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Bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, prefer to feed alone

Anke F. Bullinger [a,*], Judith M. Burkart [b], Alicia P. Melis [a], Michael Tomasello [a]

[a] Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[b] Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

Many primates share food, but the motives behind this food sharing are mostly not known. We investigated individuals' preference to feed either alone or together with a tolerant partner. Subjects (chimpanzees who are highly competitive around food, bonobos who are more tolerant around food and common marmosets who are cooperative breeders and share food actively with some partners) were tested with a door-opening paradigm. In a 2 × 2 design with the factors 'food' and 'partner', subjects had the opportunity to eat piles of sharable food, if present, and/or to open the door, thereby allowing the partner, if present, to join the subject. While food had a main effect on the subject's behaviour, the presence of the partner did not. Individuals of all species opened the door much more often if there was no food available. These results suggest that regardless of their differing social organizations, chimpanzees, bonobos and marmosets do not voluntarily co-feed, but do not mind having company if there is no food present.

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Food sharing among nonkin is considered one of the hallmarks of human evolution and has received much attention given the potential prosocial motivation behind it (Isaac 1978; Gurven 2004). The seemingly altruistic transfer of food from the possessor to the recipient raises interesting questions about the underlying motivation. Is food sharing motivated by selfish goals, that is, does the resource function as a tool for social bargaining, or is the actors' motivation to provide a benefit to the recipient? A detailed understanding of food-sharing behaviour in nonhuman primates as our closest living relatives can provide important insights into the evolutionary history of food sharing in human beings.

Food sharing takes many different forms in different primate species (Feistner & McGrew 1989; Brown et al. 2004). Two distinctions need to be made (Jaeggi et al. 2010a). One is the distinction between sharing foods among nonkin versus among kin; the other is between active sharing, that is, the possessor initiates food transfer without request (Feistner & McGrew 1989),

and tolerated theft, that is, the possessor allows scroungers to take pieces (Blurton Jones 1984; Brown 2004). Occasions of tolerated theft are often accompanied by solicitous behaviour (Apes: Nishida 1970; Jaeggi et al. 2008; New World monkeys: Starin 1978; callitrichids: Feistner & Price 2000) or even aggressive approaches (Apes: Fruth & Hohmann 2002; Jaeggi et al. 2010b; Old World monkeys: Belzung & Anderson 1986; New World monkeys: Stevens 2004; callitrichids: Rapaport 2001; Digby et al. 2007). Some researchers suggest that the social organization and associated levels of social tolerance and competition over resources have an influence on individuals' motivation to behave prosocially (Hare & Tomasello 2005; Burkart et al. 2009). Accordingly, we focused on three primate species of differing social organization: the more competitive chimpanzees, the more tolerant bonobos and the cooperatively breeding marmosets.

Among chimpanzees, food sharing is observed mainly after hunting bouts. Differences have been reported in relation to the motives of food sharing (Stevens & Gilby 2004). One possibility is that group members are coerced into sharing through harassment or the threat of punishment or eviction by dominant individuals, which makes defending the food too costly (Wrangham 1975; Nishida et al. 1979; Stevens 2004; Gilby 2006). Another possibility

* Correspondence: A. F. Bullinger, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany.
   E-mail address: bullinge@eva.mpg.de (A. F. Bullinger).

is that food is shared according to the individuals' contribution to the hunt (Boesch 2002) or in return for coalitionary support (Nishida et al. 1992; Mitani 2006), grooming (Nishida et al. 1992; de Waal 1997; Mitani 2006) or mating opportunities (Tutin 1979; Gomes & Boesch 2009; but see Gilby et al. 2010). Outside of the hunting context, food sharing in chimpanzees is rare (Bethell et al. 2000; Nakamura & Itoh 2001; Slocombe & Newton-Fisher 2005; Hockings et al. 2007) and occurs mainly between mother and dependent offspring, in which mothers usually give only food of low quality or leftovers (McGrew 1975; Nishida & Turner 1996).

Among bonobos, very few sharing events are described in the wild. In accordance with their limited hunting activity and meat consumption, meat sharing is very rarely seen. Reports mainly mention observed sharing events but do not give further details relevant to underlying motives (Hohmann & Fruth 1993; Surbeck & Hohmann 2008). Few observations specifically mention that food is not shared, but instead that the food owner tries to ignore begging scroungers (Badrian & Malenky 1984; White 1994; Fruth & Hohmann 2002). Overall, active tension reduction behaviour such as genito-genital rubbing and copulation is widely described in the context of food sharing (Kuroda 1980; de Waal 1987; Hohmann & Fruth 1996; Wobber et al. 2010a), giving reason to question the degree to which bonobo food possessors voluntarily share their food with others.

