals involved in meat eating. Taï chimpanzees eat their prey more quickly than Gombe chimpanzees ($X^2 = 39.44, P < 0.001$). The speed of consumption at Taï is related to both the size of the prey and the number of chimpanzees attending the meat eating. More chimpanzees seem to feed on a prey in Taï than in Gombe; Gombe: eight chimpanzees eating, N = 12 kills (Teleki, 1973); Taï: ten chimpanzees eating, N = 52 kills). The meat-sharing frequency (see below) may partly explain this difference in meat-eating duration.

Meat sharing

Despite the capacity of chimpanzees to eat big portions of meat (up to 1.4 kg), they share meat even from small prey, which could easily be eaten by one individual. Table 16 presents the Taï data on all episodes of meat sharing. The frequency of meat sharing is 0.72 episodes per minutes in Taï (N = 3,542 minutes of observations), and 0.13 per minutes in Gombe (N = 2,580 minutes of observations; Teleki, 1973). In Taï, meat is shared 5.5 times more often than in Gombe, and thus a larger amount of meat can be eaten by a larger number of animals in the same amount of time, which may explain why prey in Taï are consumed more rapidly than in Gombe.

Sharing is influenced by the quantity of meat available. If we compare the sharing frequency in Taï for adult versus infant/juvenile prey, the difference is important: infant/juvenile: 0.49 sharing/minute, N = 15, total time of meat eating = 526 minutes; adults: 0.84 sharing/minutes, N = 22, total time of meat eating = 2,266 minutes. Tai chimpanzees share meat from small prey 1.7 times less often than from large ones. Comparisons between Gombe and Taï, only for small prey, show that in Taï, sharing is still 3.8 times higher than in Gombe.

In Taï, about 90% of the sharing implies close contact between the owner and the beggar, both touching the meat (Table 16). More

TABLE 16. Meat sharing occurrences observed during the 2-year period including 59 hours (3,542 minutes) of meat eating observed during 48 hunts (we differentiate, in addition, between recovery in the absence (S21) and presence (S22) of food owner)

	Theft (S1)	Recovery with owner absent (S21)	Recovery with owner present (S22)	Passive sharing (S3)	Active-passive sharing (S4)	Active sharing (S5)	Gift (S6)	Total
Number	13	150	87	1,321	821	140	37	2,569
%	0.5	5.8	3.4	51.4	31.9	5.4	1.4	

TABLE 17. Meat sharing observed during the 2-year period including 48 hunts in which both the meat owner and the beneficiary of the sharing were identified

Owner of meat	Beneficiary of sharing	S1	S21	S22	S3	S4	S5	S6	Total
Adult male	Adult male	6	50	42	206	84	50	14	452
Adult male	Adult female	3	30	10	543	142	63	12	803
Adult male	Subadult	—	7	4	222	26	5	—	264
Adult female	Adult male	4	8	7	144	11	7	1	182
Adult female	Adult female	—	10	6	138	11	7	5	177
Adult female	Subadult	—	2	1	189	14	18	7	231
Total		13	107	70	1,442	288	150	39	2,109

than half is passively shared, and typically the meat is put in common by the owner. Both individuals, the owner and the beneficiary, hold and eat the same piece of meat for periods of time regularly exceeding 15 minutes. In such situations, we were able to identify the food owner only because we were present before the piece was pooled. Similarly, in active-passive sharings (31.9% of all episodes) the owner, while masticating, held the meat toward another individual. As a rule, a long piece of meat (i.e., an anterior or posterior half of a colobus) is pooled by the owner with another individual (passive sharing). In contrast, with a short but large piece of meat (i.e., the complete rump or thorax of a colobus), the owner will have a bite and then hold the piece toward a beggar, allowing the beggar to have a bite while the owner is chewing his piece (active-passive sharing). Active sharing does not necessarily happen between dyads actively engaged in passive and active-passive sharing, as both eat their fill. Active sharing occurs regularly (5.4% of all sharings).

