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Chimpanzees, *Pan troglodytes*, share food in the same way after collaborative and individual food acquisition

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We investigated the hypothesis that patterns of chimpanzee food sharing are influenced by whether individuals contributed to its acquisition collaboratively. In two experiments we exposed pairs of captive chimpanzees to food acquisition/sharing situations in which we manipulated (1) whether or not the two individuals had worked together collaboratively to retrieve the food and (2) the proximity of the individuals to the food at the moment of retrieval. The first experiment resembled a scramble competition scenario, with nonmonopolizable food. Proximity of individuals to the food when it arrived was the major variable affecting amount obtained by subordinates. Whether or not the food was obtained via collaboration had no effect. The second experiment resembled a contest competition scenario, as the food was a single large piece of fruit that could be more readily monopolized. In this scenario, dominants obtained more food than subordinates, the amount of food obtained by 'noncaptors' was affected by their proximity to the food when it arrived, and again previous collaboration had no effect. These results suggest that in many food acquisition situations first-arriver and first-possessor chimpanzees, as well as dominants in general, have a significant advantage in food acquisition, but being a collaborator brings no extra benefits.

Chimpanzees live in fission–fusion communities which split temporarily into small parties of different size and composition as they forage across their territories. They engage in both scramble and contest competition for food. In contexts where a food resource is relatively dispersed, individuals will scramble to harvest as much as possible. For example, when a group of chimpanzees finds a fig tree, individuals scramble up the tree such that, ideally, each finds a suitable location with sufficient figs. Individuals who get to a good patch first have some advantage in that they get a head start eating, and if a late-arriving dominant finds another satisfactory patch, s/he may not attempt to displace the early arriver.

A different dynamic emerges when items of food are more concentrated, and therefore more easily monopolizable. Of course, dominants can in theory monopolize and try to control the totality of the food. But chimpanzees also show some respect for 'possession' (Kummer 1991). In a situation in which a subordinate individual has some food already in her grasp, it is not necessarily the case that the dominant individual will try to take it. Because subordinate individuals are likely to fight to some degree to retain food they already have in their possession (they show an endowment effect; Brosnan et al. 2007), dominants often demur, perhaps depending on such things as who the possessor is, how attractive the food is, how easily the food may be defended by the possessor, and what the alternatives are.

One special situation arises in chimpanzees' group hunting of monkeys (Goodall 1986; Boesch & Boesch 1989; Watts & Mitani 2002). Since chimpanzees are frugivores, a first hypothesis was that chimpanzees hunt to compensate for shortages in food availability (Teleki 1973; Stanford 1996). However, recent studies have shown that at Ngogo, Kibale National Park, Uganda, a large chimpanzee community hunts mainly during times of food abundance (Mitani & Watts 2001), suggesting exactly the opposite, namely, that hunting, which is a costly activity, might take place when individuals can easily meet their daily energy needs because there is enough food available (Mitani & Watts 2001). Group hunts have been described as collaborative in some chimpanzee groups with several individuals coordinating their actions in time and space to catch the prey (Boesch & Boesch 1989). Typically, during a group hunt several adult males work to surround a monkey prey, but only one makes the actual capture, after which the others arrive, joined sometimes by bystanders and other nonhunters (including females). The typical prey is a red colobus monkey, *Colobus badius*, which is too large to monopolize (and which would take too long to consume alone) in the face of numerous other contestants. And so the outcome is that

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the captor almost always gets the most meat (and typically the best parts), but others get significant amounts of meat as well (Goodall 1986; Boesch 1994; Gilby 2006).

There is currently controversy over what factors determine how much meat is obtained in this situation by noncaptors. Boesch (1994) found that within a chimpanzee group in the Tai Forest in western Africa, age and dominance are the two principal criteria influencing meat acquisition by noncaptors, such that older and more dominant individuals profit the most. In their study groups in eastern Africa, Wrangham (1975) and Gilby (2006) found that the major factors are how much and how vigorously a noncaptor begs and harasses the captor. In yet another group in eastern Africa, Mitani & Watts (2001) observed that being a coalitionary partner of the captor (and of noncaptors who have already obtained meat) allows one to acquire more meat. Finally, Gilby et al. (2006, 2010) claimed that meat possessors do not share more with sexually receptive females, as Stanford et al. (1994) suggested (although see Gomes & Boesch 2009).

The most debated claim is Boesch's (1994) proposal that the share of prey obtained by noncaptors depends on the work they put into the group hunt. Boesch reported that individuals get more meat when they actively participate in the hunt than when they are either bystanders in the general vicinity or latecomers to the party, suggesting the possibility that meat is divided based on participation. However, bystanders still get plenty of meat (83% of bystanders in Tai get at least some meat) and they get more meat than latecomers. The pattern of meat acquisition suggests that another main variable affecting the chances of obtaining meat may be proximity to the kill at the time of capture: the captor has the largest share, followed by those in the immediate vicinity (whether they hunted or not), and finally latecomers who get the least amount. Boesch & Boesch-Achermann (2000) reported that, of the hunters who are not captors, the individual who obtains the most meat is the 'ambusher', the hunting role requiring the most skill in anticipating the prey's movements. But, as ambushers tend to be older individuals and close to the kill site, it remains unclear whether the portion of meat they receive is in fact due to their skill or rather to their age or position at time of capture.