Among callitrichids, food is shared almost exclusively from adults to their offspring/siblings owing to their social organization of groups consisting of a breeding pair and related offspring helpers. Rare occasions of food offers to related adults (Rapaport 2001) and to infants of different species (Feistner & Price 1999) are observed. Active food offers are usually preceded by the food possessor soliciting another's approach with a food call (Ferrari 1987; Price & Feistner 2001; Jaeggi et al. 2010a). Most described sharing events, however, fall under the category of tolerated theft occurring in response to begging behaviour of the infants signalling their needs with specific begging calls (Feistner & McGrew 1989; Feistner & Price 2000; Brown et al. 2004). There is also a high percentage of resistance reported (Stevenson & Poole 1976; Feistner & McGrew 1989; Rapaport 2001). The degree to which food is shared voluntarily is therefore debatable.

Experimental research on collaborative problem solving involving food sharing has shown that the level of tolerance and the intensity of the social relationship among partners correlate positively with the ability to solve such problems (bonobos: Hare et al. 2007; callitrichids: Werdenich & Huber 2002; Cronin et al. 2005). More competitive species such as chimpanzees collaborate with others only after tolerance constraints are eliminated and only if the reward is not monopolizable (Chalmeau 1994; Melis et al. 2006a). It has been shown that this effect does not depend on contributed effort (Hamann et al. 2011; Melis et al. 2011a), but rather that subjects act as mandatory collaborators using their partner as a social tool to reach their otherwise inaccessible selfish goal (Melis et al. 2006b; Bullinger et al. 2011a). Levels of tolerance between individuals also affect chimpanzees' aversion to inequity. Specifically, it has been found that chimpanzees are more tolerant to disadvantageous inequity with group members than nongroup members (Brosnan et al. 2005).

In contrast to the evidence of the importance of tolerance, another line of research focusing on other-regarding preferences weakens the idea that increased social tolerance enhances the motivational predisposition towards active food sharing. Some researchers have found that callitrichids are motivated to provide benefits to their partners (Burkart et al. 2007; Cronin et al. 2010; Burkart & van Schaik 2012), whereas others have not (Cronin et al. 2009; Stevens 2010). Results for chimpanzees point mostly in one direction: they make their choices based only on personal gain and are indifferent to rewards for others (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008; Yamamoto & Tanaka 2010; but see Horner et al. 2011). This is true not only for contexts in which they can deliver benefits to others when acting alone but also in a collaborative context (Bullinger et al. 2011a). The only situations in which chimpanzees behave prosocially towards the partner helping her to access food is in instrumental tasks in which the potential helper himself has no access to that food and the recipient signals her needs/goals (Warneken et al. 2007; Yamamoto et al. 2009, 2012; Melis et al. 2011b). Equivalent studies with bonobos have not yet been conducted.

Experimental studies specifically investigating food-sharing events have all used the same paradigm, that is, they have provided individual primates with clumped food to explore spontaneous food interactions (Apes: Nissen & Crawford 1936; Jaeggi et al. 2010b; callitrichids: Feistner & Chamove 1986; Kasper et al. 2008). In such situations it is hard to disentangle voluntary from coerced sharing and hence it is difficult to draw any conclusions about the underlying motivation of the observed sharing behaviour. Only one recent study approached this question by giving unrelated subjects the choice of either seeking or avoiding the presence of a partner while feeding. Hare & Kwetuenda (2010) found that bonobos preferred to open a door for a partner and feed together with them. Notwithstanding the methodological improvements, this study had no condition in which the subject could open the door for a partner when no food was involved, just for 'company', and so it is not clear whether bonobos' preference could be explained by their motivation to feed together or on a more basic level by their motivation to be together with another bonobo more generally.

In the current study, therefore, we aimed to investigate specifically individuals' preference to be or feed either alone or together with a tolerant partner among three primate species of differing social organization: the more competitive chimpanzees, the more tolerant bonobos and the cooperatively breeding marmosets. We predicted that chimpanzees would preferentially choose to stay alone when food was involved, but would not mind having a companion if no food was present. In contrast, we predicted that bonobos and marmosets would preferentially choose to be together with the partner regardless of whether food was present or not.

EXPERIMENT 1

To get additional data for the marmosets, prior to our main experiment (experiment 2), we attempted to run Bullinger et al.'s (2011a) experiment with the same marmosets, that is, the subject had the choice between pulling a platform to within reach either individually or collaboratively with a tolerant partner, both strategies having equivalent payoffs. As we found that subjects were unable to collaborate well enough with the apparatus, we devised an alternative design in which subjects were required to choose between eating alone and eating together with a tolerant partner, with both options resulting in the same payoff.

