THE EFFECTS OF LEOPARD PREDATION ON GROUPING PATTERNS IN FOREST CHIMPANZEES

by

CHRISTOPHE BOESCH[1])

(Department of Ethology and Wildlife Research, University of Zürich. Switzerland, and Centre Suisse de Recherches Scientifiques, Abidjan. Côte d'lvoire)

(With 1 Figure)

(Acc. 20-I-1991)

Introduction

Composition and size of groups arc (bought to have evolved as adaptations that increase efficiency in exploiting and defending food resources and that reduce the risk of predations (BERTRAM, 1978; DUNBAR, 1988; TERBORGH, 1983; TERBORGH & JANSON, 1986). Disagreements persist over the relative contribution of the two factors, some advocating an exclusive role for resource exploitation (WRANGHAM, 1980), while others favour the predation hypothesis (DI/NBAR, 1988; van SCHAIK, 1983). Lastly, some support the optimal-group-size hypothesis where animals adapt to both factors (TERBORGH & JANSON, 1986). A great deal ol evidence suggests that both factors play a role in group formation (CHENEY & WRANGHAM, 1987; KUMMF.R *el al..* 1985; Pui i IAM *&* CARAGO, 1984).

All chimpanzee studies report a fission-fusion grouping system (BADRIAN & BADRIAN, 1984; KUMMER. 1971; KIRODA, 1979; GOODAEL, 1986; NISHIDA, 1968, 1979). This system, observed in 8 other species ol

large arboreal primates, is thought to allow greater flexibility in exploiting resource patches of different sizes in a species free from predation (DUNBAR, 1988; KUMMER, 1971; SYMINGTON, 1988; TERBORGH & JANSON, 1984; WRANGHAM, 1980). Under this view, chimpanzee social structure is presented as an adaptation to better use and intergroup defense of food resources by the females, with males primarily concerned with gaining access to females (DUNBAR, 1988; WRANGHAM, 1980, 1986).

However, it is hard to confirm that a species in the wild is really "free from predation", for predation is a rare event and has to be so for the prey species to survive. Scepticism of this lack of predation should have increased as evidence of aggressive interactions between chimpanzee and leopard accumulated throughout the areas of sympatry (BOESCH & BOESCH, 1989; GANDINI & BALDWIN, 1978; GOODALL, 1968, 1986; HIRAIWA-HASEGAWA et al. , 1986; IZAWA & ITANI, 1966; KORTLANDT, 1963; NISHIDA, 1968). Although it was not clear whether the chimpanzees attacked the leopards because they were predators or simply because they were intruders, the question remains, why should a chimpanzee take the risk of chasing a leopard away or killing one of its cubs (HIRAIWA-HASEGAWA et al., 1986), if the leopard is simply a disturbance? Until recently, faeces analysis of potential predators showed no chimpanzees remains (STRUHSAKER & LEAKEY, 1990, for Tai: HOPPE-DOMINIK, 1984), except in Mahale where newly intruding lions were found to have eaten chimpanzees (TSUKAHARA & NISHIDA, 1990 in BARTON, 1990) confirming their vulnerability to huge predators. CHENEY & WRANGHAM (1986) argue that successful predation, if it exists, is too rare to represent a serious threat. However, I agree with DUNBAR (1988) that it is the potential risk of encountering the predators which is important rather than the actual mortality rate, which may be a measure of the effectiveness achieved by the prey's defenses or evasive counter-strategies.

Most long-term studies on chimpanzees have been done m the savanna, and hence, most chimpanzee-leopard interactions are reported from habitats where leopard density is as much as 10 times less than m the tropical forest (MYERS, 1976). This might explain why reports of predations there arc rare. Recent observations in the rainforest of Tai National Park, Ivory Coast, have enabled us to document the predatory relations between the two species more precisely. I shall lust present these observations and then compare social parameters from several studies on common and pygmy chimpanzees in relation to leopard predation pressure.

Methods

In September 1979, Hedwige BOESCH and I began a study of the wild chimpanzees living in the Tai National Park, Cote d'lvoire (BOESCH & BOESCH, 1983, 1984, 1989). We habituated a community of chimpanzees to our presence without any artificial provisioning and followed them by their drumming, vocalizations and finally by sight. Observations were never made by more than two persons; similar green clothes were always worn; observers remained silent with the chimpanzees, maintained a quiet, peaceful attitude throughout, and never carried a weapon such as a bushknife. Habituation was slow, but since March 1984, we have been able to follow all the males by sight and remain within their group during their daily foraging. At the time of writing (November 1990), only a few shy females cannot be followed a(a distance of 20 m for the whole day.

Following the definitions of GOODALI. (1968), the community comprises all the chimpanzees ranging together in a territory. They form parties consisting of individuals of all ages that move together by remaining in visual contact with each other. Whenever the party composition changes, a new count is made of the individuals present. Due to the loose cohesion of such parties, their composition is monitored whenever visibility allows such a check, considering only the members whose presence I can verify regularly even if I know the party to be larger. Large parties will thus be underestimated. I use the term "group" for all the parties that move together in the same region and are in auditory contact with each other. The number ol chimpanzees in the study community fluctuates from 68 to 51 individuals, with 9 to 6 adult males and a sex-ratio always above 3 (number of adult females per number of adult males).

Since November 1985, our observations have been continuous thanks to students and an African held assistant, Gregoire NOHON, who has been trained to follow target chimpanzees recording on check-sheets the behaviour of mother-infant pairs. In August, 1986, we noticed for the first time an adult male, Ulysse, bearing various wounds that could only have been caused by a leopard. I attribute wounds to leopards when they are clear-edged and sharply cut, and typically appearing as two or three parallel strokes, as would be expected from a ripping paw with protracted claws. Clear-edged punctures also occur, probably resulting from a rapid strike with a paw. Bites from leopards were only inferred twice (Tina's and Salome's cases below); the difference between the effects of the canines and the incisives was very distinct. Leopards are the only big cats in Tai able to inflict such injuries. The other major causes of wounds in chimpanzees are those inflicted by conspecifics during conflicts. Chimpanzees bites produce large wounds with very irregular edges, typically at the extremities, the ears or the rump.

The following episodes all took place between November, 1985.and October, 1990.

Results

1.   Interactions between chimpanzees and leopards.

The encounters between the two species always appeared to be aggressive and were normally very brief, but it is possible to distinguish three kinds of encounters.