Here we report two experiments with captive chimpanzees designed to address some of the questions left open by these results from the wild. In both experiments, pairs of chimpanzees were exposed to food-sharing situations, in which we manipulated (1) whether or not the two individuals had worked together collaboratively to retrieve the food and (2) the proximity of the two individuals to the food at the moment of retrieval. To manipulate the individuals' proximity, we let them enter from different rooms. However, we set things up so that the dominant in each pair would most likely be the first arriving to the food. In the first experiment, which resembled a scramble competition scenario, the food consisted of many small pieces of fruit spread out over a small area. The pieces were thus monopolizable to a degree, but only with agonistic effort. In the second experiment, which resembled a contest competition scenario, the reward consisted of a single large piece of fruit (more similar to a monkey carcass), initially grabbed by one individual (the captor) which forced the noncaptor (in our experiments mostly the subordinate individual) to rely on means other than direct claim to get a share. One hypothesis (following Boesch 1994) was that subjects (noncaptors or individuals with less power, when the food was not monopolizable, i.e. 'subordinates') would acquire more food if they had collaborated in retrieving the food, regardless of proximity. An alternative hypothesis was that the major variable affecting the levels of sharing would be subjects' proximity to the food at the time of retrieval, regardless of whether individuals collaborated in procuring the food. In addition to assessing the effect of these two manipulated variables, we were also interested in how the begging and harassing behaviour of the noncaptor affected her acquisition of food.

EXPERIMENT 1

Methods

Subjects

Twelve chimpanzees, six males and six females, ranging between 7 and 16 years of age participated in this study (see Table 1). They live in a social group of 42 individuals in Ngamba Island Chimpanzee Sanctuary in Lake Victoria, Uganda (www.ngambaisland.org) established in 1998 to care for confiscated orphan chimpanzees. All subjects were unrelated. During the day the group of 42 chimpanzees is released onto the 40 ha island to roam freely and forage within a primary forest. At night all chimpanzees sleep in a large holding facility (4 m high and approximately 140 m^2) consisting of seven rooms with interconnecting raceways. Chimpanzees are fed four

Table 1
The sex and estimated age (at the beginning of the study) of each subject tested in the present study

Pair	Subject	Sex	Estimated age (years)	Experiment 1		Experiment 2	
				No. of trials where they pulled	No. of trials where they shared	No. of trials where they pulled	No. of trials where they shared
1	**Umugenzi**	**Male**	10	**5**	3	**6***	0
	Nkumwa	Female	11	1	0	0	
2	**Bwambale**	Male	7	**6***	4	**6***	0
	Namukisa	Female	8.5	0		0	
3	**Bili**	Female	9	**6***	3	**5**	1
	Indi	Male	8	0		1	0
4	**Becky**	Female	16	**6***	3	**6***	1
	Sally	Female	16	0		0	
5	**Yoyo**	Female	8.5	**6***	1	1	1
	Okech	Male	8	0		**5**	0
6a	**Kalema**	Male	11	**6***	1	————	————
	Asega	Male	9	0		—————	————
6b	**Kalema**	Male	11			**6***	0
	Baluku	Male	9			0	
7	**Umutama**	Male	11			**4**	2
	Asega	Male	9			2	0

Pairs 1–6a participated in experiment 1 and pairs 1–5, 6b and 7 in experiment 2. Results of the dominance tests: the number of trials (maximum = 6) in which each subject in a pair pulled the tray and shared its food (only one dish was baited, with two banana pieces) in the dominance test. The individuals in each dyad who were considered dominant are indicated in bold.

* An individual that pulled significantly more often than her partner (binomial probability: $P < 0.05$).

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times a day with fruits, vegetables, posho (maize flour cake) and millet porridge. Subjects were tested in pairs in one or two rooms of the holding facility (15 m^2 each).

The subjects were never food deprived and water was available ad libitum. They could choose to stop participating at any time. All subjects had participated in several studies investigating their collaborative problem-solving abilities (Melis et al. 2006a, b, 2008, 2009; Hare et al. 2007). They had all shown that they understood the need to synchronize and coordinate their behaviour with that of their partner to succeed in the collaboration task used in the present study.

Apparatus

The collaboration apparatus consisted of a flat platform (17 cm × 3.4 m) with three food dishes, two of which (17 × 27 cm) were placed at either end of the platform and a third (17 × 80 cm) was positioned in the centre of the tray. The apparatus was placed 1 m away from the metal bars of the test room (15 m^2), out of reach of the subjects. The pulling mechanism (Hirata & Fuwa 2007) in the Collaboration conditions consisted of a single rope (5.8 m or 8 m long depending on the condition) threaded through loops on top and across the length of the platform so that both ends of the rope extended from the platform through the metal bars into the test room(s). Pulling from only one end of the rope was ineffectual because the rope would come out of the loops and thus lose its connection to the platform. Since the two ends of the rope were too far apart for a single individual to reach both at once, subjects could only pull the platform within reach if two individuals each simultaneously pulled one end of the rope towards the room. In the Solo (no Collaboration) conditions a rope (1.6 m) was attached to the centre of the tray, so that a single individual could pull the tray within reach.

Procedure

Pretests. Before starting the test phase, it was important to ensure that pairs could succeed in collaborating and maintaining collaboration in simpler situations in which subjects could not easily monopolize the food rewards. For this purpose, we conducted several pretests designed to (1) test whether tolerance levels between subjects were high enough to guarantee successful collaboration in a situation with low potential for competition over food rewards, (2) assess the most dominant individual in each dyad and (3) test whether dyads would successfully collaborate when one individual was required to pull from a disadvantageous position more distant from the food rewards.

(1) Tolerance and basic collaboration. The two individuals in a pair were allowed to enter the test room (room 1) at the same time, and were required to pull simultaneously to gain access to the food in the out-of-reach tray. Pairs had to collaborate and share some of the food to be considered tolerant enough to participate in the study. Subjects participated in two sessions. In each session they received six trials in which the two dishes on the tray (2.5 m from each other) were baited with six to eight banana slices per dish, and one trial in which only the middle dish on the tray was baited with 30–45 banana slices (three or four bananas depending on the subjects' age).