Table 17 presents the details of the sharing episodes classified according to the age/sex classes of the owner. Male owners initiate 78.6% of the active sharing and 66.6% of the gifts. The difference between the sharing behavior of female and male owners is significant ($X^2 = 50.87$, df = 3, excluding S1, $P < 0.001$). Males tend to share meat more often in an active-passive manner (S4) or in an active manner (S5 and 6) than do females. In addition, males actively share significantly more with other males than with females ($X^2 = 94.98$, df = 3, $P < 0.001$). This higher generosity of the males toward other males is illustrated by the gifts. Gifts are normally observed when the owner has almost finished his meat and then presents the remains to another individual (Gombe descriptions are similar for such gifts; Goodall, 1986; Teleki, 1973). In Taï, occasionally at the beginning or during the meat consumption, males may cut off a small piece for themselves (commonly 3–5 vertebrae) and give the much larger piece to a nearby male, which gives an impression of generosity. For the males, sharing seems to have an important social value, and we hypothesize that such generosity is related to social status; the higher a male is in the hierarchy, the more generous he is in meat sharing.

Active sharing accounts in Gombe only for four sharings out of 335 observations (Teleki, 1973). This frequency is significantly lower than in Taï ($X^2 = 16{,}45$, $P < 0.001$). Taï chimpanzees share meat more frequently than Gombe chimpanzees, and the sharing quality seems to differ as well.

Taï adult males, as regular owners of large portions of meat, are the providers of meat in 72% of the sharing episodes observed (see Table 18). Adult females provide meat in 28%

TABLE 18. Proportion of meat shared, measured in percentage of sharing occurrences observed between the different age/sex classes in Taï (see Table 17) and Gombe (calculated from Teleki, 1973, p. 147, Fig. 11, including 623 sharing occurrences)

Owner of meat	Beneficiary of sharing	Taï (%)	Gombe (%)
Adult male	Adult male	21.43	38.47
Adult male	Adult female	38.07	40.90
Adult male	Subadult	12.51	9.53
Adult female	Adult male	8.62	0.51
Adult female	Adult female	8.39	1.03
Adult female	Subadult	10.95	9.18

of the episodes, which is, nevertheless, higher than the frequency of their involvement in hunting (only 13%). It is relevant that adult females provide meat to adult males in 61% of their sharing episodes with adults and that adult males obtain meat from adult females in 29% of the cases.

Comparisons with Gombe are not straightforward, because Teleki (1973, p. 147) pools requesting and meat sharing behaviors. A first look at the interactions between the adults shows that males are targets of requesting and meat taking in 98% of the interactions, whereas Taï males are significantly less often providers of meat through sharing (in 77% of the sharings events between adults) ($X^2 = 101.30$, df = 1, $P < 0.001$). In opposition, the interactions of adult males and females with the subadults are highly similar in both populations ($X^2 = 0.12$, df = 1, $P = > 0.05$). These comparisons are justified only if the meat requests were equally successful in both populations. However, the data to test this assumption are not available.

These comparisons between Taï and Gombe suggest qualitative differences in the sharing patterns between the two population. Sharing in Taï occurs more frequently and more actively between more individuals, and females seem more often to be important providers of meat for adult males and females. It may be relevant to note that Taï chimpanzees generally eat meat on the ground (65% of the cases), whereas Gombe chimpanzees consume meat typically in trees, apparently to avoid the beggars (Goodall, 1986; Wrangham, 1975).

Tool use during hunting and meat eating

Wild chimpanzees regularly use tools in many different contexts and often manufacture them from vegetable material, i.e., grass, leaves, or wood. In social contexts they may throw clubs and stones at other group members to impress or threaten them (see also Goodall, 1986). In Gombe, tool use was observed three times in a *hunting context* (Goodall, 1986; Plooij, 1978). Stones were thrown in order to put the animals at which they were aimed (one bushpig and two baboons) to flight; the intent was not apparently to harm the target and facilitate its subsequent capture.

