

## Cooperative hunting in wild chimpanzees

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**Abstract.** A model for the evolution of cooperation shows that two conditions are necessary for cooperation to be stable: a hunting success rate that is low for single hunters and increases with group size, and a social mechanism limiting access to meat by non-hunters. Testing this model on Tai chimpanzees, *Pan troglodytes*, showed that (1) it pays for individuals to hunt in groups of three or four rather than alone or in pairs, and (2) cooperation is stable because hunters gain more at these group sizes than cheaters, owing to a meat-sharing pattern in which hunting, dominance and age, in that order, determine how much an individual gets. In addition, hunters provide cheaters (about 45% of the meat eaters) with the surplus they produce during the hunts. Thus, cooperation in Tai male chimpanzees is an evolutionarily stable strategy, and its success allows cheating to be an evolutionarily stable strategy for Tai female chimpanzees. In Gombe chimpanzees, cooperation is not stable, first, because hunting success is very high for single hunters, and second, because no social mechanism exists that limits access to meat by non-hunters. The analysis showed that some assumptions made when discussing cooperation in other social hunters might be wrong. This might downgrade our general perception of the importance of cooperation as an evolutionary cause of sociality.

Group hunting has been described in about 22 vertebrate species. In mammals, the most famous examples include hyaenas, *Crocuta crocuta* (Kruuk 1972; Mills 1990), lions, *Panthera leo* (Schaller 1972; Packer et al. 1990), wild dogs, *Lycaon pictus* (Estes & Goddard 1967; Fanshawe & FitzGibbon 1993), wolves, *Canis lupus* (Mech 1970) and chimpanzees, *Pan troglodytes* (Teleki 1973; Nishida et al. 1983; Goodall 1986; Boesch & Boesch 1989). The size of the hunting groups, hunting frequencies and successes vary between different populations of lions and chimpanzees; sharing tendencies of chimpanzees also vary (Schaller 1972; Van Orsdol 1984; Goodall 1986; Boesch & Boesch 1989; Uehara et al. 1992). Tai chimpanzees hunt systematically in groups (95% of hunts), and the individuals collaborate in two-thirds of all hunts, while Gombe chimpanzees hunt much less often in groups (12% of hunts) and have been seen to collaborate in only 7% of all hunts (Busse 1978; Goodall 1986; Boesch & Boesch 1989).

A game theoretical model of the evolution of cooperation in hunting has recently been proposed

(Packer 1988; Packer & Rutan 1988). This model considers four hunting strategies: 'solitary', when an individual always hunts alone; 'cooperator', when it always hunts with a companion; 'cheater', when it hunts only when alone and never when in groups; and 'scavenger', when it never hunts. The model also considers two meat-distribution patterns: no sharing (prey that is too small to be divided), and sharing for all group members (prey large enough to be divided). When meat is not shared, 'solitary' is the evolutionarily stable strategy (ESS): cooperators have to compensate for the cost of hunting although they eat only when they capture the prey, whereas cheaters that never hunt in groups never have access to meat. When meat is shared by all group members, cheater is always an ESS, since cheaters eat as much as cooperators without having the cost of the hunt. Cooperator has been proposed to be an ESS under this last condition, if 'the increased performance of cooperative pairs overcomes the two-fold disadvantage of dividing the prey in half' and 'if the hunting success of cooperative pairs is sufficiently greater than that of singletons to overcome the costs of participating in a cooperative

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hunt' (Packer & Ruttan 1988, pp. 167–168). Fulfilling these conditions would make the evolution of cooperation possible; however, for cooperation to be an ESS an additional condition is necessary, namely the ability to resist invasion by cheaters. Thus, we have to compare the meat intake of cheaters and cooperators for the same hunting group size. Packer & Ruttan failed to address this question. In their model under 'the sharing to all group members' pattern, cheaters and cooperators eat the same amount of meat and cooperation is not stable. Therefore, more conditions and meat-sharing patterns must be investigated to understand when cooperative hunting should evolve.

Sociality is proposed to precede cooperative hunting in species capturing a single prey (Packer & Ruttan 1988), as would be the case for most social carnivores and the chimpanzees. A recent analysis of lion grouping data in the Serengeti suggests that cooperative hunting may be a by-product of group living rather than the evolutionary force resulting in group living (Packer 1986; Packer & Ruttan 1988; Packer et al. 1990): group size seems to be determined by other factors, such as infant protection and territorial defence. However, this interpretation relies on some assumptions. First, tests of the hypotheses were done with foraging group size and not with actual hunting group size, for which data are not available (Packer et al. 1990). As non-hunting group members are known to be attracted by a successful hunt (Kruuk 1972; Lamprecht 1978; Packer 1986; Cooper 1990) or by motivated hunters before they start to hunt (personal observation), in these tests cheaters and hunters are treated alike and the discrepancy in group size may simply reflect the cheaters' ability to manipulate hunters. For example, in a population of spotted hyaenas, the hunting group size was close to the optimum group size for maximizing food intake, but the group size feeding on the meat was much larger because clan members converge on the kill (Cooper 1990). In other words, lions, like hyaenas, might hunt in optimal group sizes, but the additional individuals seen in the foraging groups are cheaters exploiting the situation. Second, data combine feeding on prey acquired either by scavenging or by hunting (Packer 1988; Packer et al. 1990), thereby testing foraging rather than hunting optimization. More detailed data are needed to test the possibility that hunting may be the driving force for sociality. Lastly, successful

hunters should be able to control their kill. Lions in Botswana may lose up to 20% of their prey to hyaenas, and these losses increase the smaller the group size (Cooper 1991). Thus, group size may be adapted to both hunting and controlling the prey.

I first present a model developed to understand the evolution of cooperation in hunting and then test it with data collected on wild chimpanzees living in the tropical rainforest of the Taï National Park, Côte d'Ivoire, as well as on those living in the savanna-woodlands of Gombe Stream National Park, Tanzania.

## METHODS

### The Study Communities

In September 1979, Hedwige Boesch and I began a study of the wild chimpanzees living in the Taï National Park, Côte d'Ivoire. We habituated one community to our presence without any artificial provisioning. Habituation was slow, but since March 1984, we have been able to follow all the males by sight and remain within their groups during their daily foraging. At the time of writing (February 1993), only a few shy females cannot be followed at a distance of 20 m for the whole day. In the present analysis, only hunts for 1987–1990 are considered, when the community included 60–70 members with seven or eight adult males.