(2) Dominance test. Only the middle dish in the tray was baited with two banana pieces (each piece was placed in one end of the dish, i.e. the two pieces were 80 cm from each other). A single rope (1.6 m) was attached to the centre of the tray, so that an individual could obtain the food by pulling the rope alone. The two individuals in the pair were allowed to enter Room 1 simultaneously. We recorded who pulled the tray and whether or not subjects shared the food (see Table 1 for results). Each pair participated in a single session of six trials. The individual who monopolized the tray in the majority of the trials was considered to be the dominant one.

(3) Collaboration in the 'separated' condition. The purpose of this pretest was to determine whether dyads would still collaborate in a situation in which one of the subjects had to pull from a disadvantageous position more distant to the food rewards. Unlike in the test trials, we baited the two distant dishes on the tray to facilitate sharing after successful collaboration. The tray was positioned outside Room 1 and the two dishes (2.5 m apart) were baited with six to eight banana slices each. The dominant individual in a pair (as assessed in the dominance test) was allowed to enter Room 1 (from an adjacent room) at the same time as the subordinate individual was allowed to enter Room 2 (from an overhead runway). The two rooms were separated by a sliding door which was slightly open, so that subjects could see it was open but still had to push it aside to go through. After successfully pulling the tray within reach, the subordinate individual had to enter Room 1 to reach the pieces of food on the tray (see Fig. 1b). All pairs participated in two sessions of six trials each for a total of 12 trials.

Test phase. All pairs participated in four conditions (see Fig. 1). In all conditions the tray was placed outside Room 1 and was baited with 16 banana pieces (3 cm each) spread across the totality of the middle dish.

(1) Collaboration/Together. A single rope (5.8 m) was placed through the loops on top and across the length of the tray, so that both individuals needed to collaborate to pull the tray within reach. The two individuals entered simultaneously from a room adjacent to Room 1 (Fig. 1a).

(2) Collaboration/Separated. A single rope (8 m) was placed through the loops on top and across the length of the tray, so that both individuals needed to collaborate to pull the tray within reach. One end of the rope was in Room 1 and the other was in Room 2. The dominant individual in each pair (as assessed in the pretest) was allowed to enter Room 1 (from an adjacent room) at the same time as the subordinate was allowed to enter Room 2 (from an overhead runway; Fig. 1b).

(3) Solo/Together. A single rope (1.6 m) was attached to the centre of the tray, extending 76 cm into the room. One individual could pull the tray within reach alone. The two individuals entered simultaneously from an adjacent room (Fig. 1c).

(4) Solo/Separated. A single rope (1.6 m) was attached to the centre of the tray, extending 76 cm into the room. The dominant individual in each pair (as assessed in the pretest) was allowed to enter Room 1 (from an adjacent room) at the same time as the subordinate was allowed to enter Room 2 (from an overhead runway; Fig. 1d).

In the 'Separated' conditions, we always let the dominant individual in each pair enter the room with food first. This was the best method to guarantee a controlled comparison across conditions. We did not counterbalance who entered first, since such a manipulation would have been unsuccessful in the 'Collaboration/Separated' condition, in which typically (as observed on pilot observations) dominants would refuse to pull from the more distant position. Subjects received six trials per condition (total of 24 trials). Each pair participated in six sessions of four trials each (one trial per condition per session). The order of the conditions was randomized across pairs and sessions. Trials in which subjects did not succeed in pulling the tray were repeated a maximum of two times per session. If they did not succeed on the third trial, the next condition was conducted.

Coding and analysis

All trials were filmed and recorded with two video cameras. One was positioned in front of the baited dish and the second one on the side of the tray capturing who pulled when and from which position. The number of banana pieces each subject obtained was coded live by

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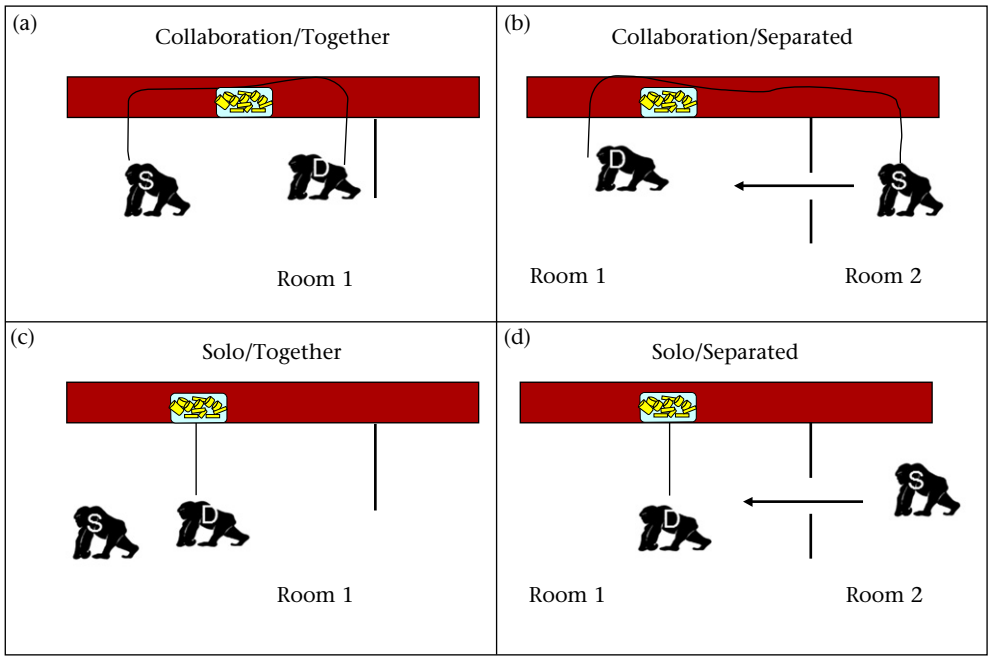

Figure 1. The four test experimental conditions. In the Collaboration conditions (a and b) subjects had to collaborate by pulling together to get access to the tray, whereas in the Solo conditions (c and d) one individual alone was able to pull the tray within reach. In the Together conditions (a and c), both subjects entered Room 1 simultaneously. In the Separated conditions (b and d), the dominant individual of each pair (D) entered Room 1 directly whereas the subordinate partner (S) was allowed to enter Room 2 from an overhead raceway, and she then had to slide a door aside to enter Room 1.