In Tai, *one use of tools as a defense weapon during a hunt* was observed:

> On March 23, 1985, Darwin, a young adult male chimpanzee, was surrounded by a threatening group of adult red colobus, as soon as he went into the trees. He tried to avoid them, but they followed him. After 4 minutes he broke a fresh branch and threatened them once with it, by waving it towards them. Then he threw the branch at the two nearest colobus, hitting them. The colobus retreated.

In Taï, tools are also regularly used for *processing the prey during the consumption.* Chimpanzees use them in two different ways in order to facilitate access to the brain and bone marrow:

1. *To open skulls* (proto-tool use). The skull of an adult colobus is quite hard, and opening it with the teeth requires a lot of strength. In some cases (3 out of 15 adult skulls observed to be opened by the chimpanzees in Taï), the opening process was facilitated by banging the skull held in the hand against a hard surface, a root or a tree trunk. Taï chimpanzees are also regularly observed to use such a banging behavior for three species of large or hard fruit (*Treculia africana, Strychnos aculeata, and Landolphia hirsuta [?]*), and the same activity has been observed in East Africa for *Strychnos.* Thus we conclude that Taï chimpanzees have generalized this movement to hard skulls. The behavior has been labeled as proto-tool use by Parker and Gibson (1977).
2. *Marrow extraction.* A true tool use is performed to extract the marrow from bones. After having broken the head of the large bones (femur, tibia, and humerus) with their teeth, the chimpanzees repeatedly dip small sticks (which they have previously fashioned) into the soft marrow material of the bones; they then lick the end of the stick. Out of 28 observations, such sticks were used for emptying bones in 26. In one of the exceptions, a juvenile who could not break open the skull tasted some of the brain by poking a stick through the foramen magnum. In the second case, a stick was used to clean the vertebral canal of some tail vertebrae of a colobus.

DISCUSSION

Environmental influences on hunting behavior

Our comparisons of a forest-living population of chimpanzees (Taï) with two populations living in a more open savanna/woodland habitat (Gombe and Mahale), lead to the conclusion that the forest population seems more efficient in hunting than the savanna ones. Taï forest chimpanzees tend to hunt more frequently for larger prey, with a higher rate of success, and they hunt more often in groups with a higher level of organization than do chimpanzees living in a more open environment. Sharing of meat is more frequent and more generalized in forest-living chimpanzees. These results contrast with the widely accepted influence of the environment on these behaviors in the evolution of the hominids. Paleoanthropologists were struck by the fact that all remains of early hominids found in East Africa were east of the Rift Valley, in savanna regions, and that all known living pongids live mainly in a forest environment west of the Rift Valley (see for example, Coppens, 1983; Isaac, 1978; Johansen and Edey, 1981; Leakey, 1981; Leakey and Lewin, 1978; Pilbeam, 1980). They suggest that the transition from a forest to a savanna-like environment in early hominids has favored some important physical changes, such as bipedalism, and some major behavioral adaptations, including the appearance of hunting, tool use and tool making, food sharing, cooperation, and use of a home base. In this perspective, the data on the behavior of wild chimpanzees in these two environments could serve as a test of this hypothesis. We conclude that the superior huntings performances of the Taï chimpanzees clearly contradicts it. The challenges of forest life may have been underestimated relative to those presented in the savanna. For example, it is easier to solve the visibility problem in the savanna by standing momentarily upright or climbing a tree, whereas this problem may never be solved in the dense tropical forest. In the forest, social animals are forced to rely on acoustic rather than visual means for group cohesion, for group movements, and sometimes for recognition of individuals. Unexpectedly, some animal species live in larger groups in the forest than in the savanna, i.e., bushpigs or chimpanzees (in Taï, groups of seven chimpanzees or more account for 50% of the encounters and in Gombe for only 18%; Goodall, 1986). Spatial orientation in a dense environment with a visibility of 20 m at most, as in the Taï forest, represents a bigger challenge in finding more or less patchy food sources than in a savanna. This factor may be critical when moving in large areas. Taï chimpanzees live in home ranges larger than Gombe or Mahale chimpanzees (Tai = 27 km^2, Gombe = 9.6–24 km^2, according to the number of males; Goodall, 1986; Mahale = 10.4 km^2 for K-group and 13.4 km^2 for M-group; Nishida, 1979). In such situations, important demands act on cognition to solve orientation tasks (see, for example, stone transportation in Boesch and Boesch, 1984a). Our study also shows that forest-living chimpanzees developed nut-cracking behavior, one of the most sophisticated tool uses observed in chimpanzees (Boesch and Boesch, 1981 1984b; see also Goodall, 1986; p. 545). In conclusion, the "open environment hypothesis" for hominization should be revised in the light of these results.