A.   *Chimpanzees attacking leopards.*

Tai chimpanzees seem to search systematically for leopards whenever they are aware of their presence, either because they hear one, or when

leopard prey, such as a duiker, call in distress. Keeping together, with hair on ends, they silently move in the direction of the supposed leopard, looking around as they progress and waiting to listen for indications of the leopard's position. If they find the leopard or happen to encounter one by chance, they very aggressively and noisily chase it away. During the study period, Tai chimpanzees were seen to chase leopards away 9 times and to rush the rescue alarm-calling chimpanzees 11 times (twice we saw leopard footprints at the site and twice we heard the growl of the fleeing leopard). In the following examples, two types of reaction by the leopard, depending upon the number of chimpanzees chasing it, were recorded.

Example 1. A leopard discovered by two male chimpanzees.

"On 18th September 1989, Ulysse and Rousseau (two young low-ranking adult males), on their own, were silently approaching a mixed group of noisy monkeys when suddenly . following an alarm shriek of a diana monkey *(Ccrcopithecus dinna),* the soft growl of a leopard was heard. Immediately, Ulysse stood upright and, facing Rousseau, sought reassurance by touching the other's mouth before moving towards the growl, followed by Rousseau. The leopard growled twice more while moving westwards, Ulysse accordingly changing his direction of approach. Very deliberately and silently, Ulysse led the approach, 10 meters ahead of Rousseau. Suddenly he stood upright and, with wild aggressive barks, rushed ahead followed by Rousseau. The surprised leopard ran further west pursued by the two males and, like a hare in flight, suddenly made an abrupt turn and dashed away from the closing chimpanzees passing right beside rne with its ears flat down. Delayed by this swerve, Ulysse and Rousseau stopped, looked around and drummed aggressively on buttress roots several tunes."

Example 2. A leopard discovered by a large group of chimpanzees.

"On 6th March 1989, our field assistant, Gregoire Nohon, was observing a party of 2 adult females and an adult male, Rousseau, resting 20 m nearby a large windthrown tree At 12.10 hrs. he heard loud calls from another party of chimpanzees behind that tree. Then he saw Rousseau rushing towards the fallen tree while an adult female leopard was running out from under the tree, avoiding Rousseau who made a shortcut lo catch up with it. Four adult males appeared now by jumping over the tree and followed the leopard behind Rousseau. The 2 females that were still close to Nohon now joined in the pursuit and the leopard was seen running away with 7 chimpanzees behind it, Rousseau being as close as 3 meters. Forty meters further on, tremendous screams from chimpanzees and roaring by the leopard were heard. Nohon rushed back to camp and informed me. 1 arrived at the site at 13:45 hrs and saw the chimpanzees around another large fallen tree under which the leopard was trapped in a deep and narrow hole. The leopard roared without interruption for the rest of the observation, barking loudly whenever it tried to strike the chimpanzees with its paw. For the next 42 minutes, they settled around the entrance, some grooming, others just sitting or even laying on the ground near the hole entrance. Now and then, females with youngsters neared the entrance and look advantage of the rare opportunity to have a close and safe look at a leopard. Some regularly threatened the animal. Seven times different Chimpanzees were seen to take a piece of a fallen branch and use it as a club, repeatedly trying to hit or stab the leopard in its hole (average, of 4.44 strikes per instance), each time the leopard

barked in response and jumped forward out of its shelter to hit the hand of the chimpanzee holding the club, seemingly unsuccessfully. But before it could try to escape from the hole, the noisy reaction of the group, with a minimum of 3 adults rushing towards it, forced it back to its refuge. The small entrance hole (about 70 cm at its highest point and narrowing down towards the leopard) prevented the chimpanzees from taking effective action and at 14.32 hrs *i.e.* 2 hours 22 minutes after the first sighting, they left the site, the leopard silently leaving the hole 11 minutes later."

The leopard's behaviour in this sequence seemed appropriate. Followed by 7 adult chimpanzees, swerving would not have shaken off all the pursuers, since some at the rear could have taken shortcuts; hiding was obviously the best choice. We do not know what would have happened if the chimpanzees had actually succeeded in getting hold of the leopard. In two other encounters, we have seen one, respectively two chimpanzees rush in very close behind a leopard that escaped, but despite their proximity it was difficult to judge if they chased it away or wanted to capture and harm it.

The repeated use of clubs as weapons in example 2 seems to indicate that the chimpanzees intended to harm the leopard, and only the low entrance of the hole prevented them from hitting powerfully. They hit at the leopard up to 11 times in a row and usually threw the club into the hole afterwards. Some actually tried to stab it with one end of the club, but the leopard seemed to deflect the club with a paw. Furthermore, the leopard appeared to be familiar with such weapons, as it obviously tried to reach for the hand holding the club and not the dub itself.

B. *Leopards attacking adult chimpanzees.*

During the last 5 years, 7 chimpanzees—2 adult males (Falstaff and Ulysse) and 5 females (4 adults: Ella. Gitane, Hera, Malibu and 1 adolescents: Fossey)—have born numerous fresh wounds (between 5 to 19) that could only be attributable to leopard attacks. Four were attacked while member of a party within a large and noisy group (Falstaff, Ella, Malibu and Fossey), when we were following a nearby party, while the others were attacked when we were absent. However, Hera, was known to have been absent from the group for two days, probably with another adult female, at the time she received the wounds. All recovered completely except for one mak[1], Falstaff, who died two months later, most probably from an infection following the perforation of the pleural membrane caused by one of the claws of the leopard. I found Falstaff very shortly after the presumed attack, attracted by tremendous alarm calls of the chimpanzees and all the monkeys in the area. He was covered in

blood and bore 16 wounds that all healed rapidly, except one neat little hole in his side from which a whitish secretion continually oozed. His general state of health deteriorated until he looked very ill and could not follow the group any more. We encountered him a few times and could tell his presence by an awful smell. We never found his corpse, but the chance of his having been eaten by the leopard that had attacked him so much earlier seems remote. The fragmentary nature of these observations does not enable us to explain why leopards should attack chimpanzees when they are in groups and apparently able to defend themselves. However, Falstaff's death proves that leopard attacks can be fatal, even for a full-grown male chimpanzee.