All the hunt observations were made by myself to avoid the inevitable inconsistencies between observers when following a fast-moving group activity. During the hunting season (from September to November), I followed the keenest hunters, switching from one to the other according to my perception of their motivation to hunt in order to increase the chance of being with the hunters before a hunt started.

The Gombe chimpanzees, in Tanzania, have been studied since 1960 and are well habituated to human observers (see Goodall 1986). To investigate the cooperation of hunters, I spent 19 weeks (April to June 1990 and 1992) following the habituated chimpanzees of the Kasakela community in Gombe Stream National Park and recorded their hunting behaviour with the same methodology used for the Taï chimpanzees. This community included during the study period 32 chimpanzees with seven adult males. In addition, Jane Goodall gave me access to the Gombe predation files from 1970 to 1975, and I reanalysed

the hunts with the most details in the same way as Tai hunts. For both chimpanzee communities, only hunts on arboreal monkeys are considered.

### Costs and Benefit of Hunting

Once a hunt started, I recorded all movements of the males present and of any individual starting to hunt as well as the duration of their participation. To transform these observations into energy costs, I used the following estimations. First, Taylor & Rowntree (1973) measured the steady oxygen consumption of captive chimpanzees at various running velocities on a treadmill: for quadrupedal running, the energy expenditure equals  $(0.25 \text{ ml O}_2/\text{kg}/\text{km}) + (0.79 \text{ ml O}_2/\text{kg}/\text{h})$ . Thus for a chimpanzee of 40 kg walking at a speed of 4 km/h, this expenditure is 24 kJ/min, whereas for one running at 16 km/h, it is 64.5 kJ/min. Second, from human work physiology (Spitzer et al. 1982), I could estimate the supplementary work required when conditions are more natural than a treadmill: walking on a forest floor increases the energy expenditure by a factor of 1.50 over the treadmill data, whereas climbing a steep slope of 45° increases it by a factor of 10.18 (a figure I shall use as equivalent for climbing trees, because this is the closest figure I could find in the literature). Therefore, for a hunter that spends 60% of the hunting time running on the forest floor and 40% climbing in trees, the energy expenditure equals 156 kJ/min. This is an overestimate, because hunters do spend time watching colobus and other hunters. I intentionally overestimate this figure because of the uncertainties in applying data from the human physiology to chimpanzees and because such an overestimate makes the subsequent analysis more robust.

The benefit of the hunt consists in the amount of meat eaten. Once a capture was made, I recorded the size of the pieces of meat secured by an individual, the time I saw it eating meat, and all occurrences of sharing. As chimpanzees sometimes disperse once they have obtained a share, I either estimated how long they ate for from the size of the piece of meat they carried away based on previous observations with the same individual eating a similar piece of meat, or relied, in Tai, on H. Boesch's observations of some of the hunts.

To transform these figures into an energy benefit for each individual, I estimated the average time to eat 1 kg of meat as follows. First, I

determined the species and the age class of the prey caught by the chimpanzees as quickly as possible following the capture. I used estimated weight for *Colobus* and *Cercopithecus* species (Haltenorth & Diller 1977): infants of all species (*Cercopithecus diana* and *petaurista*, *Colobus badius*, *polykomos* and *verus*, *Cercocebus atys*)=1 kg, adult *Cercopithecus* sp. and *Colobus verus*=4 kg, juvenile of *Colobus badius* and *polykomos*=3–6 kg, adolescent of *Colobus badius* and *polykomos*=9 kg, adult *Colobus badius*=13 kg and adult *Colobus polykomos*=18 kg. No juvenile *Cercopithecus* monkeys were captured. With these estimates, I could calculate the total amount of meat captured. Second, I recorded for how long each individual ate meat. From these two figures, the average time to eat 1 kg of meat equals 46.15 min. Using such a measure underestimates meat intake at the beginning of a meat-eating episode, when chimpanzees are very hungry and excited, and overestimates meat intake at the end of the meat-eating episode, when individuals are less hungry. However, it remains the best measure I could find, because it is unreliable to attempt to evaluate the amount of meat taken per mouthful.

Lastly, the meat intake of an individual was transformed into energy gain by using the energy value of bushmeat (4440 kJ/kg; Wu Leung 1968). This value was corrected for incomplete assimilation of the food because of incomplete resorption and the specific-dynamic action of the nutrients. In humans about 12% is lost in that way (Astrand & Rodahl 1977; Ulmer 1985), whereas in non-human animals, such as porcupines, *Hystrix indica*, the energy indigestibility can be as high as 80% (Alkon et al. 1986). I used the human figure because of the close physiological resemblance between these two species (same basal metabolic rate). From these calculations, each individual gained 3908 kJ per kg of meat eaten.

## RESULTS

### The Model

My model has the following characteristics.

(1) Two strategies are considered. A Hunter is an individual that hunts either alone or together with at least one other hunter for the same prey. A Cheater is an individual that takes part only in the meat-eating episode of a hunt and not in the hunt itself.

(2) The number of individuals taking part in the hunt is variable.

(3) The amount of meat eaten is the benefit of the hunt.

(4) All individuals, hunter or cheater, present during a meat-eating episode have access to the same amount of meat.

The benefit  $H$  to an individual taking part in a hunt depends on two factors:

$$H_i = W_{mi} - E_{hi}$$

where  $i$  = number of hunters,  $W_{mi}$  = average meat intake per individual (in kJ) and  $E_{hi}$  = cost of performing a hunt (in kJ).

The average meat intake per individual is:

$$W_{mi} = (W_{pi} \times S_i \times a) / \text{number of meat eaters}$$

where  $W_{pi}$  = energy value of the prey captured in kJ,  $S_i$  = average hunting success and  $a$  = digestibility of the meat.

Cheaters have no costs as they never hunt ( $E_{hi} = 0$ ) and so  $H_{ci} > H_{hi}$  ( $H_{ci}$  is the net benefit per cheater and  $H_{hi}$  is the net benefit per hunter). However, in a group of pure cheaters no hunting occurs and cheater is, therefore, a conditional strategy dependent upon the presence of at least one hunter.

Thus, the questions we have to ask are (1) when should a single individual hunt (evolution of hunting), (2) when should an individual join other hunter(s) (evolution of cooperation) and (3) when should an individual remain a cheater while a hunt is performed by others (stability of cooperation). The last two questions are intermingled but the first has to be answered before resolving the others.