Cross-population differences

Clearly not all the differences observed between these chimpanzee populations are related to environmental differences. The forest structure imposes constraints, but the solutions adopted by the chimpanzees are functions of their physical and cognitive abilities. One way to discriminate between these parameters would be to make a comparison involving a close match of as many different independent variables as possible. The hunting behavior illustrates, first, interactions between two animal species involving mainly their physical and cognitive abilities. Second, we compare the same species of predator, the chimpanzee (*P. troglodytes*) and its actions relative to one main prey species, the red colobus (*C. badius*). Third, biases due to observational conditions are limited, as the studies are basically similar, i.e., all are long-term studies of natural and spontaneous behavior of wild-living chimpanzees.

The important and numerous differences we find between the three chimpanzee populations already exclude any unique or simple explanation. We shall discuss only the most obvious differences because they are the least dependent on observational procedure differences.

One first set of differences seem to be related; prey choice, frequency of intentional search for the prey, hunting group size, hunting duration, hunting success, and level of organization of the hunt. Taï chimpanzees hunt in groups for the most common middle-sized mammals (colobus monkeys). Our data show that duration of the hunt, hunting success, and organization of group hunts are all related to the number of hunters (see Table 9). In Gombe and Mahale, where chimpanzees most often begin to hunt opportunistically, the prey choice is less specialized, and the hunting group size is smaller. Three other parameters (hunting duration, success, and organization level) are also smaller, as would be expected if they were related to the number of hunters as they are in Taï.

So the important questions are: 1) why do Taï chimpanzees hunt in larger groups than other chimpanzee populations; and 2) does the much lower hunting success for lone hunters in Taï justify this important behavioral change? We assume here that the solitary hunt, the most commonly observed type of hunting in other chimpanzee populations, is more primitve than the group hunt.

1. Busse (1978) suggests that the hunting group size is related to the size of the social group prior to encountering a prey. However, because he did not distinguish between hunters and bystanders, this relation is obvious. If the motivation of adults to hunt was the same in both populations, however, then the size of the hunting group would be directly related to the size of the group prior to the hunting. As Taï chimpanzees forage in larger groups than do Gombe chimpanzees, this explanation may be true. However, data are difficult to compare. From Goodall (1968), the mean foraging group size is 4.83 individuals and the hunting group size is somewhere between 2 and 4 individuals for Gombe. In Taï, the foraging group size is 10.28 individuals, and the hunting group size 4.11. It may be that the greater sociability of the Taï chimpanzees can explain the larger number of hunters, as the ratio of bystanders to hunters seems to be about the same as in Gombe. This leads us to a new question: why are Taï males (the hunters) in larger groups than Gombe males? Boesch and Boesch (1984b) observed that the Taï males, contrary to the females, prefer to abandon nut-cracking when there is a risk of losing contact with other male group members. Therefore there seems to be a pressure for the males to keep strong contact among themselves and to forage in larger groups than do East African chimpanzees. Predation alone cannot explain the higher sociability of the Taï males. Leopards, the only natural predators of chimpanzees, can be repelled without tools by a lone male (personal observation) and are also present in Gombe.

