Cooperative hunting in chimpanzees: kinship or mutualism?

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8.1
Introduction

Cooperation characterizes human societies today and is thought to have been important in our evolutionary past as one of the main characteristics that allowed humans to dominate the planet (Isaac 1978, Mithen 1996). The fundamental role of cooperation is, for example, evident in hunter-gatherer societies, where the prevalence of food-sharing combined with a sexual division of labor is the basis of the economic system (Kaplan et al. 2000, Heinrich et al. 2001, Hill 2002). Analysis of the factors favoring the evolution of cooperation is, therefore, vital for the understanding of the course of human social evolution.

Cooperation can be defined as two or more individuals acting together to achieve a common goal. Cooperation can evolve when two basic conditions are fulfilled. First, the benefits of the common action must be shared sooner or later between the participants, and second, the benefits to the participants must exceed the costs of the common action. However, cooperation can be rather unstable, as it is very susceptible to cheaters, individuals that are not investing in the cooperative task, but are nonetheless trying to gain access to the benefits. The greater the extent of cheating, the less likely cooperation is going to occur (Axelrod & Hamilton 1981, Maynard Smith 1982). Therefore, theories of the evolution of cooperation rely on four different mechanisms to explain its evolution. First, kin selection can facilitate cooperation among related individuals, as each agent will not only benefit directly, but also indirectly from the gains of the others the more they are related to them (Hamilton 1964). Second, in a mutualistic scenario, all partners in a cooperative act would directly profit from the outcome. Third, reciprocity in repeated interactions could allow each partner in turn to obtain the benefit of the cooperative act (Trivers 1971). Finally, the byproduct of sociality scenario suggests that individuals have been selected to live together for other reasons and, by virtue of their proximity, may happen to engage in cooperative acts even when not directly profiting from them (Mesterton-Gibbons & Dugatkin 1992). It is important to note that these explanations for cooperation are not mutually exclusive and several mechanisms may operate simultaneously. Kin selection theory has convincingly explained the evolution of some dramatic forms of cooperation, such as worker sterility in eusocial insects (Reeve et al. 1998). However, it is possible that the indirect benefits of cooperative behavior have been overestimated and little consideration given to direct benefits in other animal societies. This is illustrated by the exemplary work of Clutton-Brock and colleagues, in which careful field observation and experimentation using large numbers of wild meerkats has led to a greater appreciation of direct benefits as an explanation for helping in that species (Clutton-Brock et al. 2001b, 2001c, Clutton-Brock, this volume).

An important distinction between mutualism and reciprocity is that in a mutualistic scenario, the benefits to actors are immediate, whereas the benefits to one partner are deferred in a reciprocal interaction. This is important because some observations have shown that most animals appear wholly or mostly incapable of keeping track of past or future exchanges and so mutualism rather than reciprocity might be more likely to be observed in nature (Clements & Stephen 1995; but see de Waal & Brosnan, this volume).

Many carnivores hunt in groups, but even studies of the same species differ with regard to explanations of the mechanisms promoting this possibly cooperative behavior. In some populations of lions and cheetahs, group hunts have not been observed to provide a direct benefit to all hunters, so that in many instances it would seem better for individuals to hunt alone (Packer et al. 1990, Caro 1994). Accordingly, byproduct mutualism has been suggested to be the main mechanism explaining the observed group hunting in those populations. In other populations living in more difficult or less prey-rich habitat, lions and cheetahs were observed to hunt in groups more frequently and it could be shown that under these conditions, individual benefits increased with group size (Cooper 1991, Stander 1992, Creel & Creel 1995c). In carnivores, group hunting and the benefit extracted from it is not a fixed characteristic of a species, as it is the conditions of the habitats where the hunt take place that will determine the outcomes for the different participants in the hunt. Thus, viewing cooperation in hunting as a constant in a species living in different populations in different habitats is misleading and additional studies may be required to understand the features of the cooperative abilities of a particular species.

We are going to concentrate in this chapter on group hunting in wild chimpanzees (*Pan troglodytes*) and discuss which mechanisms could be responsible for its evolution and maintenance.