A.P.M., who also verified the number by watching the videofiles. We further coded whether subordinates were delayed in gaining access to the food relative to their dominant partners or whether both individuals gained access simultaneously (Delayed versus Simultaneously). We considered the subordinate to be delayed when (s)he gained access to the food at least 2 s after the dominant partner. Interobserver reliability comparisons were performed on a randomly chosen 25% of the trials, with the second coder blind to the hypotheses (number of banana pieces obtained by each subject: $r_S = 0.992$, $N = 36$, $P < 0.01$; subordinate delayed at gaining access to the food: Cohen's $k = 0.72$, $N = 36$). All analyses were done on SPSS 15.0 and 16.0 (SPSS Inc., Chicago, IL, U.S.A.) using parametric tests. The dependent measure for all analyses was the percentage of the total number of pieces that a certain individual obtained. We conducted a 2×2 repeated measures ANOVAs (general linear model) with Collaboration (Collaboration versus Solo) and Proximity (Together versus Separated) as the within-subjects variables. A second ANOVA was also conducted with Collaboration (Collaboration versus Solo) and Delay (Delayed versus Simultaneously) as the within-subjects variables. The normality of the residuals was checked by visual inspection of Q–Q plots and their homoscedasticity was checked by plotting residuals against fitted values. None of the plots indicated a severe deviation from the assumptions for the ANOVA. All *P* values reported are two tailed.

Results

Subjects successfully retrieved the tray in 100% of the trials. Overall, dominants did not obtain more banana pieces than subordinates (paired *t* test: $t_5 = 1.49$, $P = 0.20$; Fig. 2a). However, the number of food pieces that subordinates were able to obtain varied as a function of the condition they were in. A 2×2 repeated measures analysis of variance revealed that subordinates obtained more food in the 'Together' than the 'Separated' conditions (ANOVA: $F_{1,5} = 8.46$, $P = 0.03$; Fig. 2a). Subordinates also tended to obtain more food in the 'Collaboration' than in the 'Solo' conditions, although this effect was not statistically significant (ANOVA: $F_{1,5} = 4.75$, $P = 0.08$) and, as we explain below, this was due to the two variables ('Collaboration' and 'Proximity') being confounded. There was no interaction between the two variables (ANOVA: $F_{1,5} = 0.05$, $P = 0.83$).

During the test we observed that the delay with which subordinates obtained the food was a function not only of the condition they were in ('Together' versus 'Separated') but also of other variables. For example, the delay was often confounded with the Collaboration variable, since in the 'Solo/Separated' condition when the subordinate came from a different room, dominants did not need to wait for the subordinates and had a head start in most of the trials, whereas in the 'Collaboration/Separated' condition dominants needed help to get access to the tray and had to wait for the subordinates. Furthermore, subordinates learned to pull in a way that reduced their delay entering the room (e.g. pulling with the door open and very close to the door). Therefore, we coded whether subordinates gained access to the food with at least a 2 s delay from their dominant partners or not and categorized all trials based on this new variable 'Delay' (delayed versus simultaneously; dominants arrived with a delay with respect to their subordinate partners in only 5 (3%) of the trials). A 2×2 repeated measures analysis of variance with Collaboration and Delay as the within-subjects variables revealed a main effect of delay (ANOVA: $F_{1,5} = 19.06$, $P = 0.01$) with subordinates obtaining more food when they acted simultaneously with their partners than when they were delayed (see Fig. 2b). However, there was no effect of Collaboration (ANOVA: $F_{1,5} = 1.66$, $P = 0.27$) or interaction between Collaboration and Delay (ANOVA: $F_{1,5} = 4.96$, $P = 0.09$).

Discussion

Overall, dominants did not obtain significantly more food than subordinates. However, the amount of food that both subordinates and dominants obtained varied across conditions. We found that subordinates obtained more food in the 'Together' conditions,