Methods

Ethical note

Subjects came from groups of common marmosets housed at the primate station of the Anthropological Institute at the University of Zurich, Switzerland. All subjects lived in social groups of various sizes with access to indoor and outdoor areas equipped with branches, ropes, resting places and various enrichment devices. Dyads were tested in familiar rooms of the holding facility (48 × 55 cm and 33 cm high) and could choose to stop participating at any time. The marmosets were regularly fed with gum, mealworms, fresh fruits and vegetables, and cheese, egg, fish or nuts.

They were never food deprived and water was available ad libitum. In the experiment, monkeys received one mealworm per trial. Animal husbandry and research comply with the 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria' and the 'WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums'.

Subjects

Twelve common marmosets (1–9 years) participated in this experiment (eight females and four males). All marmosets were mother reared. All individuals played the role of the subject as well as the partner, with the exception of one male marmoset who only participated as a subject and another male marmoset who only participated as a partner (Table 1). Some subjects had participated previously in partner studies (e.g. Burkart et al. 2007).

Apparatus and set-up

The study was conducted in three adjacent rooms with a choice room in the middle. The rooms were separated by sliding doors (15 × 20 cm) that could only be opened from the choice room but not from the outer rooms. We used two platforms (11 × 40 cm and 0.5 cm high), each with two circular feeding dishes (diameter 3.5 cm and 0.5 cm high) at either end. These platforms were placed outside the outer rooms (20 cm), one on each side, and moved within the marmosets' reach upon the subject entering the choice room. The dishes on the platforms were baited according to their function and were closed with a transparent lid until the subject had made a choice.

Procedure and design

Training. Before entering the test, subjects received thorough training to ensure that they understood how they could manipulate the door. Only subjects showing full understanding and easy handling of the door were allowed to participate in the test.

For that purpose, subjects entered the choice room through another door and had 20 s to open the door to enter one of the adjacent rooms where food was presented on the platform. Subjects had to enter each outer room and obtain the food in four consecutive trials (average of 8.25 trials; range 8–10 trials).

Pretests. Subjects sat in a room above the choice room and could observe the experimenter baiting the platforms. Afterwards the subject entered the choice room and had 1 min to choose (by opening the door) to enter one of the two outer rooms where the respective options were presented. Once the subject opened one door the other door was irreversibly closed so that the other option was no longer accessible. The position of the different options was counterbalanced across trials and within subjects. Four pretests were conducted before starting this test. Pretest 1 served to test whether subjects understood that once they had chosen, they could not switch to the other option. For that purpose the same amount of food was placed in front of each outer room. Subjects had to choose one room and obtain the reward and not try to enter the other room within 1 min in four consecutive trials. On average, subjects needed five trials to pass pretest 1 (mean ± SE = 5.08 ± 0.69). Pretest 2 served to test subjects' ability to pay attention to the baiting process. For that purpose one platform was baited with one and the other with two mealworms. Subjects had to choose the room with the bigger amount of food within 1 min in four consecutive trials. On average, subjects needed seven trials to pass pretest 2 (mean ± SE = 7.25 ± 0.99). Pretest 3 served to test whether subjects were tolerant to a conspecific partner feeding in the same room. For that purpose both dishes of one platform were baited and the conspecific waited in that room, while the other room was empty and the platform was not baited. Subjects had to choose the room with the food and the partner within 1 min in four consecutive trials and both individuals had to receive their food. On average, subjects needed eight trials to pass pretest 3 (mean ± SE = 7.92 ± 1.05). To avoid subjects being biased by the pretest order, and also to test the subjects' ability to attend and switch reliably between the different options, we gave the subjects sessions of eight more trials (pretest 4), four of which were pretest 2 trials and four of which were pretest 3 trials, conducted in a random order. Subjects had to choose the correct option and obtain the reward in three of four trials of each pretest type. On average, subjects needed one session (mean ± SE = 1.17 ± 0.11) to pass pretest 4.

Test. In the test trials, the subject could choose within 1 min between the social and the solo option. In the social option, the partner was waiting in the outer room and both dishes of the platform were baited. In the solo option, the outer room was empty and only one dish of the platform was baited (Movie S1 in the Supplementary Material). Both platforms yielded the same payoff for the subject (and partner), that is, one mealworm for each individual. Subjects participated in 12 trials, administered in two sessions of six trials each. The subject within the pair being tested first had to complete an entire set of 12 trials before the same pair was tested in reverse. Subject–partner order was assigned randomly. The position (left/right room) of the different options was counterbalanced across trials and within subjects, with the only constraint that the same option was never placed in the same location for more than two consecutive trials.