8.2
The puzzle of chimpanzee hunting

Wild chimpanzees live in large multi-male, multi-female communities that may contain from 10 to more than 100 individuals. Membership in these communities is very stable, except for females that normally transfer once, upon reaching maturity. Males are philopatric, remaining in their natal group their entire lives (Goodall 1986, Nishida 1990, Boesch & Boesch-Achermann 2000, Mitani & Watts 2002). Cooperation in chimpanzees has been observed in two main contexts. First, the territory of one community is defended by macro-coalitions of adult and adolescent males that regularly patrol the borders, repelling all intruders they see or hear (Goodall 1986, Boesch & Boesch-Achermann 2000). Encounters between communities are normally aggressive and in some instances, have been seen to lead to the deaths of individuals (Goodall et al. 1979, Goodall 1986, Boesch & Boesch-Achermann 2000, Wilson & Wrangham 2003). Hunting of small mammalian prey is the second typical context in which cooperation among varying numbers of males has been observed (Boesch & Boesch-Achermann 2000). Hunting by wild chimpanzees has been observed throughout the area of distribution of the species and it represents a special challenge, as it involves the pursuit and capture of small monkeys fleeing through the forest canopy. As in many apparently cooperative activities, the outcome of a hunt is dependent upon the spontaneous participation of different actors. In fact, hunting success increases with the number of individuals actively hunting (Boesch 1994, Boesch & Boesch-Achermann 2000).

Hunting seems to be a universal behavior in chimpanzees as it has been observed in all populations subject to long-term study (Boesch & Boesch-Achermann 2000). However, detailed observations have been limited to only a few of the long-term studies on that species. First, Geza Teleki (1973) described hunting behavior of the Gombe chimpanzees and detailed some of the tactics used by the male hunters. Subsequent studies at Gombe have complemented our understanding of the hunting behavior in that population (Busse 1978, Goodall 1986, Stanford et al. 1994, Stanford 1998). Studies of hunting behavior have also been conducted on the chimpanzees in Mahale Mountains National Park, some 200 km south of Gombe, and revealed a rather similar picture of the hunting behavior (Nishida et al. 1983, 1992, Uehera et al. 1992). Our understanding of this behavior in chimpanzees was broadened when new observations of the behavior of the Taï chimpanzees in Côte d'Ivoire became available (Boesch & Boesch 1989), revealing surprisingly large variation in the hunting behavior within this species. Lastly, observations of an exceptionally large community in Ngogo, Uganda, have complemented this view of a very flexible behavior in chimpanzees (Watts & Mitani 2000, Mitani et al. 2002a).

Hunting in chimpanzees is puzzling because while there are many similarities in hunting behavior between different populations, important differences have also been observed (Nishida et al. 1983, Goodall 1986, Boesch & Boesch 1989, Uehara et al. 1992, Boesch 1994, Boesch & Boesch-Achermann 2000, Mitani et al. 2002a). First, all chimpanzee populations have been observed to hunt mainly arboreal monkey species and, of those, red colobus monkeys (*Procolobus badius*) are generally the preferred species whenever they are present (Table 8.1). Second, since monkeys are the preferred prey, hunting occurs mostly in the trees. Finally, hunting success in chimpanzees is rather high, compared to many other predatory animal species (Table 8.1). For example, wolves are successful in 8% and 25% of their hunts of moose and deer, respectively (Mech 1970), which is two to five times lower than chimpanzee success rates. Similarly, lions in the Serengeti capture prey in 61% of purely opportunistic cases, but in only 19% of instances when they are stalking the prey, and in 8% of hunts that occur in the open plains (Schaller 1972). Hyenas in the Kalahari are successful in 32% of their hunting attempts (Mills 1990). One possible explanation for the chimpanzee's high rate of success may lie in the fact that, not relying on meat for survival, they tend to hunt only when the likelihood of a capture appears high, whereas social carnivores, being much more dependent on meat, hunt more depending on their level of hunger rather than according to the likelihood of success.

Table 8.1. Similarities in chimpanzee hunting behavior.

	Gombe[a]	Mahale[b]	Ngogo[c]	Taï[d]
Prey selection				
Red colobus	55%	53%	88%	81%
Hunting success	52%	61%	82%	52%

[a] Goodall (1986)

[b] Nishida et al. (1983), Uehara et al. (1992)

[c] Watts & Mitani (2002)

[d] Boesch & Boesch-Achermann (2000)