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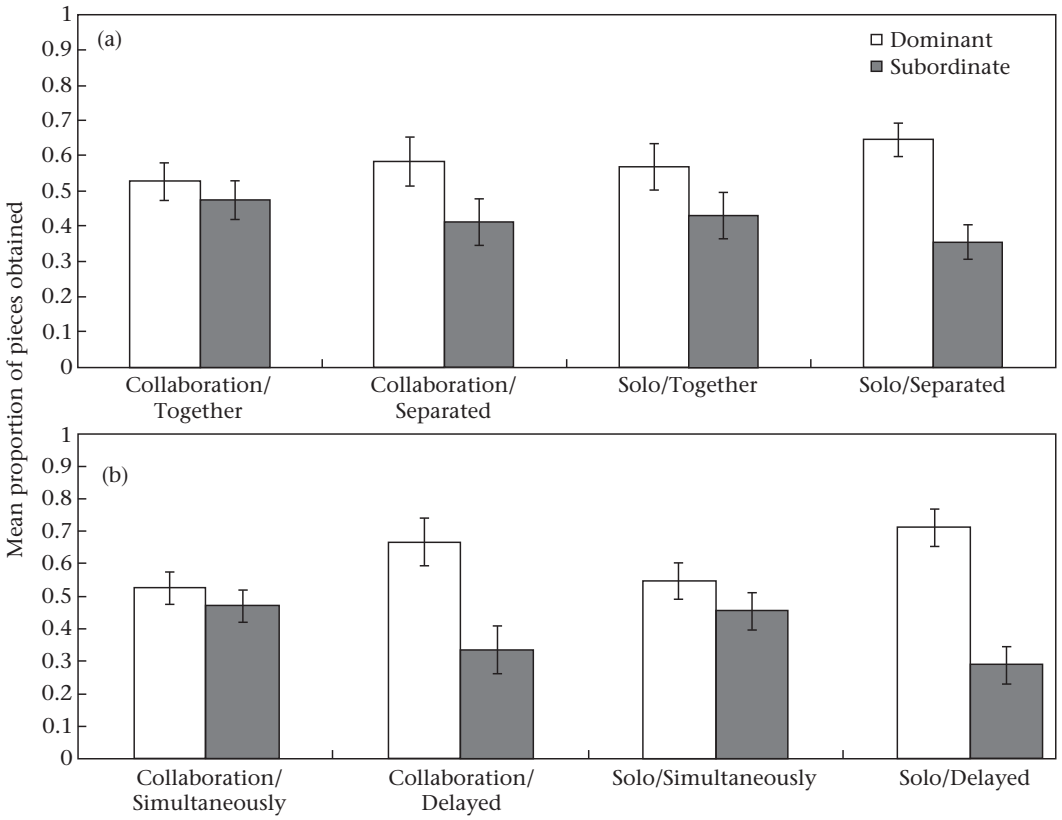

Figure 2. Mean ± SEM proportion of food pieces obtained by the dominant and subordinate individual in each pair in experiment 1 as a function of (a) the experimental condition and (b) whether they were in a 'Collaboration' or 'Solo' condition and whether subordinates obtained the food simultaneously with or later than their partners.

suggesting that whether or not they obtained the food simultaneously with their partner was the main variable influencing the levels of sharing. The initial finding suggesting that subordinates had a tendency to obtain more food in the 'Collaboration' conditions, turned out to be the result of the variable Collaboration being confounded with the second manipulation we aimed to achieve, that is, the proximity of both individuals to the food at the moment of retrieval. In particular, the partner delay we aimed to achieve in the 'Collaboration/Separated' condition did not occur in many instances because the partners employed different strategies to decrease this delay and ended up obtaining the food together. A new analysis based on the actual delay with which subordinates obtained the food confirmed that this variable, and not the Collaboration variable, was the main factor predicting how much food individuals obtained.

However, it remains unclear why subordinates obtained less food when they were delayed. Since chimpanzees show some respect for possession (Kummer 1991), one possibility is that in situations in which one individual gets the food first, partners respect the first-arriver's claim more and do not try as hard to obtain food from them. Another possibility, but along the same lines, is that the first-arrivers (in our experiment the most dominant individuals) were less willing to lose any, and defended 'their' food more strongly. However, a simpler and more plausible third explanation is that subordinates obtained less because by the time they arrived at the feeding site, dominants had already eaten or monopolized some food pieces leaving less food available to the subordinates. Using banana pieces as a reward made this last explanation particularly difficult to rule out as it allowed individuals to hoard as much as possible and chew later. That is, unlike a monkey carcass, banana pieces can be consumed very quickly, giving the first individual a significant advantage over latecomers. Furthermore, to distinguish whether levels of sharing are dependent on the food possessor's willingness to share, on beggars' insistence or potentially both factors, one would need to measure levels of begging and harassment. However, begging or harassment as observed in the wild when one individual possesses a carcass (e.g. Gilby 2006) could not really take place in the present experiment owing to the division of the food reward and the subjects' inability to monopolize it in its entirety. To address these limitations we conducted the second experiment.

EXPERIMENT 2

In this experiment we tested chimpanzees' tendency to share food in the same four experimental conditions as previously, but replaced banana pieces with a single large piece of fruit. The size of the piece of fruit and the impossibility of pulling it through the bars right away prevented first-arrivers from hoarding it completely before their partners arrived at the feeding site. We could thus manipulate whether or not subjects obtained the food together or separated and rule out the possibility that delayed partners obtained less food simply because there was less still available.

Furthermore, the first-arrivers (from now on 'captors') could seize initial control of the large piece of fruit, mimicking meat sharing in the wild, in which noncaptors have to beg or harass the captors of the carcass to obtain part of it.

Methods

Fourteen chimpanzees, the same first five pairs from the previous experiment and two new male–male pairs (Kalema – Baluku and

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Umutama – Asega) participated in this experiment (see Table 1). This experiment was conducted 2 years after experiment 1. The test procedure was identical to that of the previous experiment, except for one main modification. Instead of 16 banana pieces, the middle dish was baited with half a watermelon or papaya. Pulling the piece of fruit through the bars was not possible. That is, subjects had to reduce the size of the piece before being able to pull it inside the test room. Which food (watermelon or papaya) they received alternated across trials and sessions, since in this experiment we only conducted one trial per day. Before starting the test phase, we conducted dominance tests as in experiment 1. The only change in dominance was observed among the pair Yoyo–Okech (Okech being more dominant than Yoyo; see Table 1). The two new male–male pairs also participated in pretests to ensure that they were tolerant enough to collaborate and were able to pull in the Collaboration/Separated condition (see Experiment 1). As in the previous experiment each pair participated in the following four conditions (Fig. 1): (1) Collaboration/Together, (2) Collaboration/Separated, (3) Solo/Together, (4) Solo/Separated. Each pair participated in a total of 24 trials (six per condition and 12 of each fruit type). One pair (Kalema–Baluku) only participated in 12 trials, owing to social tensions in the group, which made it increasingly challenging to separate one of them (Kalema) from other group members.