#### Evolution of hunting

For single individuals it pays to hunt when the meat intake is larger than the energy spent hunting:

$$W_{mi} > E_{hi}$$

The costs of hunting include not only the energy required to capture and kill the prey, but also the possible risk of injuries or illness contracted from the prey, which can be evaluated only through long-term observations. If the latter exists, hunting may rapidly become too risky. Several factors could negatively influence hunting alone; these include decreasing prey weight and increasing

difficulty in capturing a prey. Cheaters could also keep hunting from being stable, if they deprive hunters of their capture before they can eat (Strum 1981).

#### Evolution of cooperation

For single hunters it pays to act in groups when the benefit of hunting increases enough so that

$$H_{(1+n)} > H_1$$

or

$$W_{m(1+n)} - E_{h(1+n)} > W_{m1} - E_{h1}$$

For the sake of simplicity, I first assume that the cost of performing a hunt ( $E_{hi}$ ) remains constant, independent of  $i$ , and the last equation can be simplified as

$$W_{m(1+n)} > W_{m1}$$

This is true when

$$W_{p(1+n)} \times S_{(1+n)} / (1+n) > W_{p1} \times S_1 \quad (1)$$

For specialized hunters (which hunt only a few prey species), the weight of the prey ( $W_{pi}$ ) can be increased only marginally. Thus, the hunting success of single hunters ( $S_1$ ) should be smaller than that of hunters in larger groups divided by the number of hunters

$$S_{(1+n)} / (1+n) > S_1 / 1 \quad (2)$$

for cooperation to evolve. The lower the hunting success of single hunters ( $S_1$ ), the larger can be the increase for group hunters. Group size will be limited to  $1/S_1$  (1 is when all hunts are successful).

For generalized hunters, the weight of the prey,  $W_{pi}$ , will be constrained by the richness of the habitat, so that generalized hunters in poor habitats (with few prey species) will have a similar situation as the specialized hunters, as they cannot easily find prey big enough to increase  $W_{pi}$ . In rich habitats, however, equation (1) applies for cooperation to appear. The higher  $S_1$  and/or the larger  $W_{p1}$ , the less likely it is that cooperation will evolve.

If the assumption that  $E_{hi}$  remains constant is wrong, and an increase in  $E_{hi}$  with more hunters (interference between hunters) is observed, then the conditions of equations (1) and (2) would be more rarely observed and cooperation accordingly rarer. If the opposite is true and  $E_{hi}$  decreases with additional hunters (synergism between the hunters), then cooperation would evolve more easily.

In conclusion, cooperation will evolve if hunting success increases with the number of hunters and this will be easier when hunting success is low and prey size is small for single hunters; however, these two factors have to be large enough to make the evolution of hunting possible at all. For generalized hunters, cooperation should evolve more frequently than in specialized ones. Switching to larger prey species when in larger groups is expected as a method of increasing  $W_{pi}$  (e.g. including large prey too difficult for a single hunter, like zebra hunted by hyaenas: Kruuk 1972).

#### Stability of cooperation

Once cooperation has evolved, it can be susceptible to cheating, for individuals may be tempted to benefit from hunting without paying the cost. This may result in the disappearance of cooperation. It pays for an individual to become a cheater when the benefit gained from hunting for cheaters ( $H_{ci}$ ) is larger than that of hunters ( $H_{hi}$ ).

$$H_{ci} > H_{hi} \quad (3)$$

or

$$W_{ci} > W_{hi} - E_{hi} \quad (4)$$

and as  $W_{ci} = W_{hi} = W_{mi}$  under our assumption, equation (3) is always true and cooperation will not be stable.

At this point, we should ask how a group of hunters could keep cheaters from invading. In other words, how could cooperation still be evolutionarily stable despite the presence of cheaters?

Because hunting costs are always present, the answer is, when

$$W_{ci} < W_{hi} - E_{hi}$$

One way to achieve such a situation is through a social mechanism that limits the cheaters' share: unequal meat distribution between group members according to their behaviour during the hunt could lead to such a difference, for then hunters eat more than cheaters and group hunters eat more than single hunters if hunting success increases with group size.

In most social groups, group members are to some degree related and kinship is expected to have two distinct effects on cooperation. First, related hunters will cooperate with smaller reward than unrelated hunters, i.e. they will cooperate with a smaller increase in hunting

success ( $S_1$  can be higher) and in larger groups. Second, hunters will be more tolerant with related cheaters. This could lead to stable cooperation of only kin even if cheaters are as successful as hunters.

In conclusion, once cooperation has evolved it can be stable despite the presence of cheaters as long as a social mechanism prevents them from getting more than the net benefit of hunters. In addition, the longer and harder a hunt, the less cheaters should be allowed to eat, and this effect will be stronger for unrelated cheaters.

This model is now tested with data from Tai and then from Gombe chimpanzees.

#### Cooperation in Tai chimpanzees

##### Evolution of hunting

For a single individual, a capture has to be achieved within 25 min per kg of meat for hunting to be profitable: the gain of 3908 kJ provided by 1 kg of meat will disappear after 25 min of hunting at 156 kJ/min (see Methods for details). In Tai, single chimpanzees hunted on average for 5.2 min with a hunting success of 13.3%, thus achieving a capture after only 39 min (Table I). However, as the prey weighs on average 9.5 kg, it pays for single chimpanzees to hunt, since they gain 794 kJ per min of hunting.

This positive margin for stable hunting would quickly vanish if the weight of the captured prey fell below 1.5 kg. Similarly, the data of Tai chimpanzees are from experienced social hunters, which should have more success than naive hunters.

##### Evolution of cooperation

Tai chimpanzees' hunting success is related to the number of hunters (Table I:  $r_s = 0.78$ ,  $N = 7$ ,  $P = 0.054$ ), and the increase in the hunting success of larger groups is more than additive (chi-squared of fit for one to five hunters,  $\chi^2 = 9.95$ ,  $df = 4$ ,  $P < 0.05$ ). This indicates a synergism between the individual hunters, which probably results from the better organization of the individuals when hunting in larger groups (frequency of collaborative hunts versus hunting group size (see Boesch & Boesch 1989 for definition of collaboration),  $r_s = 0.99$ ,  $N = 7$ ,  $P < 0.02$ ). In addition, the meat return per hunt shows a positive

**Table 1.** Different measurements of hunting success in Tai chimpanzees during 1987–1990 (only hunts during which the chimpanzees were followed before they started to hunt and until they had consumed all the meat, if successful, are included)

Number of hunters	Number of hunts	Hunting success (%)	Meat per hunt (kg)	Hunting time (min)	Net benefit per hunter (kJ)
1	30	13	1.23	5.20	4015
2	34	29	0.82	4.59	1250
3	39	49	3.12	4.91	3804
4	25	72	5.47	4.63	5166
5	12	75	4.65	5.21	3472
6	12	42	3.17	8.19	1851
>6	10	90	9.27	6.98	5020
Total	162	74			

The net benefit per hunter is estimated under the assumption that all hunters have equal access to meat.

correlation with increasing group size, with two maxima at four and at more than six hunters (Table 1:  $r_s = 0.82$ ,  $N = 7$ ,  $P < 0.05$ ). All measures of hunting success in Tai chimpanzees show an increase with larger hunting group sizes, which favours the evolution of cooperation.