Coding and analyses

All trials were recorded by one camera. A trial started when the subject entered the choice room and finished when the subject (and the partner) received the reward. Data came from live coding and coding from videotapes for the following variables: (1) subject's choice; (2) partner's behaviour during the subject's decision-making process, that is, from when the subject entered the choice room until she made a choice. The observed behaviours were separated into two categories: (1) partner waiting in front of one food dish; (2) partner trying to get the subject's attention by manipulating the door.

Results

Overall, subjects did not differentiate between the solo and the social option (paired t test: $t_{11} = 1.169$, $P = 0.267$; Table 1) and did

Table 1
The sex, age, social group, rearing history, relationship and the % of solo choices for each subject tested in experiment 1

Subject	Sex	Age (years)	Group	Rearing history	Relationship	Solo choices
Vreni	Female	9	A	Mother	Unrelated breeders	50
Juri	Male	9		Mother		83.33
Verona	Female	5	A	Mother	Adult siblings	41.67
Venezia	Female	5		Mother		75
Vesta	Female	6	A	Mother	Adult siblings	25
Venus	Female	6		Mother		75
Vito*	Male	4	A	Mother	Adult son	58.33
Vreni	Female	9		Mother	Mother	
Kapi	Male	8	B	Mother	Adult siblings	58.33
Kantor	Male	7		Mother		50
Jojoba	Female	4	C	Mother	Mother	41.67
Jet†	Male	1		Mother	Adult son	
Jupie	Female	1	C	Mother	Subadult siblings	58.33
Jaja	Female	1		Mother		50

* This individual participated only as a subject as his partner had already performed the role of the subject in a previous pairing.
† This individual participated only as a partner as he did not pass pretest 4.

not have a side preference (one-sample t test: $t_{11} = 0.582$, $P = 0.572$). Subjects chose the solo option on average in 56% (range 25–83%) of the trials.

For 84.7% of the trials, we could determine the partner's behaviour during the subject's decision-making process. Partners mainly waited in front of one food dish (96.9%, range 80–100%). In 3.1% (range 0–20%) of the trials, partners tried to get the subject's attention by manipulating the door. Neither of these behaviours had any influence on the subject's choice (paired t tests: waiting at food dish: $t_{11} = 1.000$, $P = 0.339$; getting subject's attention: $t_{11} = 1.000$, $P = 0.339$).

Discussion

Overall, marmosets were indifferent as to whether they ate alone or together with a tolerant partner. We cannot easily explain the behaviour of these subjects. Either the subjects really did not make a difference or the methods used were not ideal to test it. Maybe giving them the choice between two doors was cognitively too demanding and they did not intentionally choose one over the other room, although the pretests were aimed at showing that they could differentiate and did pay attention.

EXPERIMENT 2

Our goal in experiment 2 was to investigate whether the indifference of marmosets to feeding alone or together with a tolerant partner in experiment 1 was due to methodological problems or really to their indifference. Furthermore, the new study design aimed to compare marmosets' performance with that of two other primate species, the chimpanzee and the bonobo.

Methods

Ethical note

Subjects came from a group of captive chimpanzees and bonobos housed at the Wolfgang-Köhler Primate Research Center in the Leipzig Zoo, Germany and from groups of common marmosets housed at the primate station of the Anthropological Institute at the University of Zurich, Switzerland. The marmosets and their test conditions were the same as in experiment 1. All subjects lived in social groups of various sizes with access to indoor and outdoor areas equipped with branches, ropes, resting places and various enrichment devices. Dyads were tested in familiar rooms of the holding facility (260 × 250 cm and 250 cm high for the apes) and could choose to stop participating at any time. The apes were regularly fed with fruits and vegetables, and meat, egg, nuts or pellets. They were never food deprived and water was available ad libitum. For the study a mixture of medium-value to high-value food was used: crushed banana pellets, leaf primate pellets, crisp bread, raisins and grapes (300 g per trial) for the apes and one crushed Nuss-Stängeli (nut cracker) and three mealworms for the monkeys. The amount of food per trial was more than one individual could eat within the given trial length. Animal husbandry and research comply with the 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria' and the 'WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums'.

Subjects

The same marmosets and dyads as in experiment 1 participated in this experiment with the exception of one male marmoset that was not motivated to participate in this experiment and was replaced by another male marmoset that only acted as a partner in experiment 1. Additionally, 14 chimpanzees (6–35 years) and six

bonobos (6–28 years) participated in this experiment. There were 19 females (three bonobos, eight chimpanzees, eight marmosets) and 13 males (three bonobos, six chimpanzees, four marmosets). All adult chimpanzees and male bonobos were nursery reared, whereas all other subjects (nonadult chimpanzees, female bonobos and all marmosets) were mother reared (Table 2). Based on a previous tolerance test (see details below), individuals that were equivalent in terms of social dominance were paired into dyads, in which both individuals played the role of the subject as well as the partner, with the exception of one bonobo female who only participated as a partner (Table 2). Some subjects had participated previously in partner studies (e.g. Burkart et al. 2007; Bullinger et al. 2011b; Hamann et al. 2011).