Example 3.   An adult female attacked by a leopard.
"On 23rd February 1989, I was following a party of 4 adult females with their infants moving within a noisy but spread out group of chimpanzees. At 9.38 hrs, a chimpanzee, about 50 m away, made loud frightened calls. Instantly, 3 of the 4 mothers rushed barking aggressively towards the calls. Just before arriving, I heard them making loud mobbing calls suggesting that the rescuers were chasing a predator away. I arrived some 30 seconds later just in time to sec 5 of the 6 adult males of the community arriving and without hesitation rushing westwards, the direction the females, now in the trees, were facing. Ella, one of the dominant females, had her face, chest and legs covered in blood, and had 19 wounds visible on her body, but none looked serious. I presume that, when she was attacked, she was out of sight of others with her 5-year old son, who was now sitting unharmed nearby. For the next 2 hours, she was constantly surrounded by at least 15 chimpanzees, most of the time tending her, removing dirt and licking all the blood from her wounds. She left the site some 2 hours later and was escorted for the next 4 hours always by at least 5 adults behaving attentively towards her, regularly licking her wounds. The leopard footprints found near the site clearly showed that it had been coming from the west towards the noisy chimpanzees/'

In this case, I had the strong impression that the leopard must have directed his attack at Ella's 5-year old son and not against the adult female. Ella most certainly saved his life by facing the leopard before it could reach him.

Hera, who was attacked presumably when away from the group, seemed to have been less lucky: when she reappeared, her 2-year old son was missing. She had certainly tried to rescue him at the cost of 18 fresh wounds, of which 13 were on her head, in the ensuring battle. However, since the infant was so small, the leopard certainly killed him instantly and was able to carry him off and her rescue came too late.

The taking care of wounded chimpanzees by other group members is characteristic and results in the rapid healing of wounds not accessible to the victim, *e.g.* on the head (Ella, Hera, Malibu and Ulysse) or on the

CHRISTOPHE BOESH

back (Fossey, Gitane and Falstaff). All dirt particles and blood are removed with the fingers or the mouth, and the wounds are licked clean by adding plenty of saliva. This care is provided as long as needed and, in the case of Falstaff, was still being provided two months after the attack.

C. *Predation on chimpanzees by leopards.*

The following examples give the description of the two cases in which the death of a chimpanzee can definitely be attributed to a predatory attack and in which part or possibly all of the chimpanzee's corpse was eaten by the leopard.

Example 4: Juvenile female killed by a leopard.
"On 8th March 1989, at 7.45 hrs, Gregoire Nohon, who was following a female, heard unusual calls nearby. Rushing to the spot with the female and the alpha male, he saw Brutus, an adult male, encircle the body of a motionless subadult, some of whose viscera were visible. I arrived there at 8.17 hrs and could confirm that Tina, a 9-year old female, had been killed by a throat bite of a leopard (later examination of the skeleton showed that the leopard bite had broken her second vertebra). She presented 23 claw cuts all over her body, one cutting the skin of her belly and partly exposing the viscera, two others on the left side perforating her lungs. For the next 6¼ hrs, Tina's corpse was guarded continuously by up to 32 group members, with the dominant males remaining in immediate proximity all the time (Fig. 1). During the first 4 hours following the attack, at least one chimpanzee sat constantly within 1 meter of the body. When they eventually left the body, it was covered by thousands of flies."

I checked the body regularly and noted that the leopard had probably come back 2 days later, when no more flies were present. I found that the lower part of the body had been separated from the rest and, as traces on the ground indicated, carried 15 meters away over a 1 meter high fallen trunk. There I found the bones of the pelvis and both legs. Those of the feet were missing, presumably swallowed. No flesh nor fur remains were present, while the rest of the body, otherwise untouched, presented fur remains mixed with decomposed flesh and fly maggots. We did not see the leopard eating the prey, but the scavenger had to have been powerful to be able to carry it that far over such a big tree trunk (Tina's whole body weighed 20 kg immediately after death). In Tai forest, the leopard is the only carnivore capable of such an action. This observation is partly corroborated by our discovery of two more subadult chimpanzee skeletons comprising only the bones of the thorax and the skull; those of the legs and pelvis being absent. This suggests that these individuals met with a similar fate.

Fig. 1. Tina, a juvenile female, killed by a leopard, is guarded by two dominant males of the community. The alpha male is testing her reaction by gently shaking her leg. These males groomed her for 53 minutes during the first two hours following her death. None of them would spend such a length of time grooming a juvenile female alive.

Example 5.   Adult female killed by a leopard.

"On 28th August 1990, at 15.20 hrs, while working at camp I heard suddenly two chimpanzees giving loud calls some 80 meters west: Two single very loud screams gave me the impression of anguish whereas one of the animals emitted aggressive and at the same time frightened calls without interruption. Twenty minutes before, I had heard a party of chimpanzees calling and drumming much farther south-west. Approaching very carefully, I saw Sartre, a 10 years old male, giving these despaired calls while he climbed up into a big tree. He was staring to the ground right under him and hitting his hands on a branch in a half temper-tantrum, all hair erected. On the ground, his mother, Salome, laid motionless on the back. Eight claw stripes covered her trunk, whereas her left chest looked awful as the leopard had bitten her there, compressing all the ribs which now formed a blood-stained protrusion. One of its canines had pierced the chest wall at the sternum which led to her immediate death as the lungs collapse through a pneumothorax. The leopard may have left fearing that the group would come, attracted by Sartre's calls, but they were out of hearing distance, drumming further south. Sartre left 18 minutes after the attack, with a last look at his mother, and was seen to join the group this same afternoon. I stayed in ambush and, 1.32 hrs after the attack, saw the leopard come back in a straight line toward the body. It spotted me immediately and ran away. During the night, Salome's body (32 kg) was removed without leaving any trace on the ground. Despite careful searching we did not find any remains of her body within a circle of some 50 meters around the place she died."

The tremendous power of the leopard's bite makes him a rapid killer and, if taken by surprise, even an adult individual seems unable to prevent it from the fatal biting. Thus, all age-sex classes may suffer from predation by leopards.

2,   Predation pressure and social grouping in chimpanzees.