Coding and analysis

To quantify the level of sharing between individuals we coded how long individuals fed (time spent chewing). Analyses were conducted with the percentage of time relative to the trial duration that individuals spent feeding. Trial duration was the total amount of time from the moment one individual started feeding until the moment the last piece of food was consumed. In addition, we coded subjects' begging behaviour partly based on Gilby (2006). We distinguished the following two categories: (1) Sitting and looking (time spent by the beggar sitting within arms' reach of the fruit possessor and staring at the fruit and/or possessor), and (2) Reaching, with and without physical contact (time spent by the beggar extending the arm towards the fruit and/or possessor). We also combined the two categories into a combined score 'Begging' by adding and weighting each category by the percentage of time in which it was observed. To investigate the relationship between subjects' begging behaviour and how much food they obtained, we determined Spearman correlations for each pair using a script written for R (R Development Core Team 2010) by R. Mundry. This determines exact P values for small samples (Mundry & Fischer 1998) and otherwise derives P values through 10 000 permutations (Adams & Anthony 1996). Furthermore, to assess whether there was a consistent effect across pairs, we tested whether correlations were on average zero using one-sample t tests. All other analyses were done using parametric tests as in the previous experiment. The normality of the residuals was checked by visual inspection of Q–Q plots and their homoscedasticity was checked by plotting residuals against fitted values. None of the plots indicated severe deviations from the assumptions for this type of analysis. Interobserver reliability was good for the time individuals spent feeding ($r_S = 0.96$, $N = 32$, $P < 0.01$), sitting and looking ($r_S = 0.97$, $N = 32$, $P < 0.01$) and reaching ($r_S = 0.787$, $N = 32$, $P < 0.01$). All P values reported are two tailed.

Results

Subjects succeeded in obtaining the tray in all 'Solo' trials. However, there were several unsuccessful 'Collaboration' trials (nine unsuccessful out of 78 Collaboration trials). The majority of these unsuccessful trials occurred in the 'Collaboration/Separated' condition (eight out of the nine unsuccessful trials). But the two Collaboration conditions (Separated versus Together) did not differ with regard to level of success (paired t test: $t_6 = 1.87$, $P = 0.11$).

In this experiment, as in the previous one, both individuals could arrive simultaneously at the feeding site. However, owing to the nature of the food, only one of them could initially seize the fruit (the 'captor'). Overall, 'captors' obtained significantly more food than 'noncaptors' (paired t test: $t_6 = 6.35$, $P = 0.01$). In most of the trials it was the dominant individual in a pair who was the captor (touched and obtained the fruit first). However, in three of the pairs the subordinates were occasionally also the captors (in 19% of the trials, $N = 30$). Therefore, we investigated how much time the 'noncaptor' (the individual who obtained the food at a later point) spent feeding across conditions (see Fig. 3). The same analyses for the captors would not be very informative, since by definition 'captors' were the ones in possession of the fruit and were generally feeding nearly the whole trial. A 2×2 repeated measures analysis of variance revealed that 'noncaptors' fed longer in the 'Together' conditions than in the 'Separated' conditions (ANOVA: $F_{1,6} = 8.00$, $P = 0.03$). However, this analysis revealed no effect of the variable 'Collaboration' ($F_{1,6} = 1.15$, $P = 0.32$) and no interaction between the two variables ($F_{1,6} = 0.28$, $P = 0.62$; Fig. 3).

To understand better where this difference across conditions came from, we analysed whether individuals who were not in possession of the fruit begged differently across conditions

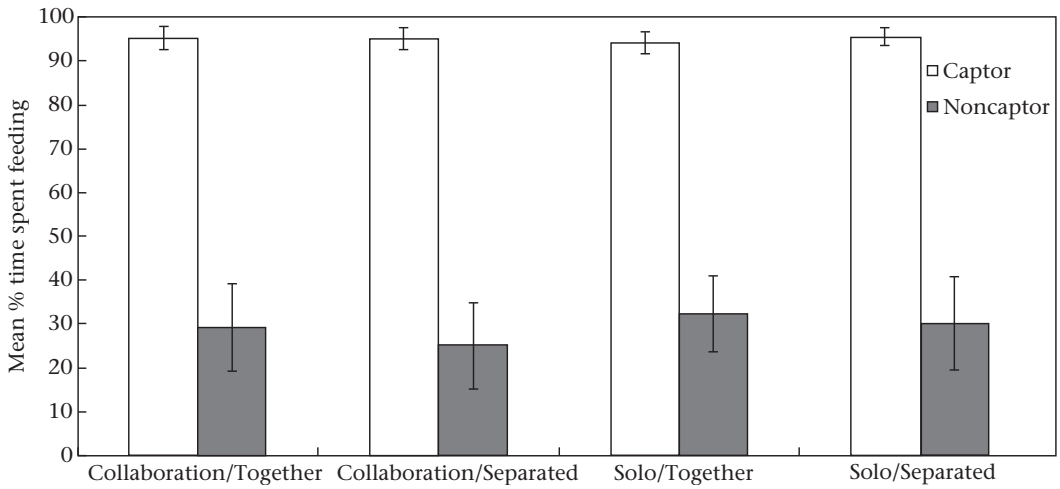

Figure 3. Mean percentage time spent feeding by the captor and noncaptor individuals as a function of the experimental condition in experiment 2.