The pressure of territorial fights could be another major factor. Encounters with neighboring communities are fairly common (29 encounters in 29 months in Taï). It might well be that the larger a male group is, the higher is its chance to win such territorial fights and the higher is its chance of enlarging its territory and its access to females (see descriptions of intercommunity encounters in Gombe; Goodall, 1986; Wrangham, 1975). In contrast, in Gombe, there were 0.25 encounters per month (33 encounters in 132 months; Goodall, 1986). Goodall (personal communication) observed that Gombe chimpanzees foraged in much larger coherent groups in 1985–87 than during the 1968–74 period, when Teleki and Busse made their observations. During the later period, they also tended to hunt in groups more systematically. This increase in group cohesion may be related to an increase in territorial pressure from neighboring communities. Thus the probably higher rate at which strangers are encountered in Taï may have forced them to adopt a more cohesive group structure, which may subsequently lead to a higher involvement of the males in social life at the cost of tool manipulation (Boesch and Boesch, 1984b).

2. The increase in hunting success with larger group size observed in Taï is intriguing, because a similar increase seems not to appear when Gombe chimpanzees hunt in groups. The higher hunting success of Taï males seems to be more related to organization than numbers. When they hunt in groups, they typically disperse under the prey, often out of sight of each other but all concentrated on the same prey, waiting until the progression of the hunt gives them an opportunity to act. With the progress of the hunt they tend to reunite while cornering the prey. Descriptions from Gombe (Goodall, 1986; Teleki, 1973) generally give the image of hunters either pursuing prey from a similar direction or dispersing while pursuing different prey. Jane Goodall (personal communication) gained the impression that, by chasing prey in different directions, Gombe chimpanzees increased the confusion of the prey and prevented them from mobbing against the hunters (Gombe males are afraid of aggressive colobus; Table 8). Thus Gombe males, when hunting in groups, seem to disorganize the prey's defense rather than increase their own hunting organization, as do Taï males.

The Taï data are still too incomplete to measure precisely the cost and benefit of both strategies (lone versus group hunt), and the second question cannot be answered fully. But the clear increase of hunting success with larger groups (see Table 9) explains why Taï chimpanzees hunt in cooperative groups more consistently than do Gombe chimpanzees. Our observations suggest that group hunting may facilitate the capture of the prey. By increasing the organization of the hunting group, the success is further increased. If this surmise is correct, then a subsequent elaboration of cooperation would lead to higher hunting success. We shall test this proposition in a future project for the four cooperation levels in Taï. In other words, cooperation could be a self-reinforcing behavior, which, once begun, provides its own feedback for more complexity.

Hunting and meat eating are highly social activities, with much excitement, many displays, and frequent meat sharing. Therefore some group hunting in Gombe and Taï could be explained by its social attractiveness as well.

As hunting group size is related to the level of cooperation in Taï, we should ask if cooperation is a consequence of hunting itself or results from the preexisting cooperative behavior in the population. Taï male chimpanzees always cooperate in territorial fights (eight observations) and always assist individuals that are giving distress calls either because they are facing potential predators (snakes and leopards) or because they are trapped in a snare (our observation was very similar to the description by Fossey [1983] of the gorilla silverback rescuing group member). These examples illustrate the possibility that cooperation among unrelated individuals could have developed in contexts other than hunting.

The next major differences we want to look at are also related: duration of meat consumption, size of sharing clusters, frequency of sharing, quality of sharing, and probably also size of prey. Taï chimpanzees have a tendency to share meat frequently, so that many chimpanzees are attracted to food owners because the success of request is high. As more chimpanzees eat more meat, the meat-eating episodes are shorter, and probably hunters try to kill the larger prey when they have the choice. This finding may explain why Taï hunters were never observed to snatch colobus infants away from their mothers' bellies without attempting to capture the mother as well. Why do Taï chimpanzees have such a high sharing tendency? We have seen that Taï chimpanzees share more large prey than small ones; large prey size could influence the sharing frequency. Hence the question is: which of these two factors was the prime mover? Availability of large prey probably does not explain the proportion of adults hunted, as Gombe chimpanzees neglect them, often intentionally (Goodall, 1986). We tend thus to think that the high sharing tendency predated the increase in adult prey. Any explanation for sharing tendencies can be only tentative, but Taï chimpanzees could be influenced by early experiences in sharing. Nut-cracking behavior is typical of the West African forest chimpanzees and provides them with a high energetic intake (Boesch and Boesch, 1984b), without requiring much energy expenditure (Günther and Boesch, in press). It also involves a high level of nut sharing between the mother and her offspring. Such nut sharing between mother and infants can last longer than the youngsters' first 5 years, and the mother may share up to 50% of the nuts she opens during the 2 years when the infants beg with greatest insistence. Sharing episode frequencies may reach 1–5 per minute (Boesch and Boesch, in preparation). Therefore it is possible that infants raised in such a sharing environment for years still have, as adults, a higher tendency to share food. One example observed after the hunt on December 4, 1985 illustrates this idea:

> Snoopy, the youngest adult male, displayed, unsuccessfully, for an hour within a large group against an adult female who was eating an adult colobus after having resisted successfully against the dominant males. Suddenly, Snoopy appeared with a large part of the upper part of the colobus followed by two adult females, Saphir and Kiri. It was the first time we saw him with such a large piece of meat, but to our surprise, after having fed for some time on the meat, he actively gave the head, the fur, and the intact thorax to both females, conserving for himself only some vertebrae on the neck. Salome, the suspected mother of Snoopy, is one of the most generous mothers that we observed, sharing up to 70% of the nuts she opened with her 5-year-old son.

In other words, the disposition to sharing within the family (as observed with the nuts in Taï) may spread out to the whole social group. Of course this difference is not unrelated to the environment; without the abundance of nuts, chimpanzees could never have learned to crack or to share them. If the hypothesis is true, however, social factors embedded in the Taï population may be crucial for the extensive meat-sharing activity.

Cultural differences

We can go on and look for differences between Taï and Gombe chimpanzees that are even more remote from environmental constraints. These differences were seen in many different aspects of meat-eating episodes.

Some could be labeled "*culinary preferences.*" For example, Taï chimpanzees keep the rump or the ribcage for last, consistently share the brain, and always swallow their leaf wadges. By contrast, Gombe chimpanzees keep the brain, which they rarely share, for last, spit out their leaf wadges, suck the blood of their prey, and eat, with delight, the fecal content of the large intestine.

Other differences could be labeled "*butchering habits.*" On the one hand, Taï chimpanzees kill adult prey by disembowelling them. They open the skull from the back, powerfully bite and tear apart the four limbs when dismembering a prey, and use sticks to extract the marrow from bones. On the other hand, Gombe chimpanzees kill adult prey by "a combination of smashing the prey against tree trunks or rocks and tearing at their limbs (sometimes breaking them)." (Goodall, 1986). They open the skull normally from the front, sometimes dismember a prey by twisting a limb round and round, but were seen once to use leaves to clean a skull.

We find it difficult to propose any ecological or sociological reasons that could explain all these different variations in a satisfactory way.

The differences in tool use for getting at the bone marrow is of particular interest. Most wild chimpanzee populations were observed to insert sticks into holes to gain access to food (either insects and insect products such as honey) or to probe (for other populations than Taï, Gombe, and Mahale, see Beck, 1980; Sabater Pi, 1974; McGrew and al., 1979; Sugiyama, 1985; Sugiyama and Koman, 1979, 1987). Gombe chimpanzees are famous for their sophisticated termite-fishing techniques, but only Taï chimpanzees were observed to use sticks for meat eating. Taï chimpanzees regularly use small sticks (maximum length about 30 cm) in many different contexts; to probe for wood-boring bees (*Xylocopa sp.*) (eight observations), to fish for insects living under the bark of fallen trees (one observation), to dip for driver ants (two observations), to dip for honey of three species of bees (*Apis sp.* and two *Melipona sp.*, 59 observations), to empty the almonds' residue of three species of nuts (*Detarium senegalensis, Panda oleosa, and parinari excelsa,* 110 observations), to inspect wounds of other chimpanzees (three observations), and to inspect dead animals (six observations). Thus it seems that the Taï chimpanzees have more largely generalized the "dipping in holes" movement with sticks than other populations, and also adopt it in the meat-eating context for bone marrow and brain.