Design and materials

The study was conducted using a 2 × 2 design with the factors 'food' and 'partner' as within-subjects variables, resulting in four conditions: (1) food–partner (FP); (2) food–no partner (FNP); (3) no food–partner (NFP); (4) no food–no partner (NFNP) with the NFNP condition serving as a baseline to measure the subjects' general motivation to open doors. Conditions were administered in blocks with four trials per condition. The order of blocks was systematically varied by means of a Latin square design. Subjects were randomly assigned to the different orders. Test sessions consisted of two conditions (eight trials) per day: one food and one nonfood condition (see Appendix for details).

The study was conducted in two adjacent rooms (Fig. 1), with the partner, if present, waiting in one room (partner's room) and

Table 2
The sex, age, social group, rearing history and relationship for each subject tested in experiment 2

Pair	Subject	Sex	Age (years)	Group	Rearing history	Relationship
Bonobos						
1	Joey	Male	28	A	Nursery	Unrelated
	Jasongo	Male	21		Nursery	
2	Yasa	Female	14	A	Mother	Unrelated
	Kuno	Male	14		Nursery	
3	Luiza	Female	6	A	Mother	Unrelated
	Bokela*	Female	7		Mother	
Chimpanzees						
4	Corrie	Female	34	A	Nursery	Unrelated
	Fraukje	Female	35		Nursery	
5	Sandra	Female	18	A	Mother	Half-siblings
	Frodo	Male	17		Mother	
6	Kara	Female	6	A	Mother	Half-siblings
	Kofi	Male	6		Mother	
7	Lobo	Male	7	A	Mother	Half-siblings
	Pia	Female	11		Mother	
8	Lome	Male	9	A	Mother	Son
	Robert	Male	35		Nursery	Father
9	Riet	Female	33	A	Nursery	Mother
	Tai	Female	8		Mother	Daughter
10	Patrick	Male	14	A	Mother	Unrelated
	Natascha	Female	31		Nursery	
Marmosets						
11	Vreni	Female	9	A	Mother	Unrelated breeders
	Juri	Male	9		Mother	
12	Verona	Female	5	A	Mother	Adult siblings
	Venezia	Female	5		Mother	
13	Vesta	Female	6	A	Mother	Adult siblings
	Venus	Female	6		Mother	
14	Kapi	Male	8	B	Mother	Adult siblings
	Kantor	Male	7		Mother	
15	Jojoba	Female	4	C	Mother	Mother
	Jet	Male	1		Mother	Adult son
16	Jupie	Female	1	C	Mother	Subadult siblings
	Jaja	Female	1		Mother	

The subject name mentioned first indicates the subject tested first in that pairing.
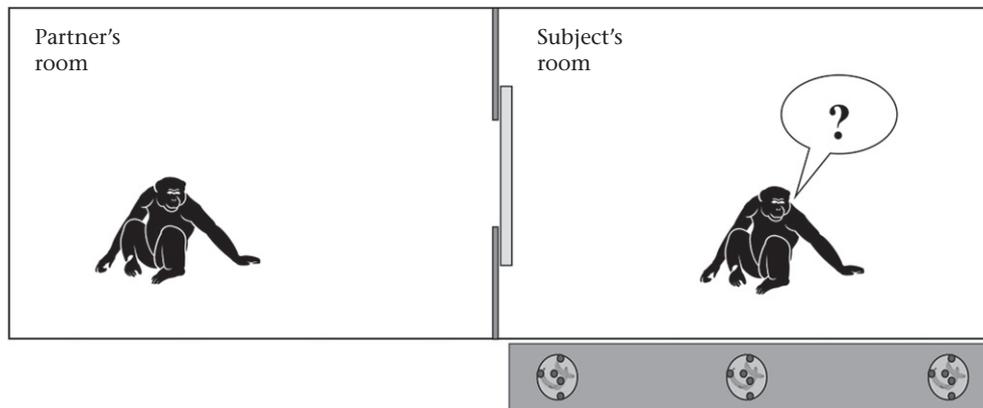* This individual participated only as a partner as she did not pass the training.

Figure 1. Room layout and set-up.

the subject waiting in the other room (subject's room). The rooms were separated by a sliding door that could only be opened from the subject's room but not from the partner's room. Small piles of shareable food, if present, were placed on three maximally distant locations on a platform that spread over the full length in front of the subject's room (see Appendix for exact measurements).