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(see Fig. 4). A 2 × 2 repeated measures ANOVA with Collaboration and Proximity as the within-subjects variables revealed that subjects tended to beg by 'sitting' close to the possessor longer in the 'Together' conditions than in the 'Separated' conditions, although this was not statistically significant (ANOVA: $F_{1,6} = 4.2$, $P = 0.085$). However, this analysis revealed no effect of the variable 'Collaboration' and no interaction between the two variables. We found no difference across conditions with regard to the begging category 'Reaching'. However, the same analysis for the combined 'Begging' score also revealed that subjects tended to beg more in the 'Together' conditions than in the 'Separated' conditions, although this was marginally significant ($F_{1,6} = 5.29$, $P = 0.06$; Fig. 4).

An analysis of the effect of the food type on the level of sharing revealed that beggars obtained more food when the fruit was watermelon than when it was papaya (papaya versus watermelon obtained by noncaptors: paired t test: $t_6 = -3.7$, $P = 0.010$). This was probably because individuals in possession of the food were more willing to share watermelon peel. Individuals needed much longer to chew on the watermelon peel, which is harder than the papaya peel, and it was often the peel that beggars obtained.

We also analysed whether, independent of the experimental condition subjects were in, noncaptors fed for longer (i.e. obtained more food) when they begged more (Sitting, Reaching and 'Begging' for longer). We found great variability across the different pairs. Three pairs showed a significant positive correlation Kalema − Baluku for all three begging measures: Sitting/looking ($r_S = 0.69$, $P = 0.01$), Reaching ($r_S = 0.69$, $P = 0.01$) and Begging ($r_S = 0.70$, $P = 0.012$) and Okech − Yoyo and Bili − Indi for Reaching ($r_S = 0.56$, $P = 0.012$ and $r_S = 0.73$, $P = 0.0003$, respectively), whereas one other pair showed a significant negative correlation and the other three showed no correlation of any type. Overall, there was no consistent pattern among the different pairs (one-sample t tests: Sitting/looking: $t_6 = 1.03$, $P = 0.34$; Reaching: $t_6 = 1.82$, $P = 0.11$; 'Begging': $t_6 = 0.88$, $P = 0.41$).

Finally, although dominant individuals were not always the captors, we analysed whether dominants fed for longer than subordinates and found that they did (paired t test: $t_6 = 3.65$, $P = 0.01$). This was the case for each condition separately with the exception of the 'Solo/Separated' condition (paired t test: Collaboration/Together: $t_6 = 3.9$, $P = 0.008$; Collaboration/Separated: $t_6 = 3.5$, $P = 0.013$; Solo/Together: $t_6 = 3.7$, $P = 0.009$; Solo/Separated: $t_6 = 1.7$, $P = 0.13$). A 2 × 2 repeated measures analysis of variance with Collaboration (yes, no) and Proximity (yes, no) as the within-subjects variables revealed a marginally significant effect of the variable Collaboration with subordinates tending to obtain more food in the 'Solo' conditions than in the 'Collaboration' conditions (ANOVA: $F_{1,6} = 5.30$, $P = 0.06$). However, no effect of the variable 'Proximity' ($F_{1,6} = 0.254$, $P = 0.63$) or interaction between the two variables ($F_{1,6} = 2.11$, $P = 0.20$) was found. In contrast to the previous experiment in which the nature of the food allowed first-arrivers to have a big advantage over latecomers, in this experiment the actual delay with which noncaptors arrived at the feeding site was no longer an issue. This is because, despite a potential delay between individuals arriving at the feeding site, by the time the partner joined the first-arriver (captor), the entire piece of fruit (which first had to be cut and pulled through the bars) remained in its entirety to be shared.

Discussion

The first goal of this experiment was to replicate the previous one with the modification that first-arrivers could not consume much of the food prior to their partner's arrival. This was achieved by baiting the tray with one large piece of fruit, instead of many small ones. Since subjects needed time to manipulate the fruit through the caging and into the room, even when the first-arriver (captor) had already grabbed the food by the time the partner joined her, the entire piece of fruit remained to be shared. This allowed us to investigate in a more controlled way the effect of both individuals arriving separately at the feeding site in the previous experiment.

Although the experiment was designed to give priority of access to the dominant individuals in each pair, occasionally it was not the dominant individual but the subordinate who obtained the fruit first. Therefore, we analysed how much food the noncaptors (independent of their rank) were able to obtain. This analysis revealed an effect of the variable 'Proximity': with noncaptors obtaining more food in the 'Together' than the 'Separated' conditions. As in the first study, there was no evidence that noncaptors obtained more food after having contributed to the acquisition process, that is, in the Collaboration conditions. However, in contrast to the first study, in this contest competition situation, dominants fed for significantly longer and ate more than their subordinate partners, with no effect of condition on this effect.

But why could noncaptors obtain more food when they gained access to it simultaneously with their partners? Are food captors more willing to share or are noncaptors more determined to obtain