Differences in hunting behavior among populations of chimpanzees are quite striking (Table 8.2). However, consideration of the differences is complicated by the fact that in arboreal hunts with limited visibility, it is not always easy to distinguish hunters from non-hunters. This makes it difficult to compare observations from different chimpanzee populations. For example, if the hunt happens in a dense part of the forest or when a large number of individuals are present, it becomes very difficult to distinguish whether a given individual is actually actively trying to capture a prey or is simply looking on. This has led some not to distinguish between hunters and non-hunters (Ngogo: Mitani & Watts 1999, 2001, Watts & Mitani 2000; Gombe: Teleki 1973, Stanford 1995, 1998, Stanford et al. 1994a, 1994b), thereby making any discussion about the evolution of cooperation impossible because per definition hunters and cheaters are treated equally. Others have concentrated their analyses on hunts in which the distinction between hunters and non-hunters was based on the behavior of the individuals present (Gombe: Busse 1977, 1978, Goodall 1986; Taï: Boesch & Boesch 1989, Boesch 1994, Boesch & Boesch-Achermann 2000). In such cases, however, individuals may alternate between hunting for some time and just looking at hunting by others. In other instances, a pursued prey may fall to the ground, whereupon one of the individuals watching the hunt would capture it and by its action immediately become a hunter. This distinction between hunters and non-hunters should be made whenever possible, because it permits the proposal of scenarios concerning the evolution and stability of cooperation in hunting.

Despite the different approaches toward observation of chimpanzee hunting, it remains possible to see some clear differences between different chimpanzee populations. First, the tendency to hunt in groups is highly variable and is observed in only one-third of the hunts by Gombe chimpanzees, while group hunting is the rule in Taï and even more so in Ngogo (Table 8.2). Even more striking is the fact that the level of organization during hunts seems very different. Collaboration, in which different hunters perform different but complementary roles during a hunt to capture a prey (Boesch & Boesch 1989), has been regularly

Table 8.2. Differences in chimpanzee hunting behavior.

	Gombe[a]	Mahale[b]	Ngogo[c]	Taï[d]
Group hunt	36%	72%	100%	84%
Collaboration	19%	0%	rare	77%

[a] Busse 1977, 1978, Goodall 1986

[b] Nishida et al. 1983, Uehara et al. 1992

[c] Watts & Mitani 2002

[d] Boesch & Boesch-Achermann 2000

observed only in Taï chimpanzees (Table 8.2). In Ngogo, despite the fact that the chimpanzees hunt exclusively in groups, collaboration among hunters has been observed only rarely (David Watts & John Mitani pers. com.).

We now are going to discuss possible explanations of differences observed among chimpanzee populations in the level of cooperation in their hunting strategies. More specifically, is chimpanzee hunting better explained by kinship or mutualism? These explanations are not mutually exclusive, in the sense that if hunting is beneficial to all participants, it would also pay to hunt with kin and we would not be able to conclude whether kin selection or mutualism favors cooperation. If, however, kin do not hunt together, even though hunting is beneficial, we may argue that kin selection is not the prime factor explaining cooperation.

8.2.1
Kin selection hypothesis

The kin selection hypothesis predicts that related individuals will experience, through indirect benefits, greater paybacks from cooperating than would non-kin. There are exceptional circumstances in which kin selection might not be favored, such as when substantial levels of competition among kin exist (West et al. 2002) or when individuals vary in other ways in their suitability as cooperative partners (Chapais, this volume). However, substantial evidence exists for a role of kin selection in the social behavior of female-philopatric primates (Pope 2000a, Chapais et al. 1997; see Silk, this volume). For male-philopatric chimpanzees, we can make three testable predictions concerning the distribution of kin in social groups. First, males should be more related than females, since males are the primary hunters in chimpanzees. Second, to explain differences between Gombe and Taï, we would expect Taï males to be more related than Gombe males, as the first hunt so much more often in groups. Third, and even if the two first predictions are not supported, we should expect individual males within a group to choose to hunt more frequently with those individuals that are more related to them.