A.   *Predation pressure by leopards sustained by forest chimpanzees.*

We can be reasonably confident of 22 interactions between leopards and chimpanzees during the last 5-year study period considered here (by "confident", I mean only those occasions in which I saw either wounds on the chimpanzee attributable to a leopard, and/or fresh leopard footprints associated with alarm calls from the chimpanzees and/or heard or saw the leopard). These certainly resulted in the death of 4 chimpanzees and led to 6 adults being wounded. If we assume that our presence does not greatly affect the leopard's behaviour, this gives a minimum estimate of the level of predation suffered by Tai chimpanzees. However, leopards are not habituated to our presence; whenever we encounter one which becomes aware of our presence, it immediately runs away. The fact that we even saw them (8 times when on our own, *i.e.* not following the chimps) shows that our smell and the noise we make has only a relative effect in deterring them. The smell and noise produced by t h e chim-

panzees we follow and which outnumber us usually, may limit further the disturbance due to our presence. Due to the chimpanzees' fission-fusion system and the limited visibility in the forest (20 m), we estimate that our presence would only directly affect the predation risk of the party we were immediately following (usually at a distance of 5-10 m) out of a minimum of 5 parties that normally comprise the group that remains in auditory contact all day long. In addition, our presence would dissuade a leopard only if it became aware of us before or during the attack. This would apply only if the party followed were smaller than 6-7 individuals, for foraging parties larger than 7 individuals are commonly scattered over distances greater than the 20 m visibility range (Malibu, for example, was attacked about 30 m from us, although a member of the party we were following). Thus, the following estimate of the effect of our presence on leopard predation can be made: Our presence may protect the chimpanzees that are members of the party we are following, *i.e.* one of the 5 parties that normally range together in a group, and only if this is smaller than 7 individuals. Since in Tai only 40% of the parties comprise less than 7 individuals, we may assume that our presence protects 8% of the parties (as we follow parties at random with respect to party size).

I estimate the risk for an individual to be attacked by a leopard, *i.e.* predation risk (Pr) and the risk of being killed in such a predatory attack, *i.e.* mortality rate (Mr) to be as follows:

$$Pr = b \, [a \, (Ne \, / \, Gs \, / \, T)]$$
$$Mr = b \, [a \, (Nd \, / \, Gs \, / \, T)]$$

where Ne = Number of encounters with the predator, Nd = Number of deaths attributed to the predator, Gs = average group size, *e.g.* number of individuals remaining in auditory contact with each other (calculated as 72% of community members in 1989-90 [N = 60 chimpanzees]), and T = Total observation time, *i.e.* 5 years.

With two correction factors: a) (Human disturbance) = 1.08, to account for the 8% of parties protected from predatory encounters due to our presence; b) (Limited observation time) = 2.78, to account for the fact that we observed the chimpanzees only for 36% of daylight time, due to incomplete day follows, days on which we could not locate them and rest days.

Thus, during the study period, individual chimpanzees suffered an estimated predation risk of 0.30 per individual per year with or without injuries and a mortality rate of 0.055 per individual per year due to predators. In other words, on average an individual will be attacked by

a leopard once in 3 years and 4 months and will be killed within 18 years. The day-light correction for the predation risk inflates the few encounters that resulted in wounds (that could be confirmed later by us anyway), but underestimates the more frequent unsuccessful leopard attacks that did not result in injuries. To account for this bias, we may estimate the predation risk to be between 0.30 to 0.60 per individual per year.

How many of the 48 individuals (including 3 adult, 1 adolescent and 5 juvenile males, 13 adult females with 15 suckling infants plus 5 adolescent and 6 juvenile females) that disappeared from the community in the last 5 years could be attributed to leopard predation? Apart from the adolescent females no other age class was ever seen to emigrate in Tai chimpanzees, therefore I have to attribute the disappearance of individuals, except that of adolescent females, to death. In forest conditions, it is very difficult to be certain of the cause of death of an individual, as corpses are eaten rapidly by scavengers or by fly maggots and are thus rarely found. Nine of these 48 individuals looked ill before they disappeared (due to striking loss of weight and difficulties in movement) and two of these were mothers with lactating infants, making 11 disappearances attributable to illness. Five adolescent females most probably emigrated from the community. Hence, 16 of the 48 disappearances could be explained by emigration and death through illness. If we use our mortality rate estimate, leopard attacks were responsible for the death of 16 to 17 chimpanzees for this 5 year period (Mr x average community size [60 chimpanzees] x observation time). Thus, predation by leopard seems to be the first cause of mortality in Tai chimpanzees (39% of the 43 deads).

B.   The fusion-fission grouping s y s t e m and p r e d a t i o n .

We can test if the grouping patterns of a population vary with different predation pressures. Between 12 February to 8 March 1989, Tai" chimpanzees experienced 4 encounters with leopards that led to one death (Tina) and two wounded (Ella, Malibu). In Table 1, I compare three aspects of grouping (party type, party size and group size) for these high predation months with the same months two years earlier, when no encounters with leopards were confirmed but fruit availability and distribution was similar. However, to control for an effect of food availability, I also checked the same months for a third year (1988), in which the fruit availability was exceptionally low and no encounter with

TABLE 1.   Party type and party size (%) in Tai chimpanzees for
                        Three consecutive dry seasons

	A	B	c:
	Low predation	Low predation	High predation
	+ Abundant food	+ Scarce food	+Abundant food
Party type:			
Mixed	66.0	30.0	63.7
Family	15.7	26.7	15.5
Male-female	3.0	0	0
All-male	6.8	18.3	12.4
Lone	8.5	25.0	8.4
Party size:			
1	5.5	18.3	5.6
2-5	21.7	K).O	33.2
6-10	28.1	21.7	30.6
11-20	31.9	13.3	20.3
Over 20	12.8	0	10.3
Total (N)	235	60	232
Average	11.7	5.7	9.5

During period A (25 January-10 March 1987). no encounters between chimpanzees and leopards were recorded, nor during period B (1 January lo 18 February 1988), while in period C (12 February-8 March 1989), encounters with leopards were frequent. Periods A and C were similar in food availability and distribution, whereas during period B. fruit availability was exceptionally low.

leopards was seen nor suspected. We could not yet observe situations with low food availability but high predation.

— Predation pressure, when food availability was high, seemed to affect some party types (columns A *vs* C in Table 1: $x^2 = 10.93$, df = 4, p<0.05); a partitioning procedure (SIEGEL & CASTELLAN, 1988) shows that, with an increase in predation pressure, chimpanzees were found more frequently in all-male parties whereas male-female part it's decreased (p<0.05). Party size decreased with an increase in predation pressure $(x^2 = 12.53$, df=4, p<0.05). Group size, which comprised 84.83% of all community members (measured as the number of identified individuals seen when following the chimpanzees each day), when predation pressure was high, remained however constant when compared to other dry-season months with lower predation pressure (December 1989 to February 1990: group size = 81% of community members: Kolmogorov-Smirnov two sample test: DN =0.66, p = 0.99).

— Food availability, when predation pressure was low, seemed to affect party type (columns A *vs* B in Table 1: $x^2 = 33.38$, df=4, p<0,001); a partitioning procedure (SIEGEL & CASTELLAN, 1988) reveals that all types were affected (p<0.001) except male-female parties; mixed parties were more frequent whereas both all-male and lone parties were less frequent when food was more abundant. Party size increased with an increase in food availability ($x^2 = 31.24$, df=4, p<0.001).