In the context of hunting, the wild chimpanzees present a large variety of differences either because of environmental factors to which the chimpanzee responds in different ways, or because of social factors inherent ot the population concerned, or for reasons not as yet understood. We think that, in this sampling, many examples can be found to illustrate all the grades of complexity that could be required to fulfil the idea of a cultural difference in a nonhuman primate.

Sex differences

Chimpanzee females present the same kind of involvement and capture rate in hunting in Gombe and Taï, although they have a smaller involvement than males. However, Taï females may reach a much higher status than Gombe females during the division of the prey and gain access to much larger pieces of meat. Furthermore, they are regular providers of meat to adult males and females during the meat-eating episodes. This observation tends to alter, somehow, the view of the females in hunting; the Taï females have a more important role in this so-called typical male activity. It is difficult for us to give a satisfactory explanation of these differences between Taï and Gombe. Taï females can be important allies of some males, i.e., Ondine is a clear associate of Brutus, the alpha male, but was also able to maintain her position in his absence. Therefore it may be that Taï females have a higher interest in some social activities.

Whatever the reasons for the great interest of some females in hunting, the view of hunting as a male activity that is antagonistic to female activities in primates (Zihlmann, 1981; Zihlmann and Tanner, 1978), does not hold true in the case of chimpanzees. It has also been proposed that, in human evolution, males traded meat for sex with estrus females, an exchange that helps form privileged long-lasting bonds with these males (Lovejoy, 1981, cited in Johanson and Edey, 1981; Hill, 1982). We have rarely observed this kind of trade in Taï chimpanzees, where males mostly share meat with females with which they have a good relationship independently of their sexual cycle.

Predation in wild chimpanzees

Comparisons of all studies of wild chimpanzees show that hunting is observed almost everywhere (see Goodall, 1986); the present study shows that Taï forest chimpanzees hunt in a more elaborate way than savanna populations. But not all chimpanzees living in forests hunt so much: chimpanzees living in the Kibale Forest, Uganda, rarely hunt (one hunt suspected in 2 years of study; Ghiglieri, 1984). However, this contrasting observation was obtained during a short period of time with minimally habituated chimpanzees that were rarely followed in their daily movements (observations were focused at the fruiting fig trees). If this result holds true, then the suspected divergence between forest and savanna in terms of hunting behavior would become questionable. However, it is also possible that Kibale chimpanzees may hunt quite frequently; for example, in Taï during the first 2 years of our study we saw only seven hunts!

Teleki (1981) and Wrangham (1975) propose a mean meat intake in Gombe of about 27 g per day for each individual. We think that such mean estimations may be misleading in a certain sense as individual meat intake can vary greatly, some eating hardly any or no meat and others (mainly the dominant males) eating a large portion of meat each time (see also description in Goodall, 1986). Dominant males may eat more than 300 g of meat per session. Such an intake will be relevant not only qualitatively but also quantitatively for those individuals that generally are also the hunters. In a chimpanzee population with a hunting rate similar to Gombe and Taï, we can understand why some individuals hunt. The benefits probably compensate the costs. However, Mahale chimpanzees hunt much less frequently, and meat may play a marginal role in their diet. Thus the supplement of nutrients (proteins, vitamins, minerals) provided by meat (Teleki, 1981) could be covered by a low hunting rate.

Chimpanzee versus carnivore hunting

Schaller and Lowther (1969) have proposed that the hunting behavior of the social carnivores could be a better model for understanding the behavior of early hominids than that of primates. Some comparisons of the carnivores with the primates have sharply underestimated the hunting behavior of the latter (Hill, 1982; Thompson, 1975, 1976). In Table 19, we present another attempt to compare hunting behaviors in social carnivores and chimpanzees, using our definitions of the group hunt. Such a comparison, including numerous different works, stumbles over the problem in defining such words as "hunt" and "cooperation." We tried to consider only the hunts for which it was possible to be reasonably sure that the respective observers defined these terms similarly. Therefore this table should not be considered as representative of all hunts engaged in by a particular species, especially for social carnivores in which solitary hunts on small prey tend to be underestimated.