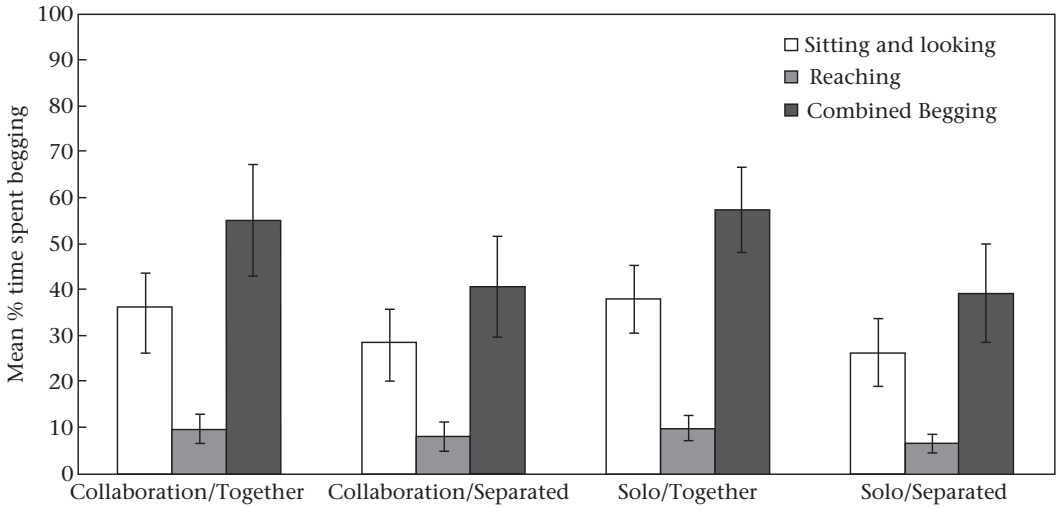

Figure 4. Mean percentage time spent begging for the three categories (1) Sitting and looking, (2) Reaching and (3) combined score 'Begging' as a function of the experimental condition in experiment 2.

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more? Since subjects tended to beg more in the 'Together' than in the 'Separated' conditions, one possible explanation is that the phenomenon is primarily determined by the noncaptors' begging behaviour. However, this is not completely clear, since we found a positive correlation between begging and food obtained only among three of the pairs.

GENERAL DISCUSSION

The present study was designed to determine what factors influence chimpanzees' sharing behaviour after collaboration. Based on observational data suggesting that chimpanzees preferentially share meat with individuals that have contributed to the hunt (Boesch 1994), we designed an experiment that allowed us to measure food-sharing behaviour and manipulate (1) whether or not the two individuals worked together collaboratively to retrieve the food, and (2) whether or not the two individuals were in proximity to the food at the acquisition time. In the first experiment, which resembled a scramble competition scenario, we found that both individuals in a pair were able to obtain a significant proportion of the food, and dominants did not monopolize the majority of it. However, in the second experiment which was more like a contest competition scenario, captors (and dominants as well) did monopolize the resource and ate most of the food.

We found no evidence in either experiment supporting the hypothesis that chimpanzees obtain more food when they have contributed to the collaborative task. There was also no evidence suggesting that the individuals with less power (either because they were the noncaptors or the subordinates) begged more (maybe because of heightened expectations) after collaboration. That is, even though subjects had a great deal of experience collaborating to retrieve food and had previously demonstrated an understanding of the need to work together with a partner in order to succeed (Melis et al. 2006a, b, 2008, 2009; Hare et al. 2007), in these two experiments, neither captors nor noncaptors (or dominants and subordinates) altered their behaviour depending on whether or not they had collaborated to obtain the food.

In contrast, in both experiments we found evidence supporting the hypothesis that proximity to the food at the time of acquisition influenced how much an individual was able to obtain. The results of the first experiment suggest that, in scramble competition scenarios, latecomers obtain less simply because more food has already been monopolized and/or taken away by the time they reach the feeding site (they lose the scramble competition). The results of the second experiment suggest that, in more contest competition situations, latecomers obtain less because the captors might deny them access (they lose the contest). But if they are nearby at the moment of capture they tend to beg more, perhaps because they are more aroused by the sight of the capture or they feel more entitled to the food, and thereby hope to obtain more from the captor.

Although overall we did not find a clear relationship between levels of begging/harassment and sharing, there were almost no instances of active sharing; the majority of food transfers were of a passive nature initiated by the beggar, as has already been reported in many other studies (Boesch & Boesch 1989; de Waal 1989; Ueno & Matsuzawa 2004; Gilby 2006). Nonpossessors obtained some of the food only after sitting in close proximity to the possessor, reaching towards the fruit and/or its possessor, and collecting pieces, mostly peel, dropped by the possessor.

We are aware that chimpanzees' sharing behaviour after group hunts could represent a unique situation that is difficult to mirror in captive settings. For example, we used fruits and not meat and the nature of the food itself, as we have found in the present study, might have a large influence on subjects' feeding and harassment opportunities. In addition, many of our subjects were females and most of the subjects were younger than typical hunters. However, the strength of the experimental approach is that we tested individuals who, although young, were very experienced in the collaborative task and understood the role of the partner for success, which is a key prerequisite if individuals were to share with others based on a sense of fairness (rewarding contributors and punishing laggards in the collaborative act). In addition, the current study permitted the separation of the influence of proximity from that of collaboration, which might be very difficult if not impossible in the wild.

Although further experiments and systematic observational studies are necessary to understand fully chimpanzees' food-sharing behaviour after collaboration, the present study in addition to other studies on chimpanzees' inequity aversion (Bräuer et al. 2006; Jensen et al. 2007; although see Brosnan et al. 2005) does not provide any evidence in support of the 'fair meat distribution' hypothesis. Variables such as dominance, age (Boesch & Boesch-Achermann 2000), harassment (Wrangham 1975; Gilby 2006), possessor–beggar interindividual relationships (Mitani & Watts 2001; Nishida et al. 1992), reciprocal exchange (Mitani & Watts 1999, 2001), and proximity to the kill (present study) all seem to be more important variables in determining how chimpanzees share the spoils.

Rewarding partners' contributions to the collaborative task is a key mechanism for promoting and maintaining collaboration in human societies, especially in collective action situations where individuals are tempted to free-ride. The results of this study suggest that the proximate mechanisms underlying group-level collaboration in humans and our closest living primate relatives could be very different in this regard. Future studies investigating collaboration and its associated payoffs in groups rather than in dyads will be key to identifying primates' solutions to social dilemma situations.

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