Thus, Tai chimpanzees social response to increase of predation or food is specific; party size response is opposite and the type of party favoured is different.

Differences between Tai chimpanzees and those living in environments with different predation pressures should be expected. The chimpanzee population of Gombe Stream National Park, Tanzania, seems to experience very low predation pressure, as the park has for years been inhabited by only one old leopard (GOODALL, 19(38, 1986, pers. comm.). Since Gombe Stream National Park comprises about 150 sq km, leopard density may be as low as 0.007 individual per sq km, whereas in Tai leopard density reaches 1 individual per sq km (MYERS, 1976; BOESCH, pers. obs.). In addition, no predatory episodes have been witnessed in Gombe in more than 30 years' observation (GOODAI.L, 1986, pers. comm.). Although I know of no data concerning the density of leopards in the Mahale Mountains, Tanzania, several reports (NISHIDA, 1968; HIRAIWA-HASEGAWA *el al.*, 1986) indicate that the density may be higher than in Gombe, for they are encountered by chimpanzees and there seems to be a resident breeding leopard population. If this impression is correct, I would expect to see a decreasing occurrence of party types presenting an effective predator defense (mixed and all-male) in the order Tai-Mahale-Gombe. Prediction about party size is more hazardous for the following reasons: In theory, party size is expected to increase with predation pressure in a high visibility environment (BERTRAM, 1978; DUNBAR, 1988; HAMILTON, 1971; PULLIAM & CARACO. 1984). However, as visibility varies between the three sites in the opposite way than prcdation pressure, the two factors may nullify each other. Second, no data on food availability between these three sites exist which would enable prediction on its impact on party size.

The data (Table 2) support the predictions on party type, as predator-safe parties are found less frequently when predation pressure decreases; Tai' chimpanzees forage less alone or in male-female parties than Mahale chimpanzees ($x^2 = 12.42$, df=4. p<0.05: Partitioning procedure; p<0.05 and p<0.001) and Mahale chimpanzees forage less in family,

TABLE 2.   Party type and size (%) of three populations of common chimpanzee, one living in a tropical forest (Tai) and two living in wooded savannas (Gombe and Mahale)

	Tai	Gombe	Mahale
Party type:			
Mixed	61.8	30.0	51.8
Family	12.7	24.0	13.3
Male-female	2.0	18.0	4.3
All-male	9.9	10.0	10.6
Lone	13.6	18.0	21.0
Total (N)	2123	498	218
Party size:			
1	8.5	13	11.5
2-4	27.1	49	30.3
5-6	14.2	20	12.8
7-9	16.0	9	11.5
10-20	27.9	8	28.-1
Over 20	6.3	1	5.5
Total (N)	2123	350	218
Average	8.4	5.6	6,1

Party size following GOODAI.I.'S classification (1968). Tai data were collected for 12 months period between December 1986 to March 1989. Gombe data from GOODAI i (1968), Mahale data from NISHIDA (1968).

male-female and lone parties than Gombe chimpanzees ($x^2 = 48.96$, df=4, p<0.001: Partitioning procedure; p<0.001). Similarly, Tai chimpanzees are more frequently in mixed groups and less in family, male-female and lone parties than Gombe chimpanzees ($x^2 = 262.99$, df=4, p<0.001: Partitioning procedure; p<0.001). Gombe chimpanzees forage in smaller parties than Tai ($x^2 = 180.2$, df = 5, p<0.001) or Mahale chimpanzees ($x^2 = 75.25$, df = 5, p<0.001). Party size in Tai and Mahale is the same (p>0.05). However, Mahale data are only from the artifical feeding site (NISHIDA, 1968) and could, therefore, be inflated (see also WRANGHAM, 1974). If we assume that all three chimpanzee populations react in a similar way to a leopard predation and food availability, then the results confirm that grouping patterns in these populations reflect varying predation pressure.

A comparison between different chimpanzee populations living in forest habitats ought to indicate if social groupings are similar when food availability and predator pressure are more comparable than under forest *vs* savanna conditions.

TABLE 3. Party type and size (%) for three forest chimpanzee popula-
tions: the common species (Taï) and the pygmy species of Lomako and
Wamba

	Taï	Wamba	Lomako
Party size:			
Mixed	62.9	74.2	68.4
Family	13.5	4.9	5.2
Male-female	0.8	2.5	7.9
All-male	11.9	2.5	4.5
Lone	10.8	6.1	13.7
Unknown	—	9.1	—
Total (N)	2123	163	191
Party size:			
1	6.6	6	11
2-5	32.9	12	35
6-10	27.7	15	27
11-20	25.2	30	23
Over 20	7.5	36	4
Total (N)	2123	147	268
Average	8.4	16.9	7.9

Party size follows BADRIAN & BADRIAN's (1984) and KURODA's (1979) classification.
Wamba data from KURODA (1979), Lomako data from BADRIAN & BADRIAN (1984).

Data from two studies on the bonobo or pygmy chimpanzees *(Pan paniscus)* of the tropical rainforest in the bassin of the Zaire river are available (Lomako and Wamba).

— Party type (Table 3): Family and all-male parties are more frequent in Tai than in Lomako forest ($x^2 = 38.04$, df = 4, p<0.001: Partitioning procedure; p<0.001, p<0.05), male-female parties are less frequent in Tai (p<0.001) and mixed parties seem equally common.
Family, all-male and solitary parties increase from Wamba to Tai $(X^2 = 27.71$, df=4, p>0.001: Partitioning procedure; p<0.001), and from Wamba to Lomako, mixed parties increase but male-female and lone parties decrease ($x^2 = 10.47$, df=4. p<0.05: Partitioning procedure; p<0.05).

— Party size is similar in Tai and Lomako ($x^2 = 4.80$, df = 4, p>0,05) and bigger in Wamba chimpanzees (compared to Tai; $x^2 = 198.48$, df=4, p<0.001, and to Lomako; $x^2 = 96.16$, df=4, p<0.001).

The similarity in party size, but the lower all-male party frequency suggest that, in a comparable habitat, the Lomako chimpanzees suffer a

lower predation pressure than the Tai chimpanzees. The bigger arboreality of the bonobos (DORAN, 1989; SUSMAN, 1979) may either explain such a lower predation pressure, as leopards have less opportunity to attack them, or be the bonobo answer to a high predation pressure. The singular Wamba grouping patterns might be attributable to the constant use of fixed and mobile artificial provisioning that may-attract chimpanzees towards the observers (artificial provisioning is not used in either Tai or Lomako) and unable us to forward any hypothesis about predation in Wamba.