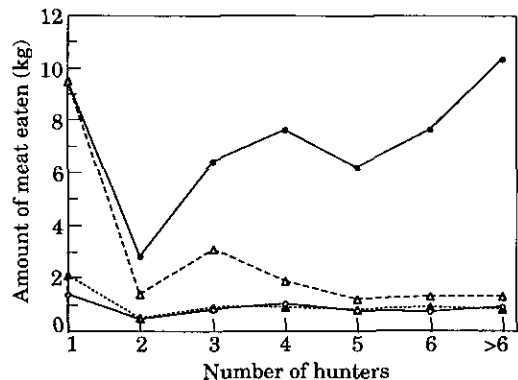
This is not, however, enough to account for the evolution of cooperation. I assume here that the population includes only hunters that share equally between themselves as was the case in the model. Table 1 shows the net benefit per hunter in Tai chimpanzees; cooperation in hunting should evolve and favour groups of four hunters.

#### Stability of cooperation

Once cooperation has evolved, cheaters having the same access to meat as hunters might invade the Tai chimpanzee community. Does a social mechanism in Tai chimpanzees limit the success of cheaters? If it does, is it strong enough to make cooperation stable?

Figure 1 compares the observed amount of meat eaten by Tai chimpanzees with that predicted by three patterns of meat sharing. Tai observations do not differ from the predictions of the 'equal sharing between all group members' pattern (Mann-Whitney  $U$ -test,  $N_1 = N_2 = 7$ ,  $P > 0.05$ ; for the comparisons with the two other patterns of meat sharing,  $P < 0.02$ ). No social mechanism is obvious at this stage; however, before drawing any conclusion, one must see if the average values in Fig. 1 are equally distributed among group members.

To check for this, I differentiate between the proportions of hunters and bystanders, equivalent to cheaters in Tai chimpanzees as they are present during the hunt but do not take part in it, that were seen eating once a capture was achieved (Table 2). Bystanders were present at most kill sites but their number tended to decrease, although not significantly so, as the number of hunters increased ( $r_s = -0.1$ ,  $N = 7$ ,  $P > 0.05$ , but for one to six hunters:  $r_s = -0.79$ ,  $N = 6$ ,  $P = 0.07$ ). Their success in eating a piece of meat tended to be slightly superior to that of hunters although again not significantly so ( $P > 0.05$ ). Cheaters in Tai chimpanzees represent 47% of the meat-eaters and have good access to meat. Thus, the social



**Figure 1.** Comparison of the observed (○) individual meat consumption for all members of the Tai chimpanzee community with the predictions of three meat distribution patterns. ●: No sharing; △: equal sharing for all hunters; ▲: equal sharing for all group members.

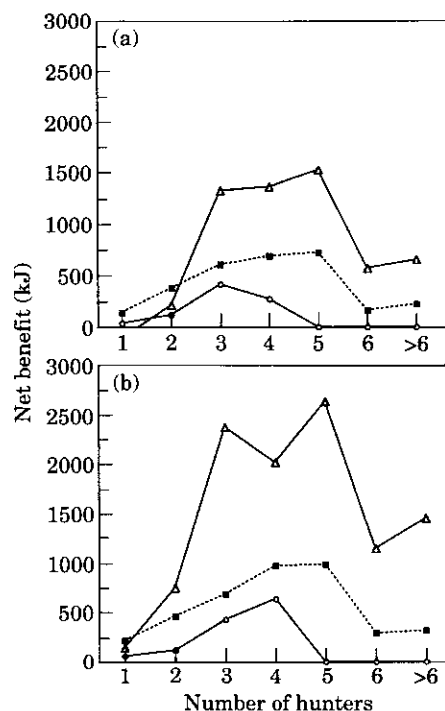
**Table II.** Success of hunters and bystanders in obtaining meat from captures between 1987 and 1990 in the Tai chimpanzee community

	Number of hunters		Number of bystanders	
	Hunting	Eating	Present	Eating
1		0.7	3.5	3.0
2		1.6	3.6	2.6
3		2.5	3.6	3.0
4		2.5	2.7	2.1
5		3.5	2.7	2.3
6		4.7	2.4	2.2
7-7		6.2	4.9	4.2
Total	28.7	21.7	23.4	19.4
Percentage of:	Hunters eating 75.6%		Bystanders eating 82.9%	

mechanism, if it exists, does not limit the access to meat of cheaters per se.

The critical test, however, for the stability of cooperation is the net benefit ( $W_{hi} - E_{hi}$ ) per individual. One possible social mechanism is uneven food distribution between group members according to their contribution during the hunt. This implies individual recognition, and therefore the analysis should be done at the individual level. Figure 2 presents the pay-off of three strategies seen adopted by the adult males in Tai; 'hunter' as defined in the model, and two cheating strategies; 'bystander' which is an individual present in the group during a hunt but which does not actively take part in it and 'latecomer' which is an individual absent from the group during a hunt but which joins it after a capture has been achieved. I limit myself here to the adult males, for which I have the most detailed data, as they represent about 90% of the hunters at Tai (see below).