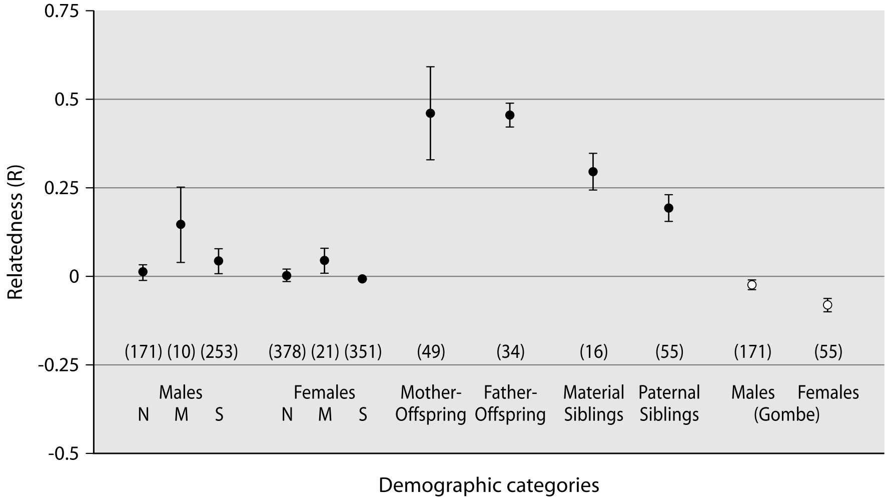

Fig. 8.1. Estimated relatedness (R) of the various demographic categories at Taï and Gombe.

Fig. 8.1 shows the average relatedness of the Taï chimpanzees as measured with microsatellite nuclear DNA markers (Vigilant et al. 2001). It shows very clearly that despite the fact that in Taï chimpanzees, males are philopatric and almost all females transfer between groups before reaching maturity, in each of the three groups on average the males are not significantly more related than the females. In addition, males in Taï chimpanzees and in Gombe chimpanzees have very similar, near zero average relatedness values. Therefore, the presently available data do not support the first two predictions that would originate from a kin selection explanation for male cooperative hunting.

However, the most interesting test is at the individual level, because males may selectively hunt with the individuals most related to them. The matrix in Table 8.3 shows the relevant data for joint hunting in Taï chimpanzees during two different time periods in 1987–1989 and in 1990–1994. Taï chimpanzees hunt mainly in groups containing an average of 3.5 individuals. To test for selective hunting according to relatedness, we established a second matrix with a pairwise comparison of genetic similarity for those males that we could sample (three individuals observed during the first period could not be sampled as they died before the initiation of the genetics project). Table 8.4 reveals that only one dyad out of 21 was judged significantly more likely to represent a half-sibling rather than an unrelated pair (using the program Kinship). The ability to determine a half-sibling from typical genotype information alone is limited (Blouin 2003), as is illustrated by the fact that a known maternal brother pair (Kendo-Fitz) was not significantly supported as a sibling pair when using Kinship. Nonetheless, all other dyads had low or negative (indicating lower relatedness than a random pair from the population) relatedness estimates, suggesting that no other pairs of relatives were present.

Table 8.3. Dyadic frequency of joint hunting in Taï males between 1987 and 1989 (upper half), and between 1990 and 1994 (lower half). Joint hunting was calculated as the number of hunts where two individuals were actively hunting divided by the number of hunts where both were present regardless of whether they were hunting or not.

	Bru	**Dar**	**Ken**	**Mac**	**Rou**	**Sno**	**Uly**	**Ali**	**Fit**
Bru	*	0.22	0.47	0.47	0.29	0.50	0.48	0.57	0.44
Dar	0.26	*	0.32	0.28	0.18	0.57	0.28	0.22	0.33
Ken	0.36	0.15	*	0.29	0.24	0.67	0.46	0.35	0.44
Mac	0.54	0.33	0.44	*	0.26	0.48	0.47	0.42	0.63
Rou					*	0.50	0.26	0.17	0.21
Sno						*	0.43	0.33	1.00
Uly							*	0.54	0.61
Ali	0.64	0.17	0.31	0.42				*	0.43
Fit	0.60	0.31	0.42	0.68				0.67	*
Mar	0.54	0.27	0.33	0.67				1.00	0.86

Table 8.4. Pairwise relatedness estimates for Taï male chimpanzees. In bold is the only dyad that was judged from genotype information to be significantly likely to be related at the half-sibling level, and underlined is the only dyad known to have the same mother.

	Bru	**Dar**	**Ken**	**Mac**	**Ali**	**Fit**	**Mar**
Bru	*	−0.186	−0.197	0.019	−0.080	0.002	−0.225
Dar		*	**0.218**	−0.166	0.038	−0.102	0.096
Ken			*	−0.021	−0.054	*0.184*	−0.065
Mac				*	−0.129	−0.033	0.016
Ali					*	−0.064	−0.092
Fit						*	−0.074
Mar							*

Table 8.5 presents the results of the correlation between these two matrices and clearly shows that relatedness had no significant relationship with joint hunting over both time periods. We checked for the importance of two additional factors, age and social rank, often proposed to be important in social interactions in chimpanzees. Of these, age had no effect but social rank played a significant role, in that males tended to hunt more frequently with males of

Table 8.5. Rowwise matrix correlations (Kr-test) of joint hunting with relatedness, age and rank in Taï male chimpanzees.