Procedure
Training and tolerance test. Before entering the test, subjects received thorough training to ensure that they understood how they could manipulate the door. Only subjects showing full understanding and easy handling of the door were allowed to participate in the test. For that purpose, subjects entered the subject's room through another door and had 20 s to open the door to enter the partner's room where food was presented on the platform that spread over the full length in front of the partner's room. Subjects had to open the door and obtain the food in four consecutive trials (average of 17.48 trials; range 8–45 trials). After reaching that criterion, they experienced four trials (1 min each) in which the food was placed in the subject's room and they were in the partner's room. The purpose of these trials was to make subjects understand that they could not open the door from the partner's room.

For the purpose of the study we also needed to make sure that subjects were tolerant of each other feeding in the same room. Therefore we paired potential partners in the subject's room with the door to be potentially opened and checked whether they were able to feed together in the same room with the food presented, as in the test, in piles of shareable food on three maximally distant locations on the platform. If both individuals got food and neither opened the door to seek more distance from the partner, the pair was considered tolerant.

Test. Once everything was set up according to condition (food and/ or partner being present or not), the subject was allowed to enter the subject's room through another door. Marmosets had 1 min, bonobos and chimpanzees 2 min to eat the food, if present, and/or to open the door, thereby allowing the partner, if present, to join the subject (Fig. 1 and Movie S2 in the Supplementary Material).

All subjects except one male chimpanzee opened the door at least once throughout the test, proving that they were skilled at opening the door.

Coding and analyses
All trials were videotaped. A trial started when the subject entered her room and finished after 1 min for the marmosets/2 min for the apes. Data came from coding from videotapes for the

following variables: (1) opening door; (2) time of opening door; (3) food left at time of opening door; (4) partner's behaviour directed at the subject's room (i.e. indicating their intent to enter or potentially harass the subject; the observed behaviours were separated into two categories: (a) silent, i.e. partner waiting silently at the door and looking into the subject's room, and (b) audible, i.e. partner moving the door, trying to reach into the room or vocalizing); (5) subject's first behaviour after opening the door (the observed behaviours were (a) interacting with the partner such as co-feeding, playing, sexual interaction, greeting each other; (b) remaining in close proximity versus sitting apart from each other; (c) entering the adjacent room). Reported differences are significant at $P < 0.05$ (two-tailed) for all tests.

Preliminary analyses for 2 min trials showed that different partners, kinship and trial length had no effect on door opening (see Appendix for results). For comparability to the marmoset data set, the subsequent analyses were therefore based only on data of the first pairing and the first minute of a trial. Further analyses revealed that subject–partner order and condition order did not have any effect on whether subjects opened the door. Subsequent analyses were thus performed on data ignoring these factors.

To assess interobserver reliability, a second coder, ignorant of the hypotheses and the procedure of the experiment, coded 25% of the videotapes. Excellent agreement on whether subjects opened the door (Cohen's $K = 0.98$), partners' behaviour (Cohen's $K = 0.82$), subjects' behaviour (Cohen's $K = 0.93$) and on the time of opening the door was achieved (Spearman correlation: $r_S = 1.000$, $N = 80$, $P < 0.001$).

Results

The major variable affecting door opening for all three species was whether or not food was present (see Fig. 2a): they all opened the door much more often if there was no food available ($2 \times 2 \times 3$ (food $\times$ partner $\times$ species) repeated measures ANOVA: main effect of food: $F_{1,28} = 48.678$, $P < 0.001$, $\eta^2 = 0.635$). There was no main effect of partner and all interactions were nonsignificant. There were no significant effects of gender on subject's tendency to open the door between partner and no-partner conditions ($2 \times 2 \times 3$ (condition $\times$ gender $\times$ species) repeated measures ANOVA: no significant effects or interactions).