We may conclude from this table that first, some social carnivores may be specialized group hunters, as are wild dogs and hyenas for some prey, but the proportion of their group hunts are still comparable with Taï chimpanzees' group-hunting tendency. Moreover, important variations are found in this tendency according to the prey. Hyenas almost always hunt zebras in groups, whereas with wildebeest this tendency drops to 35% (Kruuk, 1972). Comparably, wolves seem always to hunt moose in groups (94.5%), whereas this tendency decreases to 66.6% for the white-tailed deer and drops to 27.7% for successful hunts upon caribou (Mech, 1970). Therefore group hunts in social carnivores seem to be an adaptation to the prey defense potential: zebras always present a coherent group defense while the wildebeest, which can easily be singled out, do not. Moose are very powerful and dangerous prey, whereas deer and caribou rely mostly on flight for their safely. For chimpanzees, such a relation is more difficult to document, as most prey present a similar defense potential, except for bushpigs in Gombe.

Second, level of cooperation and group hunting do not seem to be related in social carnivores: group hunts rarely involve high coordination of the hunters, most of them just pursuing the prey in a string (wolves and wild dogs) or as a pack fanning out behind them (wild dogs and hyenas). A collaborative hunt has been reported only for lions and wolves. Schaller (1972) describes precisely how hidden lioneses wait for others to drive the prey against them and only then rush toward the prey (29 observations). Among wolves, three hunts are described in which one or two wolves hid in ambush while waiting for another to drive the prey toward them (Mech, 1970). This disjunction of the frequency of group hunts and level of cooperation in carnivores suggests that the performance of different roles during a hunt may be somewhat difficult for such animals. If the comparisons in Table 19 are reliable, higher organization of the hunt as a normal

TABLE 19. Hunting strategies of social predators classified according to our definitions of cooperation[1]

	No. of hunts	Group hunt (%)	Similarity (%)	Synchrony (%)	Coordination (%)	Collaboration (%)
Primates						
Chimpanzee	80	92	6.5	11.5	14.5	63
Taï						
Gombe	86	36	←	29	→	7
Mahale	34	23	23	—	—	—
Papio anubis	147	14	← 14	→	—	—
Social carnivores						
Lion	523	52	←	46	→	5
Hyena[2]	46, 164	91, 35	24	91, 11	—	—
Wild dog	54	91	—	←	91 →	—
Wolf[3]	103	86.5	←	78.5 →	2	3

[1] In some cases, we could not differentiate from the description between different cooperative levels, and we pooled them. The baboon data are from Strum (1981), who presents the most elaborate observations of hunting within this species. The lion data are from Schaller (1972), including all hunts he observed. The spotted hyena data are from Kruuk (1972) and present hunts on two different prey species to illustrate the variability of their hunting behaviors; zebra hunts are the most elaborate in this predator species. The wild dog data are from Goddard and Estes (1969); we include captures they describe of small prey, which are solitary actions made while searching for larger prey. The wolf data are from Mech (1970).

[2] Zebra and wildebeest hunts, respectively.

[3] Moose, caribou and white-tailed deer hunts pooled.

means of hunting appears only in the chimpanzees. Some abilities of the higher primates may be necessary for cooperation. However, the differences seen within the chimpanzees require more study to understand what factors are responsible for the increase of the level of cooperation in primates.

In conclusion, we propose that Taï chimpanzees hunt in the most elaborate way known for animal hunters. With the results of the studies on the Gombe and Mahale chimpanzee populations, we shall be able to analyze precisely the factors that influence behaviors such as group hunts, cooperation sharing, and sex differences. Such a cross-population analysis within chimpanzees may shed some light onto the enigma of how these factors evolved in the primate order and how they may have appeared in the early hominids.

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