		Relatedness	Age	Rank
Joint hunt	Kr	1018	1480	1
1987-1989	p value	0.203	0.296	0.0002
Joint hunt	Kr	2308	232	1
1990-1994	p value	0.461	0.046	0.0002

similar social rank. Social rank was important in both time periods considered, despite the fact that some individual males died between the two periods and others occupied different social ranks (e.g. Macho decreased from the alpha position during the first period to the third position in the second, while Fitz was the seventh-ranking male in the first period but the alpha male in the second one).

Therefore, we can say that none of the three predictions were supported by the data and therefore kin selection generally appears not to be an important factor in explaining the hunting behavior of chimpanzees in the Taï Forest.

8.2.2
Mutualistic hypothesis

We now turn our attention to a mutualistic explanation, whereby we expect chimpanzees to hunt because they profit directly from taking part in this activity. Here again, we can make three different predictions. First, hunters should gain more when hunting in groups than when hunting alone. This would provide males with a strong incentive to wait for others to join or enlist others in the hunting activity. Second, for a given group size, we should expect hunters to gain more than non-hunters. If that were not true, we would not expect to see group hunting, as it would be better to cheat rather than to invest energy in a hunt. Third, we expect the first two predictions to apply more clearly to the situation in Taï chimpanzees than in Gombe chimpanzees and that this would explain the difference we have observed in the group hunting tendencies observed between these two populations (Table 8.2).

Fig. 8.2 shows the net benefit of three hunting strategies of male chimpanzees of the Taï Forest; namely hunter, bystander and latecomer. With regards to the first prediction, the success of hunters increases steadily and reaches a maximum when five individuals hunt together. This increase is significant and individual hunters gain significantly less when hunting in groups of three to five ($r_s = 0.78$, $n = 7$, $p < 0.05$; Boesch 1994). Similarly, Fig. 8.3 reveals that for hunting groups of three to five individuals, it pays an individual to be a hunter rather than a bystander or a latecomer (Wilcoxon signed-rank test: Hunter versus By-

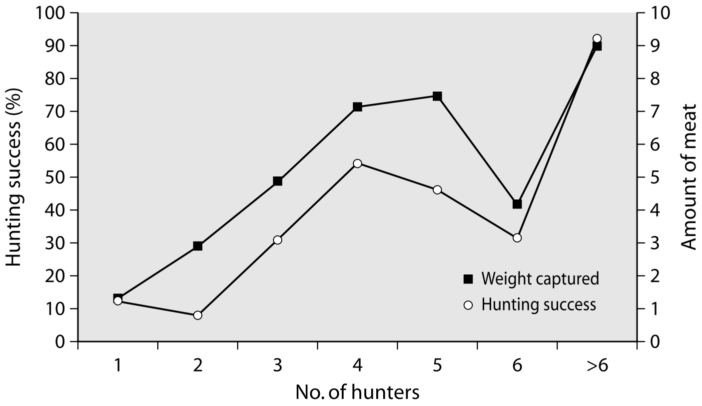

Fig. 8.2. Hunting success and weight captured as a function of the number of males participating in the hunt.

stander: for group size 3: $T^+ = 32$, $n = 8$, $p < 0.05$; for group size 4: $T^+ = 31$, $n = 8$, $p < 0.05$; Hunter versus Latecomer: for group sizes 3 to 5; $T^+ \geq 30$, $n = 8$, $p < 0.05$) (Boesch 1994). Therefore, there is not only an incentive for hunters to hunt in groups, but also for non-hunters to become hunters.

In Fig. 8.3, it is also possible to compare the relative success of both hunters and bystanders in Taï or in Gombe chimpanzees. There is a clear difference, for in Gombe bystander success does not differ from hunter success, except for groups of five hunters, in which case it is better to be a bystander (Wilcoxon signed-rank test: $T^+ = 30$, $n = 8$, $p < 0.05$) (Boesch 1994).