Discussion

Despite the fact that chimpanzees have been the subject of intensive studies for many years at various sites, this is the first time that predation of chimpanzees by leopards is reported. Predatory interactions may be rarer in sites other than Tai forest partly because of lower predator densities, but another factor could contribute. In Tai, chimpanzees are followed at most by two observers and we never use a bushknife. In Wamba and Lomako, chimpanzees are followed by larger human groups and bushknifes are commonly used to cut a path through the undergrowth (Diane DORAN, pers. comm.; IHOBE, 1990). Shy leopards are thus probably kept away by such noisy groups. In Gombe, Mahale and Wamba, artificial provisioning was supplied which concentrated chimpanzees near humans (IHOBE, 1990; WRANGHAM, 1974; NISHIDA, 1979), a proximity possibly discouraging non-habituated predators.

Chimpanzees in the Tai forest suffer from heavy predation by leopards, which appears to be the first cause of mortality. In the last 5 years, 17 disappearances could be attributed to predation, 11 to illness, 5 to emigration and 15 to unknown causes[1]). For the same period, 26 infants were born while 6 females immigrated, giving a negative balance of 16 individuals. For an animal species that is adult when 115 for the females and 15 for the males (GOODALL, 1986), a mortality rate of once within 18 years does not give much prospect for reproduction. However, predation effect may be limited if it affected particularly vulnerable individuals, *e.g.* the sick (Salome, the adult female in example 5, was very old, just lost her one year old baby and showed signs of being

[1]) Under unknown causes, poaching, with guns or snares, may be the most probable one for the community under study.

heavily parasitised), or handicapped ones (Tina, the juvenile female in example 4, had badly misshaped hands with 2 lingers missing on each one). Only if this was the case would the community compensate with its birth rate for illness and predation mortality (Death due to unknown cases would increase proportionally). However, the reproductive value of the juvenile, adolescent or adult victims of leopards is higher than that of new-born infants and in such a slowly developing species predation cost would even so remain high.

In addition, the ratio between the predation risk and the mortality risk (0.30 to 0.60/0.055) reveals that 9-18% of the leopard attacks could result in the death of a chimpanzee. The high success of predator attacks forces us to question the chimpanzee[1] aptitude to face leopards.

On a social level, Tai chimpanzees have reacted to the threat of predation in two ways: First, they forage in relatively small parties and keep auditory contact between parties. Theories tend to link an improvement m predator detection, defense and lower mortality risk with larger groups (BERTRAM, 1978; DUNBAR, 1988; HAMILTON, 1971; PULLIAM & CARACO, 1984). However, in a low visibility environment, as Tai forest, predators detect prey mainly be sound and the predator is, if at all, detected in the last instant (TERBORGH, 1983). Therefore, detection of predators through increased vigilance and number of eyes is minimally increased by group size (see also DEHN, 1990), whereas the noise level of such larger groups will inevitably increase detection by predators (KILTIE, 1980). These considerations may explain why Tai chimpanzees decrease their party size with higher predation pressure but increase party types which offer the best defense potentialities against predators, all-male parties. The fact that 5 out of 9 individuals wounded or killed were attacked whilst members of a large party (see example 3 and 4) may illustrate the vulnerability of such group members and the limited detection abilities of large parties. Dilution, however, remains effective in decreasing the individual risk of being attacked (DEHN, 1990; HAMILTON. 1971) and the reduced distance between parties, while allowing dilution, also allows a response whenever needed by a group comprising 4 to 5 times more individuals than the average size of the parties. Second, to improve anti-predator defense, Tai chimpanzees are mostly found in parties with the best defense capacities (mixed and all-male) that allow both sexes to profit from the others' support, this benefit being more obvious for females. Such greater defense potential is hampered, however, when facing an ambushed rapid killer, as defense, whatever rapid, can materialize only after an attack has occurred, which may be too laic. Note that both adap-

tations are also effective in coping with the more frequent territorial encounters in Tai than in Gombe (see BOESCH & BOESCH, 1989).

On an individual level, Tai chimpanzees respond to any alarm calls with immediate assistance. As illustrated in example 3, this rescue behaviour is a condition for the two social adaptations to be effective. An indication of stronger solidarity between individuals than in the savanna can also be concluded from the fact that Tai chimpanzees take care of injured group members independently of kin relationships and their age or sex. This is in marked contrast with Gombe chimpanzees who are rarely attentive to injureds others than family members, and seem even fearful moving away of non-kin woundeds (GOODALL, 1986). In addition, whenever Tai chimpanzees notice the presence of a leopard, they search for it and chase it away cooperatively. When confronted with an "'ambushed rapid killer", these preventive attacks may be more effective than defense against actual attacks, as leopards with young (HIRAIWA-HASAGAWA *et al.*, 1986) or surprised when asleep (pers. obs.) could be at risk. Mahale chimpanzees, when killing the cub of a female leopard that had not molested them, acted in a similar way.

Given the high mortality of chimpanzees due to leopards at Tai, both social and individual adaptations to predation seem not to deter sufficiently this powerful predator. 1 cannot exclude the possibility that in the last years Tai chimpanzees were dominated by the leopards and that the reduction of the community size (iron; 68 to 51 individuals) reflects their inferiority. An alternative explanation might be that usually they cope with the leopards but that one "chimp-killer" has recently appeared and is responsible for all or most attacks; two points may favour such an explanation; first, all attacks leading to injuries or death, where I was present (7 out of the 9 bloody attacks), happened between two rivers, in an area barely exceeding 4 sq km (out of the 27 sq km large community territory). Second, 6 of the 9 bloody attacks happened during the last 20 months. However, even so the chimp-killer explanation could account only for an increase in the mortality rate not for the existence of predation.

Weapon use (hitting and stabbing with a stick without releasing it) seems to be the only possibility left to the chimpanzees to cope effectively such a predator: By using constantly weapons during their preventive attacks, they could induce fear in the leopard that would start to apprehend them. It seems to me the safest way they have to harm an adult leopard. Tai chimpanzees do use weapons with leopards, as seen in example 2, but it is not clear if they could be able to kill or harm a

leopard with such a tool? As similar spontaneous weapon use has never been observed in another context (KORTLANDT, 1963, GOODALL, 1968, NISHIDA, 1968, 1979), it may well be a specific reaction of the chimpanzees when facing a powerful enemy.