The different species had different tendencies to open the door ($F_{2,28} = 3.548$, $P = 0.042$, $\eta^2 = 0.202$), especially in the NFNP condition when they were simply alone without food and no partner was next door. We thus attempted to correct for this species' difference by using difference scores as a dependent measure; that is, each subject's door opening in the NFNP condition
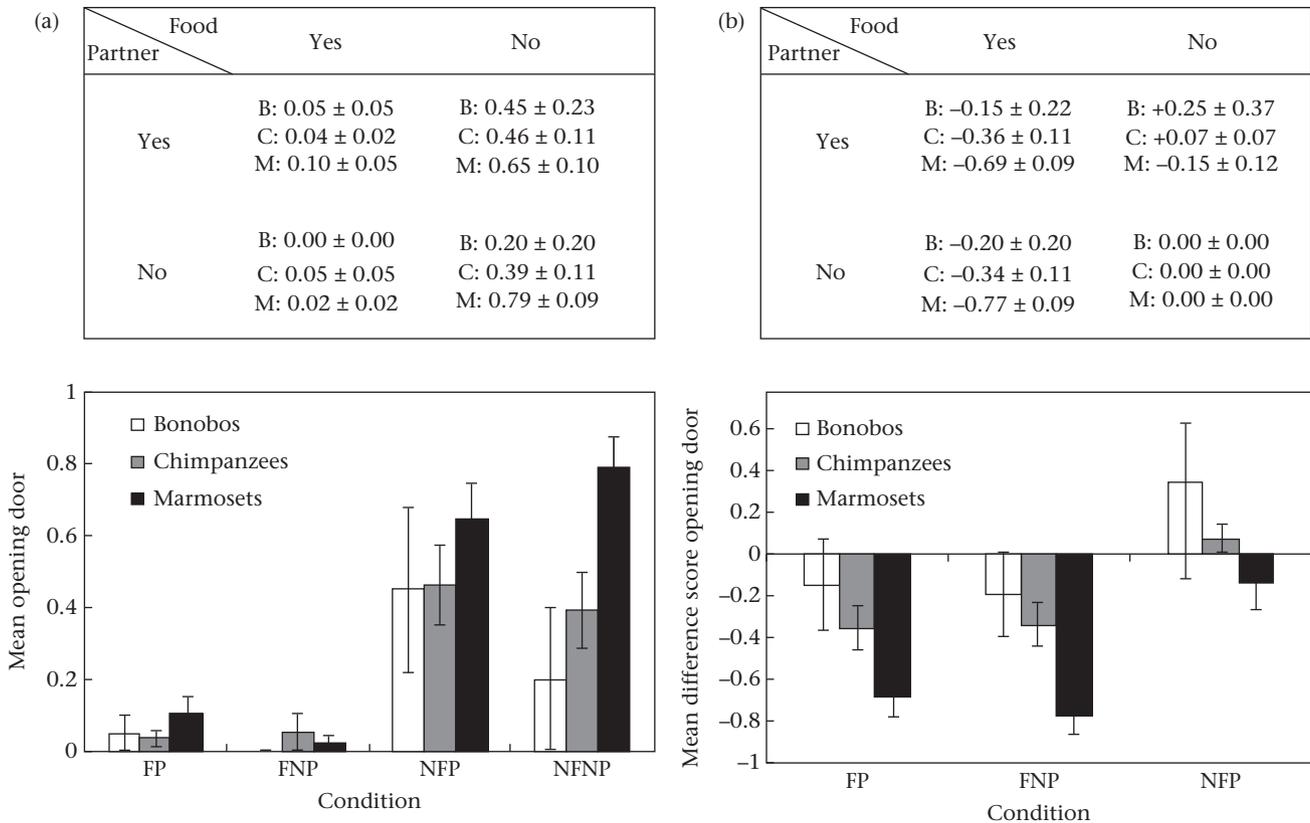
(a)

Partner \ Food	Yes	No
Yes	B: 0.05 ± 0.05 C: 0.04 ± 0.02 M: 0.10 ± 0.05	B: 0.45 ± 0.23 C: 0.46 ± 0.11 M: 0.65 ± 0.10
No	B: 0.00 ± 0.00 C: 0.05 ± 0.05 M: 0.02 ± 0.02	B: 0.20 ± 0.20 C: 0.39 ± 0.11 M: 0.79 ± 0.09

(b)

Partner \ Food	Yes	No
Yes	B: –0.15 ± 0.22 C: –0.36 ± 0.11 M: –0.69 ± 0.09	B: +0.25 ± 0.37 C: +0.07 ± 0.07 M: –0.15 ± 0.12
No	B: –0.20 ± 0.20 C: –0.34 ± 0.11 M: –0.77 ± 0.09	B: 0.00 ± 0.00 C: 0.00 ± 0.00 M: 0.00 ± 0.00

Figure 2. (a) Mean and SE of opening the door for species across the four conditions. (b) Mean difference scores and SE of opening the door for species across the three conditions. B = bonobos; C = chimpanzees; M = marmosets; FP = food–partner condition; FNP = food–no-partner condition; NFP = no-food–partner condition; NFNP = no-food–no-partner condition.

was subtracted from its score in the FP, FNP and NFP conditions to yield different score measures for each of the three conditions in which food or partner or both, were present (Fig. 2b). A 3 × 3 repeated measures ANOVA of the mean difference scores with species as a between-subjects factor and the three conditions (FP; FNP; NFP) as within-subjects factors revealed a main effect of condition ($F_{2,56} = 31.340$, $P < 0.001$, $\eta^2 = 0.528$) and species ($F_{2,28} = 4.572$, $P = 0.019$, $\eta^2 = 0.246$). There was no interaction between the two factors (condition * species: $F_{4,56} = 0.664$, $P = 0.619$, $\eta^2 = 0.045$). Post hoc comparisons using the Fisher LSD revealed that marmosets opened the door significantly less often than bonobos ($P = 0.012$) and chimpanzees ($P = 0.026$) and that subjects opened the door significantly less often in the FP ($P < 0.001$) and FNP ($P < 0.001$) condition than in the NFP condition. There was no significantly different pattern between chimpanzees and bonobos.