In conclusion, a mutualistic explanation, in which hunters receive direct benefits from cooperating appears to explain hunting in Taï chimpanzees. However, this does not appear to be the case in Gombe and this may explain why group hunting there is less frequent. An interesting correlate of this result is that meat-sharing among the males is done according to different rules in each population. In Taï chimpanzees, it is the behavior of the male that is the strongest predictor of the amount of meat he receives, with hunters receiving more than non-hunters and good hunters receiving the most (Boesch 1994, Boesch & Boesch-Achermann 2000). In Gombe, social dominance is the strongest predictor of meat access, with higher-ranking individuals receiving more, either through sharing or through stealing from the owner (Goodall 1986, Stanford et al. 1993, Boesch 1994). In Mahale chimpanzees, the dominant males secure the captured prey in the vast majority of the cases and favor allies when distributing meat (Nishida et al. 1992). Similarly, in Ngogo chimpanzees, meat-sharing occurs reciprocally with coalition partners of the meat owners (Mitani & Watts 2001). Thus, it seems that within each chimpanzee population, additional social factors are important and interact with the hunting behavior to result in different meat-sharing rules. It is notable that only in Taï chimpanzees do the sharing rules appear to support the stability of cooperation between individual active hunters.

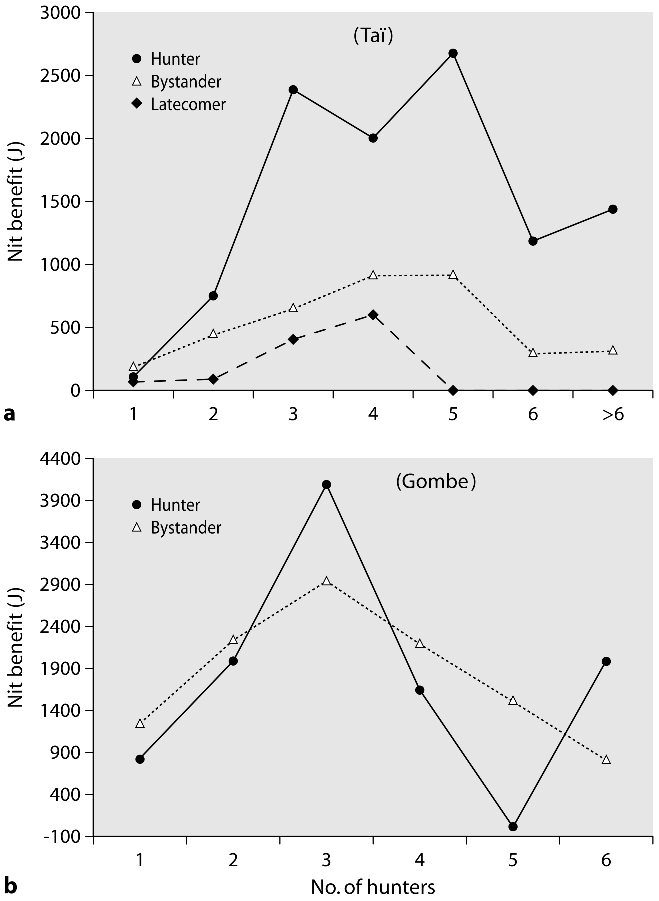

Fig. 8.3. Net benefit of different strategies used by chimpanzees when hunting red colobus monkeys in (**a**) Taï and (**b**) Gombe.

8.3
Discussion

Our analyses have revealed that cooperation in hunting among Taï chimpanzees is not readily explained by kin selection, but rather is the result of a mutualistic process in which all participants gain more than if they were acting alone. This result is consistent with investigations in two other chimpanzee populations of the importance of kin selection in explaining social behavior. A first study of the Kanyawara chimpanzees in the Kibale National Park of Uganda revealed that maternal genetic relatedness, estimated using mitochondrial DNA (mtDNA), did not predict social interactions such as association patterns or grooming interactions between individuals (Goldberg & Wrangham 1997). Similarly, in Ngogo chimpanzees of the Kibale National Park, Uganda, maternal genetic relatedness did not predict association patterns, grooming interactions, alliance between individuals, meat-sharing interactions or patrol participation among the males (Mitani et al. 2000).

The role of kinship in influencing behavior in social insects has been well documented, and there has been an expectation that kin selection would be a major factor for explaining social behavior in other animal taxa as well (Hamilton 1964, Wilson 1975, Maynard Smith & Szathmary 1995). In mammals, the role of kinship has been generally confirmed in social systems where dispersal patterns allow for related individuals to remain together, as in cooperatively breeding species in which helpers are often close kin or within female matrilines found in different primate species where social support may be given according to degree of relatedness (Chapais et al. 1997, Clutton-Brock 2002, West et al. 2002). However, in other studies, such as those on chimpanzees mentioned above, the influence of kin selection has not been found (Clutton-Brock et al. 2001b).