Being a hunter is a superior strategy over latecomer for all group sizes larger than two (Wilcoxon signed-rank test comparing for each individual male's net benefit for the two different strategies considered for each hunting group size:  $T+ \geq 31$ ,  $N=8$ ,  $P<0.05$ ), whereas the large individual variations keep the trend favouring hunter over bystander from becoming significant (Fig. 2a). Thus, although being a latecomer is not a good strategy, cooperation is not stable, as



**Figure 2.** Net benefit of three strategies for Tai male chimpanzees when hunting red colobus monkeys taking into account either (a) only the amount of meat eaten by each individual, or (b) both the amount eaten by them and the amount that they have shared with other group members.  $\Delta$ : Hunter;  $\blacksquare$ : bystander;  $\circ$ : latecomer.

bystanders have pay-offs similar to hunters. By considering only the amount of meat eaten, however, we underestimate the true success of the individuals, because part of the secured meat is shared with other group members. On average, hunters share 45% of their part with other group members, while bystanders share only 15%. Thus, meat sharing is very important and not including it in this analysis penalizes hunters. If we do the same comparison by including the meat that individuals share with group members (Fig. 2b), hunter is a better strategy than bystander for groups of three and four hunters (Wilcoxon signed-rank test for group size 3:  $T+ = 32$ ,  $N=8$ ,  $P<0.05$ ; group size 4:  $T+ = 31$ ,  $N=8$ ,  $P<0.05$ ) and better than latecomer for most groups larger than two hunters (Wilcoxon signed-rank test for group size over 2:  $T+ \geq 30$ ,  $N=8$ ,  $P<0.05$ ; except for six hunters where  $T+ = 29$ ,  $P=0.07$ ). Thus, a social

**Table III.** Net benefit (kJ), including meat shared by owners, for the adult males of the Tai chimpanzee community depending on their strategies during hunts in 1987–1990 and the effective time they were seen hunting per hunt

Name of adult male	Hunter	Bystander	Latecomer	Hunting time (min)	Age	Dominance
Brutus	3830	1863	597	5.3	1951	3.4
Macho	2529	1185	67	5.5	1964	1.8
Ulysse	2014	762	130	8.8	1967	3.3
Kendo	1718	169	61	3.1	1969	2.0
Rousseau	1457	931	324	2.6	1966	5.0
Snoopy*	1078	169	22	7.2	1971	6.0
Fitz†	791	762	225	4.7	1975	5.8
Darwin	686	1185	8	3.2	1970	6.0

For age the estimated year of birth is given and for dominance the average year dominance rank for this 4-year period.

\*Snoopy disappeared at the end of the 1987 hunting season.

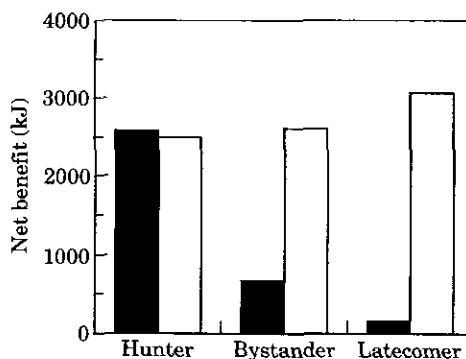
†Fitz was considered as adult only for the 1990 hunting season.

mechanism regulating access to meat to the individuals does exist, but it is more complex than that previously considered, because it represents a graded response of the group, not a discrete one, and it is partly hidden by the fact that meat owners share part of their take. This social mechanism makes cooperation stable in Tai adult male chimpanzees.

Why do so many individuals cheat and why are they so readily accepted by hunters? All male hunters use a mixed strategy, as they are sometimes bystanders and latecomers, but they have access to less meat when they do not hunt (Wilcoxon signed-ranks test: hunter versus bystander:  $T+=34$ ,  $N=8$ ,  $P<0.02$ ; hunter versus latercomer:  $T+=36$ ,  $N=8$ ,  $P<0.01$ ; Table III). Thus, participation in the hunt is the prime factor affecting access to meat in males. For a given strategy, however, access to meat is quite different for each male (see Table III), and at least one other factor must explain this. I consider three: hunting time, age and dominance. The amount of meat eaten by each hunter shows a significant correlation with age (Spearman rank-order correlation coefficient;  $r_s=0.90$ ,  $N=8$ ,  $P<0.02$ ) and dominance ( $r_s=0.75$ ,  $N=8$ ,  $P<0.05$ ) but not with hunting time ( $r_s=0.30$ ,  $N=8$ ,  $P>0.05$ ). As the correlation between age and dominance is not significant ( $r_s=0.63$ ,  $N=8$ ,  $P>0.05$ ), both age and dominance contribute to the hunters' access to meat, but the data indicate that dominance is more important than age (Table III): old dominant hunters gain more meat than young dominant hunters, which have

more meat than old subdominant hunters. For the two other strategies, bystander and latecomer, neither age nor dominance correlates with the amount of meat eaten by the males ( $P>0.05$ ).

In addition to non-hunting males, adult females are tolerated as cheaters by the hunters. Figure 3 compares the pay-offs for adult males and adult females according to the strategy performed: females have very good access to meat, and this is independent of the strategies they use (Mann-Whitney  $U$ -test: hunters,  $N=16$ ; bystanders,  $N=15$ ; latecomers,  $N=18$ ,  $P>0.05$ ). This situation is quite different from the males: for both cheater types (bystander and latecomer) females receive significantly more meat than males (Mann-Whitney  $U$ -test: bystander:



**Figure 3.** Males' (■) and females' (□) net benefit according to their contribution during the hunt on colobus monkeys by Tai chimpanzees in 1987–1990.



**Table IV.** Frequency of use of the different strategies by the males and females of the Tai chimpanzee community during hunts in 1987–1990

	Hunter	Bystander	Latecomer
Males	372	305	420
Females	37	89	129

$z = -3.39$ ,  $N=15$  females, 8 males,  $P < 0.001$ ; latecomer:  $z = -3.9$ ,  $N=18$  females, 8 males,  $P < 0.001$ ). This is surprising, since females hunt much less than males (hunter versus bystander+latecomer:  $\chi^2=39.47$ ,  $df=1$ ,  $P < 0.001$ ; Table IV) and seem to specialize in cheating. Meat is shared first by the male hunters, and they favour females without any reciprocity during the hunts. Males may trade meat with the females for other privileges.

Qualitative observations show that sharing clusters are fairly predictable and that certain females always beg meat from the same male meat-owners (see Teleki 1973). This supports the idea of long-term affiliation between males and females within which such a trade could happen (Boesch 1991). During social fights, support of males by females belonging to their sharing clusters is regularly seen and indicates how such a trade-off may work.

### Cooperation in Gombe Chimpanzees

A previous comparison of the hunting performances of Gombe chimpanzees with Tai chimpanzees revealed that cooperation is much more common in the latter (Boesch & Boesch 1989). This raises two questions: are the conditions for the evolution of cooperation fulfilled for the Gombe chimpanzees and if yes, are cheaters more successful at Gombe than at Tai?