The observations presented here show that predation is relevant to the evolution of fission-fusion grouping system in wild chimpanzees and that they are not protected by their physical size. The optimal group size theory, as a balance between a tendency to aggregate for enhanced safety from predators and territorial defense on one hand, and a tendency to disperse to allow sufficient access to food to all group members (van SCHAIK & van HOOFF, 1983; TERBORGH & JANSON, 1986), may apply lo Tai chimpanzee grouping patterns. Party size and type vary with food availability but in case of food shortage decrease of party size- and variations of party types seem to be constrained by predation pressure (Tai party types in periods of food shortage [Table 1, column b] have more all-male parties than average types in Gombe [Table 2] [x^2 = 15.81, partitioning procedure; male-female parties p<0.001), all-male parties p<0.05] and party size remains bigger [x^2 = 14.86, df=5, p<0.05]).

When comparing common and pygmy chimpanzees much attention has been paid to specific differences (FURUICHI, 1989; NISHIDA & HIRAIWA, 1987; WHITE, 1988). In the light of our analysis, these could be presented as ecological differences: party size and predominance of mixed parties tend to be similar in the two species living in a rainforest habitat. Much emphasis has also been given to differences in female behaviour: common chimpanzee females were thought to be more solitary, ranging over smaller areas than males and lacking affiliative behaviour with other females, whereas pygmy chimpanzee females were the complete opposite (BADRIAN & BADRIAN, 1984; NISHIDA & HIRAIWA, 1987; WRANGHAM, 1986; WHITE, 1988). If grouping patterns are affected by the environment and the predation pressure, we should expect the relations of the sexes toward sociality to be influenced as well. For example, Tai female chimpanzees range extensively over the whole territory like males (irrespective of their oestrous cycle), as group size includes on average 72% of the community members and the sex ratio varies between 3 and 4 in favour of adult females. As females spend more time together, affiliative behaviour develop: *e.g.* 17 out of the 24 adult females

----

') Frequency of male-female parties are a direct representation of the rcproductive status of the females, the more of them have young offspring, the less male-female parties are seen, and this is not an adaptation of the chimpanzees lo predation pressure.

present in 1987 had at least one stable adult female associate with whom they shared food and formed coalitions to support each other in various contexts. These female friendships last for many years and so far we observed that only death of one of the partners put an end to it. Mother-daughter or sister-sister relationships do not explain most of them, as female migration is very important in Tai (out of 14 adolescent females in our study community, 5 emigrated and 8 immigrated). Similarly, females play an active role in assistance behaviour to other group members (see example 3). The social system of Tai chimpanzees, unlike the male-bonded system described for common chimpanzees from the wooded savanna (WRANGHAM, 1986), displays a more cohesive-fission-fusion system implicating both males and females. This system shows some parallels with the bonobos' social system.

The Tai chimpanzees social system probably evoked under high predation and territorial pressure, whereas common chimpanzees of the savanna may have been less constrained by predation pressure. Fission-fusion grouping system in primates may reflect an adaptation to both predation and exploitation of food resources. However, in arboreal monkeys possessing this social structure, predation still needs to be observed (CHAPMAN, 1990; van ROOSMALEN, 1984; TERBORGH &JANSON, 1986; SYMINGTON, 1988).

Summary

During a 5-year period, 29 interactions between chimpanzees and leopards have been observed or inferred in the tropical rainforest of the Tai National Park, Côte d'lvoire. Chimpanzees chased away leopards in 9 cases, rescued alarm calling chimpanzees in 11 cases (m 4 of these footprints or growls of leopards were noted), 9 times leopards attacked chimpanzees, injuring 6 of them and killing 4. Two of the hitters were most certain eaten by the leopard later. Predation by leopards is estimated to be the first cause of mortality in the Tai chimpanzees and individual chimpanzees may experience a risk of predatory attack of 0.30 per year and a mortality risk of 0.055 per year. Tai chimpanzees adapt specifically their grouping patterns to food availability and to predation: with abundant food and low predation, party size increases and mixed parties are more frequent, whereas with the same food condition but with hjgh predation, party size decreased and all-male party types increase. Comparisons with data on grouping patterns from Gombe and Mahale chimpanzees living in more open habitats support the hypothesis that this species adapts itself to leopard predation which is known to be lower in savanna habitats. The grouping patterns of the bonobo in I.omako forest seem more similar to Tai than to Gombe or Mahale chimpanzees, suggesting an analogous adaptation to high predation pressure.

References

BADRIAN, A. & BADRIAN, N. (1984). Social organisation of *Pan panuai* in (he I.omako Forest. Zaire. — In: The pygmy chimpanzee (R. L. SUSSMAN. ed.). Plenum Press. New York, p. 325-346.

BARTON, M. (1990). Chimpanzees at tea parties. — BBC", Wildlife 8. p. 720.

BERTRAM, B. C. R. (1978). Living in groups: Predators and prey. — In: Behavioural ecology: an evolutionary approach (J. R. KREBS & N. B. DAVIES, eds). Sinauer, Sunderland, Mass., p. 64-96

BOESCH, C. & BOKSCH, H. (198.i). Optimization of nut-cracking with natural hammers by wild chimpanzees.—Behaviour 83, p. 265-286.

----- & -------- (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. — J. Hum. Evol. 13, p. 415-440.

----- & -------- (1989). Hunting behavior of wild chimpanzees in the Tai National Park. — Am. J. Phys. Anthropol. 78, p. 547-573.

CHAPMAN. C. A. (1990). Association patterns of spider monkeys: the influence of ecology and sex on social organization. —Behav. Ecol. Sociobiol. 26, p. 409-414.

CHENEY, D. & WRANGHAM. R. W. (1987). Predation. — In: Primate societies (B. SMUTS. D. CHF.NF.Y, R. SEYFARTH, R. WRANGHAM & T. STRUHSAKER, eds). Univ. Chicago Press, Chicago, p. 227-39.

DEHN, M. (1990). Vigilance for predators: detection and dilution effects. — Behav. Ecol. Sociobiol. 26, p. 337-342.

DORAN, D. (1989). The comparative positional behavior of pvgmy *(Pan panisuis)* and common *(Pan troglodytes)* chimpanzees. — Ph.D. thesis. Univ. of Stony Brook, New York.

DUNBAR, R. (1988). Primate social systems. — Cornell University Press, New York.

FURICHI, T. (1989). Social interactions and the life history of female *Pan paniscus* in Wamba. Zaire. — Int. J. Primatol. 10, p. 173-197.

GANDINI, G. & BALDWIN, P. J. (1978). An encounter between chimpanzees and a leopard in Senegal.— Carnivore 1. p. 107-109.