Two factors have been proposed to limit the generality of kin selection. First, groups of social animals may contain a high proportion of relatives and so competition between relatives may become a problem. It has been shown that competition between relatives can drastically limit the benefit of kin selection and that this might be a much more general phenomenon than previously estimated (West et al. 2002). Second, for some tasks it might be preferable to cooperate with particular individuals regardless of relatedness, as for example in a situation in which cooperation with an individual with particular skills is likely to lead to a better outcome (Chapais, this volume). In addition, motivation and predictability might be factors that explain why in Taï and possibly in Ngogo chimpanzees, it is similarity in rank and sometimes age for Ngogo (Table 8.5) rather than relatedness that are more important in predicting the distribution of social interactions and joint participation in hunting. Individuals of similar rank and age seem to share more similar social interests and are more likely to cooperate.

Mutualism has long been recognized as one of the mechanisms leading to the evolution of cooperation, but because of its obvious nature, 'if both gain more, then they should cooperate', theoreticians have neglected it and concentrated on less obvious mechanisms, such as delayed reciprocity and altruism (Maynard Smith 1982, Dugatkin 1997). However, a growing body of studies shows that mutualism has been underestimated because the costs of participating in the cooperative act have been overestimated and the direct benefits of cooperation have probably been underestimated (Clutton-Brock 2002). Hunting in Taï chimpanzees is best explained by a mutualistic process where each hunter gains more by hunting together with others. Cheaters that try to get access to meat without investing in the hunt have some success in obtaining meat, but clearly less than hunters, and that contributes to the stability of hunting in Taï (Boesch 1994).

The variability in chimpanzee hunting behavior seems to reflect an ecological difference, namely the difficulty of the habitat where the hunt is taking place. In the dense tropical forest of the Taï Forest, where monkey prey species have the possibility to escape in all directions, the hunting success of the chimpanzees is very low if they do not hunt in groups (Boesch 1994, Watts & Mitani 2002). In contrast, if they hunt monkeys in a disrupted forest, they can more easily corner them and hunting success seems much less affected by group size (Stanford et al. 1993, Boesch 1994, Watts & Mitani 2002). An additional demographic factor plays a role in which a larger number of hunters are able to disrupt prey defenses by overpowering numbers. This is best illustrated in the exceptionally large community at Ngogo where many individuals (up to 25 adult males) have been observed to hunt at the same time in a not very coordinated way but with a very high success rate (Watts & Mitani 2002). This has been observed in Gombe as well, where many individuals hunting at the same time in a non-coordinated way are able to make multiple captures (Goodall 1986, Boesch 1994). Similarly, in the Taï Forest, the number of potential hunters, for example adult males, in the community, has been found to influence both the frequency of hunts and the number of hunters (Boesch & Boesch-Achermann 2000).

Once they hunt, chimpanzees seem to have the ability to use the benefit of the hunt in a flexible manner. We suggest that when hunting is difficult, they are constrained to guarantee the stability of cooperation and therefore meat-sharing has to favor the hunters. However, when hunting is easier, cooperation is not necessary and the meat can be used to pursue other social goals. Thus, meat can become a currency used to pay for social services, allies in Mahale, social partners in Ngogo or simply to be taken away by dominant individuals in Gombe. This is somehow reminiscent of the situation that has been described for human hunter-gatherers. Among the Hadza, meat acquisition can be a quite solitary undertaking for men and meat-sharing then follows quite flexible social goals not directly related to hunting (Hawkes et al. 2001, Marlowe 2003), while for the net hunters like the Aka pygmies, meat-sharing follows very strict rules to ensure the cooperation of the different hunters (Bahuchet 1985).

In conclusion, cooperation in hunting among Tai chimpanzees does not seem to result from a kin selection process but rather from a mutualistic process. Mutualism not only explains some of the differences in the frequency of group hunts observed within the species but also the way meat is shared after a successful hunt. The importance of mutualism seen in chimpanzees has also been reported for other animal species and might lead to a revision of the relative importance of the different mechanisms that can lead to the evolution of cooperation in nature.

Acknowledgments

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