To answer these questions, I analysed the hunting data of the chimpanzees from 1973 to 1975 collected by the collaborators of the Gombe Stream Research Center (Busse used those of 1973 and 1974 for his analysis (1977, 1978)) as well as those I collected myself during 19 weeks in April, May and June 1990 and 1992. I analysed only hunts on red colobus monkeys, *Colobus badius*, for which the number of hunters and bystanders were known, as well as the size of the captured prey (45 hunts in 1973–1975

and 17 in 1990–1992 fulfilled these criteria). As data collected on hunting at Gombe after 1975 were generally less detailed, I did not include them.

### Evolution of hunting

As shown previously, a single chimpanzee should capture 1 kg of meat per 25 min for a hunt to be profitable. Single Gombe chimpanzees hunted on average for 3.6 min with a hunting success of 50%, thus achieving a capture after only 7.2 min (Table V). As they captured on average prey of 2.46 kg, it pays for single Gombe chimpanzees to hunt, since they gain 1179 kJ per min of hunt.

Gombe chimpanzees gain 50% more per min while hunting than Tai chimpanzees, as single hunters achieve a capture five times quicker than in the Tai forest. Tai chimpanzees are able to compensate for the longer hunting time only partly by capturing prey 3.9 times larger.

### Evolution of cooperation

The hunting success of Gombe chimpanzees is high for single hunters, and there is no correlation between hunting success and number of hunters (Spearman rank correlation coefficient:  $r_s=0.26$ ,  $N=6$ ,  $P=0.55$ ; Table V). Similarly, the meat return per hunt remains fairly stable and shows no correlation with the number of hunters ( $P > 0.05$ ; Table V). Such conditions are not favourable for the evolution of cooperation.

The evaluation of the net benefit ( $W_{mi} - E_{hi}$ ) per hunter for different hunting group sizes was made in the same way as for the Tai chimpanzees, since my observations in Gombe were too limited to produce reliable figures for the time to eat 1 kg of meat. The Tai estimation overestimates the meat consumption at Gombe, because there are indications that Tai chimpanzees eat meat at least twice as quickly as Gombe chimpanzees (Boesch & Boesch 1989). This does not affect the comparison between different group sizes within Gombe chimpanzees but should be remembered when comparing them with Tai chimpanzees. An intriguing aspect of Gombe hunting is that colobus prey are often only partially eaten: of the six adult colobus killed, the chimpanzees did not touch two of them, ate only the viscera of two others, ate in addition

**Table V.** Data on Gombe chimpanzee hunts on red colobus from 1973 to 1975 analysed from the Gombe Stream predation files (45 hunts), as well as my observations of 19 weeks in 1990 and 1992 (17 hunts)

Number of hunters	Number of hunts	Hunting success (%)	Meat per hunt (kg)	Hunting time (min)	Net benefit per hunter (kJ)
1	30	50	1.23	3.6	4245
2	13	61	1.85	5.3	3201
3	9	78	1.61	5.0	1837
4	7	100	2.86	7.7	2494
5	1	100	3.00	5.0	2189
6	2	50	2.00	17.0	861
Total	62	39			

The net benefit per hunter is estimated under the assumption that all hunters have equal access to meat.

one arm of the fifth and ate wholly only the last one. Thus, the gain in weight that chimpanzees might achieve by capturing bigger prey when hunting in larger groups (five of the six adult monkeys were caught in group hunts) is counter-balanced by their lack of interest in a large portion of this gain. Cooperation is not expected to develop in Gombe chimpanzees because single hunters always have a larger net benefit than group hunters (Table V).

#### *Stability of cooperation*

As at Tai, Gombe chimpanzees may have adopted a meat distribution pattern that would make cooperation stable by diminishing the net benefit of single hunters and cheaters. Such an analysis could be done only with the 1990–1992 data, but as this sample is limited ( $N=17$  hunts), I also examined the larger set of data for corroboration of the results of this analysis.

For adult males (Fig. 4), the situation at Gombe is very different to that at Tai (Fig. 2): at Gombe, for all group sizes bystanders tend to gain more than hunters, except for three hunters, but not significantly so (Wilcoxon signed-rank test comparing individual male pay-off for each strategy depending on the number of hunters:  $P>0.05$ ). As at Tai, meat sharing may affect this comparison; however, hunters and bystanders share with others about the same amount of their meat (9% and 12%, respectively). Repeating the previous comparison with the meat shared does not alter the results except that the trend in favour of bystanders becomes significant for groups of five

hunters (Wilcoxon signed-rank test:  $T+=30$ ,  $N=8$ ,  $P<0.05$ ; Fig. 4b). Access to meat does not depend on participation in the hunt and cooperation cannot be stable.

After searching for a factor affecting access to meat, I conclude that neither age, dominance nor hunting time correlates with access to meat, except for hunters that gain more meat from shorter hunts (Spearman rank correlation coefficient:  $r_s = -0.78$ ,  $N=8$ ,  $P<0.04$ ; Table VI). The longer a hunt lasts, the more chimpanzees may join the group and the greater the risk that hunters will lose meat to other group members. Only four of the eight males (Atlas, Frodo, Goblin and Prof) gained more meat when they hunted, whereas the others had more when they were bystanders. In addition, three males acquired 66% of the meat secured by the males: the alpha male (Wilkie) and the two oldest ones (Evered and Goblin) gained more than average (19, 20 and 27% of all males' meat intake, respectively).

Is the great success of bystanders corroborated by some observations from a larger data set? Of the 25 captures I observed at Gombe, 28% (7) of the prey were stolen by higher-ranking bystanders from the captor. From 1975 to 1981 (Goodall 1986), the three higher ranking males each stole 12.5–35% of the prey from lower ranking individuals. Long-term Gombe data confirm that participation in the hunt does not relate with access to meat (Goodall 1986), but that older males tend to be more successful in gaining meat than younger ones (Wrangham 1975; Busse 1977; Goodall 1986).

Gombe females do not have the same status as Tai females in terms of access to meat (Fig. 5):

**Table VI.** Net benefit (kJ), including meat shared by owners, for the adult males of the Gombe chimpanzee community depending on their strategies during hunts in 1990–1992 and the effective time they were seen hunting per hunt

Name of adult male	Hunter	Bystander	Hunting time (min)	Age	Dominance
Goblin	7621	7452	0*	1964	4
Evered	4755	6520	1	1952	7
Wilkie	4163	6436	1	1973	1
Atlas	3824	0	1	1967	8
Prof	2482	2371	2	1972	3
Freud	2072	3133	3	1971	2
Frodo	856	0	7	1976	5
Beethoven	548	3048	3	1969	6

For age the estimated year of birth is given and for dominance the average dominance rank.

\*In this sample, Goblin captured only colobus that fell from the trees as they were chased by other chimpanzees, while he followed the hunt from the ground.