GOODALL, J. (1968). Behaviour of free-living chimpanzees of the Gombe Stream area. — Anim. Behav. Monogr. 1, p. 163-311.

----(1986). The chimpanzees of Gombe: Patterns of behavior. — The Belknap Press of Harvard University Press. Cambridge.

HAMILTON, W. D. (1971). Geometry for the selfish herd. — J. Theor. Biol. 7, p. 295-311.

HIRAIWA-HASEGAWA, M., BYRNE, R. W.. TAKASAKI, H. & BYRNE, J. M. E. (1986). Aggression toward large carnivore by wild chimpanzees of Mahale Mountains National Park, Tanzania. — Folia primatol. 47. p. 8-13.

HOPPE-DOMINIK, B. (1984). Etude du spectre des proies de la panthere. *panthera pmdus,* dans le Pare National de Tai and Cote d'lvoire. — Mammalia 48, p. 477-487

IHOBE. H. (1990). Interspecific interactions between pvgmy chimpanzees *(Pan paniscus)* and red colobus *(Colobus badius).* — Primates 31, p. 109-112. I/AWA, K. &

IZAWA, K. & ITANI (1966). Chimpanzees in Kasakati Basin. Tanganyika (l). Ecological study in the rainy season 1963-1964. — Kyoto Univ. Afr. Stud. 1. p. 73-156.

KILTIE, R. A. (1980). Application of search theory to the analysis of prey aggregation as an antipredation tactic.— J. Theor. Biol. 87, p. 201-206.

KORTLANDT, A. (1963). Bipedal armed fighting in chimpanzees. — Proc. 16th Int. .Cong. Zool. .3. p. 64.

KUMMER. H. (1971). Primate societies. — Aldine, Chicago.

----- , BANAJA, A., ABO-KHATWA, A. & GHANDOUR. A. (1985). Differences in social behaviour between Ethiopian and Arabian hamadrvas baboons. — Folia primatol. 45, p. 1-8.

KURODA, S. (1979). Grouping of the pygmy chimpanzee. — Primates 20, p. 161-183.

MYERS, N. (1976). The leopard *Panthera pardux* in Africa.   —   IUCN Monograph 5, Morges.

NISHIDA, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. — Primates 9, p. 167-224.

----- (1979). The social structure of chimpanzees of the Mahale Mountains. — In: The great apes (D. A. HAMBURG & E. R. MCCOWN, eds). Benjamin/Cummings, Menlo Park, p. 73-122.

---- & HIRAIWA-HASEGAWA, M. (1987). Chimpanzees and bonobos: Cooperative rela tionships among males. — In: Primate societies (B. SMUTS *et al.*, eds). Univ. Chicago Press, Chicago, p. 165-177.

PULLIAM, H. R. & CARACO, T. (1984). Living in groups: Is there an optimal group size? — In: Behavioural ecology: an evolutionary approach (J. R. KREBS & N. B. DAVIS, eds). Blackwcll Science, London, p. 122-147.

ROOSMALEN, M. G. M. van (1980). Habitat preferences, diet, feeding strategy and social organization of the black spider monkey *(Atelex pamxeux panixcus* Linnaeus. 1758) in Surinam. — Ph.D. thesis, University of Wageningen.

SCHAIK, C. P. van (1983). Why are diurnal primates living in groups? — Behaviour 87. p. 120-144.

---- & HOOFF, J. A. R. A. M. van (1983). On the ultimate causes of primate social systems. — Behaviour 85, p. 91-117.

SIEGEL, S. *&* CASTELLAN, N. (1988). Nonparametric statistics for the behavioral sciences. 2nd edition. — McGraw-Hill, New York.

STRUHSAKER, T. T. & LEAKEY, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. — Behav. Ecol. Sociobiol. 26, p. 435-443.

SUSMAN, R. L. (1979). Comparative and functional morphology of hominoid fingers. — Am. J. Phys. Anthropol. 50, p. 215-236.

SYMINGTON, M. MCFARLAND (1988). Food competition and foraging party size in the black spider monkey *(ateles paniscus chamek).* — Behaviour 105, p. 117-134.

TERBORGH, J. (1983). Five new world primates: A study in comparative ecology. — Princeton University Press, Princeton, N.J.

---- & JANSON, C. H. (1986). The socioecology of primate groups. — Ann. Rev. Ecol. Syst. 17, p. 111-135.

WHITE, F. (1988). Party composition and dynamics in *Pan pamxeux.* — In l. J. Primat. 9, p. 179-193.

WRANGHAM, R. W. (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. — Anim. Behav. 22, p. 83-93.

---- (1980). An ecological model of female-bonded primate groups. — Behaviour 75, p. 262-300.

---- (1986). Ecology and social relationship in two species of chimpanzee. - In: Ecological aspects of social evolution (D. I. RUBENSTEIN *&* R. W. WRANGHAM, eds). Princeton University Press,   New Jersey, p. 352-378.

Resume

Pendant une periode de 5 ans, 29 interactions entre les chimpanzés et les panthères ont été observées ou inférées dans la foret tropicale humide du Parc National de Tai. Côte d'lvoire. Les chimpanzés ont poursuivit les pantheres dans 9 cas, ont secouru des chimpanzés poussant des cris d'alarmes dans 11 cas (dans 4 de ces cas, des empreintes ou des grognements de panthères ont été constaté), 9 fois les panthères ont attaqués les chim-panzés, en blessant 6 et en tuant 4 d'entre eux. Deux de ces derniers ont certainement été mangé par la panthère plus tard. La predation par les panthères se revèle être la pre-mière cause de mortalité des chimpanzés de Tai et chaque individu endure un risque

d'attaque par Ies predateurs de 0.30 par an et un risque mortel de 0.055 par an. I.es chimpanzés de Tai adaptent specifiquernent la taille et le type des groupes à la disponibilité de la nourriture et a la predation: Pour une nourriture abondante et une faible prédation, la taille des sous-groupes augmentent et les sous-groupes mixtes sont Ies plus fréquents, alors que pour les même conditions de nourriture mais avec une forte prédation. la taille des sous-groupes diminuent et les sous-groupes de males augmentent. Lcs comparaisons avec les données sur Ies groupes de chimpanzés de Gombe et Mahale vivant dans des habitats plus ouverts supportent l'hypothèse que cette espèces s'adapte à la prédation par les panthères, qui sont connues pour être moins abondantes dans la savanne. La taille et le type des groupes des bonobos de la forêt de Lomako semblent plus similaire de ceux de Tai que de ceux des chimpanzés de Gombe ou de Mahale. suggérant une adaptation semblable à une forte pression des prédateurs.