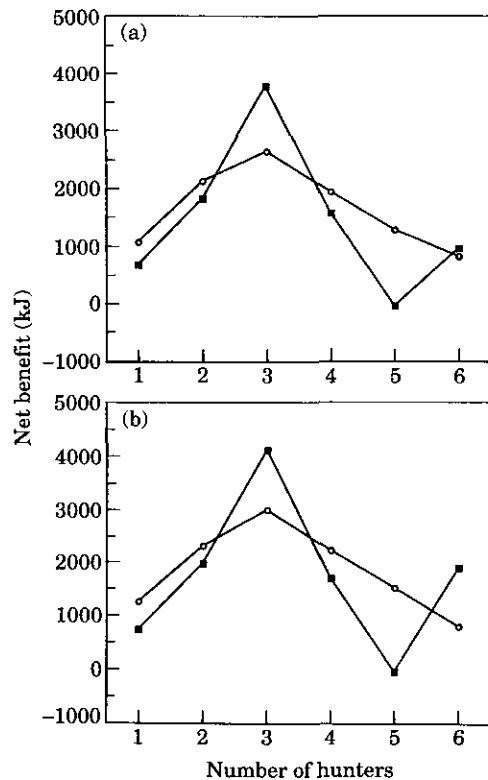
they gain more meat when they hunt than when they remain inactive during a hunt (Mann-Whitney  $U$ -test:  $U=0$ ,  $N_1=2$ ,  $N_2=8$ ,  $P<0.03$ ). In addition, their gains are similar to males when both hunt ( $P>0.05$ ), but female bystanders gain less than male bystanders (Mann-Whitney  $U$ -test:  $U=5$ ,  $N_1=6$ ,  $N_2=8$ ,  $P<0.01$ ).

Thus, at Gombe, male chimpanzees are better off remaining passive in a group where others are hunting. Nevertheless, Gombe chimpanzees hunt in groups in 52% of the cases (Table V). A precise look at the behaviour of the hunters may provide an explanation. Gombe chimpanzees, when hunting in groups, start to hunt on the same group of prey, but as a rule each follows a different target prey (Busse 1977; Goodall 1986; Boesch 1994), and they do not coordinate their movements. Thus, group hunting at Gombe is better described as simultaneous solitary hunts than true cooperation (see Boesch 1994 for a more detailed description of the Gombe hunting tactics). Single hunters profit from the confusion of the colobus that results from the other chimpanzees' hunting movements. Collaboration accounts for only 8% of the hunts at Gombe (Boesch 1994).

## DISCUSSION

### Evolution of Cooperation

The model predicts that cooperation will evolve under the following conditions: first, if hunting



**Figure 4.** Net benefit of two strategies in Gombe male chimpanzees when hunting red colobus monkeys, when taking into account either (a) only the amount of meat eaten by each individual, or (b) both the amount eaten by them and the amount that they have shared with other group members. ■: Hunter, ○: bystander.

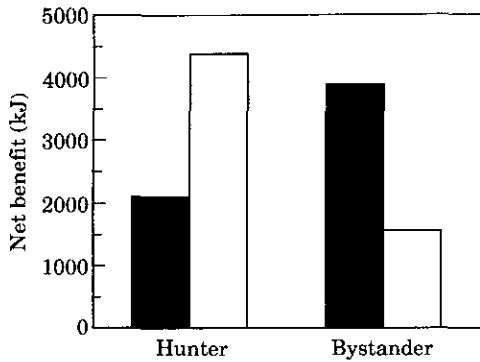


Figure 5. Males' (■) and females' (□) net benefit according to their contribution during the hunt on colobus monkeys by Gombe chimpanzees in spring 1990 and 1992.

success increases with the group size of the hunters; second, if the benefit of hunting for single hunters is small enough to allow the increased performance of group hunters to more than compensate for the costs of sharing the meat; third, if stability of cooperation is guaranteed by a social mechanism that regulates meat distribution so that cheaters obtain less meat than hunters. While the first two conditions have already been predicted (Packer & Ruttan 1988), the third is specific to this model.

In Tai chimpanzees, cooperation evolved because it pays for individuals to hunt in groups of three or four rather than to hunt alone or in pairs. Cooperation is stable because individuals gain more when hunting at these group sizes than by cheating, owing to a social mechanism that prevents male cheaters from gaining more meat from the hunt than male hunters. Moreover, hunters can afford to feed many cheaters (about 45% of the meat-eaters) on a stable basis with the benefit they produce through hunting. Thus, cooperation in Tai chimpanzees is an ESS, and its success allows cheating to be an ESS for another class of individuals, the adult females. Indeed, for mothers, hunting entails more than just energy costs, and this radically changes the analysis for them; infants are probably at risk of falling from high trees during the quick and acrobatic movements leading to a capture and of getting injured or killed. These additional risks for mothers probably suppress the benefit of hunter over bystander, so that cheating is the ESS for them.

The step-wise analysis I adopted shows that some common assumptions were false. First,

many authors have assumed that foraging group size correlates positively with hunting group size (Busse 1978; Packer et al. 1990), but, in Tai, the number of non-hunters (bystanders) tended to decrease as the number of hunters increased (Table II). Second, individual meat intake may not be equal for all group members and for all strategies: differentiation between the possible strategies is hampered either because individuals are not all identified (in some carnivore studies) or because visibility is too limited to allow detailed observations of all hunting individuals (i.e. hunting in vine tangle in Gombe chimpanzees (personal observation) and Mahale chimpanzees (Uehara et al. 1992), or hunting at night in lions (Packer 1988)). In the analysis of the lions' hunts, all females at a kill were assumed to have equal access to meat and all males twice that of the females (Packer et al. 1990). However, graded differences between individuals' meat intake might exist in lions which could be the result of pride members adopting mixed strategies, sometimes being cooperators and at other times cheaters (see Scheel & Packer 1991). Group size could maximize the net benefits of both hunter and cheater and not only the hunter's. This might account for the larger groups found in lions compared with the expectation of the hypothesis that only the hunters maximize feeding success.

Kinship may play a role in explaining the tolerance of the males towards other males. In chimpanzees, males are assumed to be more closely related than females because only females are known to transfer between communities, whereas males remain all their life in their natal communities (Goodall 1986; Nishida et al. 1990; Boesch 1991). If this assumption is true my model expects cooperation to be stable for a wider range of group sizes. Thus, both chimpanzees and lions may hunt in larger groups than predicted by the hunter-maximizing hypothesis. An illustration of a kinship effect is observed at Gombe: three of the rare cases of collaboration at Gombe (out of 58 group hunts) concerned brothers and one involved unrelated males (Busse 1977; personal observation).

True cooperation and group hunting have often been equated; however, a review of the data shows that the increase in hunting success is rarely additive with increasing group size (Packer & Ruttan 1988) as would be expected from cooperators. Such a synergistic increase seems clearly

supported only by Tai chimpanzees. The same seems to apply for true cooperation, with coordination of movements of all hunters, which is rare in social hunters and is observed in most hunts in Tai chimpanzees (Boesch & Boesch 1989). I propose that a synergistic increase in hunting success with group size is a sign of collaboration between hunters as defined in Boesch & Boesch (1989).

### Comparison of Tai and Gombe Chimpanzees

In Gombe chimpanzees, cooperation is not stable, first, because the hunting success of single hunters is very high and does not increase with the number of hunters and, second, because no social mechanism limits access to meat by non-hunters. The basic difference between Tai and Gombe chimpanzee hunts seems to lie in the hunting success of single hunters, which is an obstacle for the evolution of cooperation. Two factors may be important. First, the environment at Gombe is such that most hunts take place in woodlands where trees are between 8 and 15 m high. Therefore, the distance between the predator and the prey is so small that, once a hunt starts, in most cases the prey is caught within the first tree or one of the adjacent ones. Second, the red colobus at Gombe are not afraid of chimpanzees and tend to face and threaten them (Goodall 1986; Boesch 1994), and that gives the chimpanzees, when they occasionally intend to hunt, the necessary time to select their prey and the tree in which they want to attack. In contrast, in the Tai forest, colobus monkeys are mostly found in emergent trees (which are 45–55 m high), and when chimpanzees start to climb towards them, the monkeys have time to escape and keep their distance from the hunters. In addition, Tai red colobus are afraid of the chimpanzees and whenever they are aware of their presence, they become silent and again keep their distance (Boesch 1994).

How did these differences evolve? I propose that the Gombe technique is the primitive form of hunting in chimpanzees, mainly because the fearlessness of colobus in front of chimpanzees has been described for all long-term study sites where both species occur except Tai (Gombe: Goodall 1986; Kibale: R. W. Wrangham, unpublished data; Mahale: Uehara et al. 1992). Chimpanzees hunting with the Gombe technique in a high forest would be forced to hunt for larger prey to compensate for the longer time needed to achieve a

capture. The benefit of hunting alone would disappear if a capture required more than 25 min. This would already be the case if single Gombe chimpanzees had the same low hunting success as Tai single hunters (with 13% of successful single Tai hunts, they would need 28 min for a capture). Only the intentional selection of larger prey would make hunting profitable. This would increase the costs of predation for the red colobus which might react by becoming wary of the hunter's presence (Boesch 1994), which would in turn lower the chimpanzees' hunting success. In a further reaction of this arms race between chimpanzee and colobus, the former would have to coordinate their hunting techniques to overcome this difficulty and keep hunting profitable (Boesch 1994).

Tai coordinated hunters use two specific calls that have never been heard in Gombe chimpanzees (Goodall 1986; personal observation): first, a 'hunting bark', which indicates the hunters' location so that coordination of all movements is possible. It also attracts other chimpanzees to the hunting site. These hunting barks are quieter and have none of the aggressive tone of the 'waa bark' used in other contexts (Goodall 1986). Second, a very distinct 'capture call' is used that attracts all chimpanzees around the successful captor. This call is exclusively, but always, given when the prey is at least adolescent, since the hunt usually goes on if the prey is only an infant. This makes sense as small prey can hardly be shared, whereas larger ones are the centre of much attraction.

### Cooperation and Meat Sharing

Meat sharing is the key to the stability of cooperation; in Tai, hunters receive more meat than the others. This sharing rule is in conflict with the hierarchy order of the group, as dominance is only the second parameter ruling access to meat. Qualitative observations show that, when a large prey is subdued, all the chimpanzees scream with excitement, trying to reach it. During this excitement, dominant males may try to reach the prey by displaying against the males and some females that control meat access by allying themselves against these dominants. It took Brutus, one of the keenest hunters and the oldest and low-ranking male, rarely more than two displays before he joined the meat eaters, whereas Kendo, an average hunter, was simply unable during his first year in the alpha position to get any meat. It

took him 3 years to join the meat eaters, a period during which he hunted much more regularly. Thus, for cooperation to be stable, the selective pressure has to be strong enough to enforce such conflicting social rules.

In Gombe chimpanzees, age and dominance remain more important than hunting participation, and cooperation cannot be stable. Similarly, in Mahale chimpanzees, a recent analysis showed that the alpha male took part in 8% of the hunts, but he held the carcass of the prey in 31% of them (Nishida et al. 1992). Alpha males in Mahale are thought to share meat in order to favour coalition partners, i.e. middle-ranking old males that are close by (Nishida et al. 1992). Thus, the flexibility of the social system required for cooperation to be stable seems absent in Gombe and Mahale chimpanzees. Meat sharing in the three chimpanzee populations follows different rules and only in Tai are they such as to make cooperation stable. Baboons, *Papio anubis*, at Gilgil, stopped hunting once the keenest hunter lost his alpha position and started to lose the prey to the new alpha male, which rarely hunted (Strum 1981).

The sharing rules prevailing in Tai have allowed adult females to reach a surprisingly high status during the meat-eating episodes, with the higher ranking females gaining more meat than most of the dominant males (Boesch & Boesch 1989). This is very different in Gombe where females have to hunt if they want access to a similar amount of meat as males. This shift in some basic social rules supports my view that the male-bonded group described for Gombe chimpanzees by Wrangham (1986) may apply less generally than proposed. Tai forest chimpanzees live in bisexual-bonded groups (Boesch 1991): males and females range throughout the territory, and females have strong female associates, a central position in meat eating and in the social dominance. The major role of some females in meat eating is probably due to their important affiliative behaviour both with other females and with the hunters that allows them to fling themselves into the scramble around the prey and to enforce the social rules favouring hunters. Tai female and male hunters have a common interest in gaining access to meat and the important role of females in other social domains might have originated from this common interest.

Thus, selective pressure acting through the individuals' energy expenditure needed to achieve

a capture may result in a species hunting in groups and collaborating in some cases, but cooperation will be stable only if the social rules become flexible enough to allow particular meat-sharing rules, as observed in Tai chimpanzees, to be adopted.

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