When we calculated the difference from baseline (NFNP) as a percentage of baseline, we found that subjects chose to open the door in food conditions much less often than in the baseline (on average −89.4%; bonobos: −87.5%, range 12.5 to −100%; chimpanzees: −88.64%, range 0 to −100%; marmosets: −92.12%, range −50 to −100%). Offering the choice to have company (NFP) caused the marmosets to open the door a little less often (−18.42%, range 200 to −100%), the chimpanzees to open the door a little more often (+18.18%, range −33.3 to 100%), but the bonobos to open the door more than twice as often as in the baseline (+125%; range 100 to −100%).

Across the three species we could observe directed behaviour of the partners towards the subject's room to various extents across the partner conditions. Subjects opened the door less if partners manipulated the door or vocalized (Fig. 3; see Appendix for results).

The behaviour of dyads after the door was opened in the partner conditions differed between species. In the NFP condition, bonobos interacted in 60% of the trials, either playing (50%) or copulating (10%). Chimpanzees interacted in 58% of the trials, either playing (50%) or greeting each other and remaining in close proximity (8%). In the remaining trials, bonobos and chimpanzees sat apart from each other. Marmosets did not interact with the partner in the majority of the trials (94%), but instead moved restlessly through the rooms. Only in the remaining 6% of the trials did they seek close
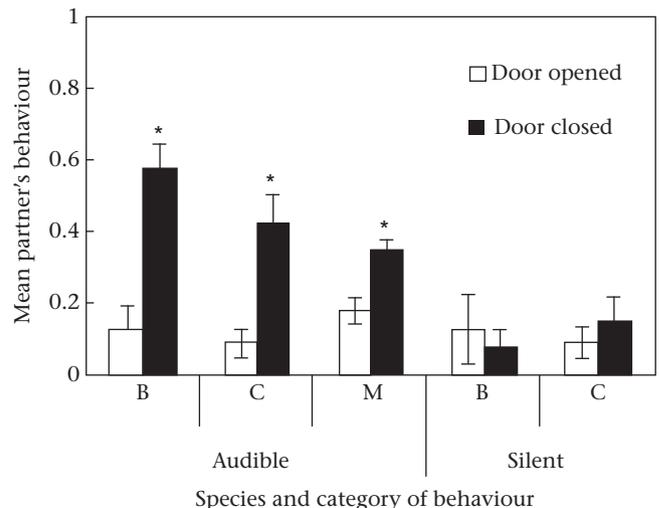

Figure 3. Mean and SE of partner's behaviour for species and behavioural categories. B = bonobos; C = chimpanzees; M = marmosets; * paired t tests: $P < 0.05$.

proximity. In the FP condition, there was always enough food left to last both individuals at the time when the door was opened. Co-feeding was observed in only one trial of each species. Co-feeding in bonobos was preceded by sexual interaction and in chimpanzees by greeting, while marmosets went straight to the food. In the remaining trials of the FP condition, in which the door was opened, no co-feeding was observed: in one trial of the chimpanzee opening the door, the two individuals did not approach the food, but started to play; in one trial of the marmoset opening the door, the partner did not approach the food, while the subject returned to the food; in three trials of the marmosets opening the door, partners approached the food, while the subject refrained from returning to the food, although no aggressive interaction could be observed between individuals.

Subjects' behaviour after the door was opened in the no-partner conditions was very similar between species. In the NFNP condition, subjects entered the adjacent room in the majority of trials (89%); in the other trials they just opened the door and remained sitting close by (11%). In the FNP condition, chimpanzees always just opened the door within the first 3 s after entering the room and immediately returned to the food to continue eating. The one trial in which the marmoset opened the door, she entered the adjacent room after 48 s upon hearing vocalizations from her group members and did not return to the food within the remaining 12 s. In all other trials, subjects went straight to the food upon entering the room and were occupied with feeding throughout the trial.

Discussion

When given the choice to open a door in order to be with or to feed together with a tolerant partner, chimpanzees, bonobos and marmosets all preferred to stay alone when food was present, but opened the door more readily for the partner as soon as food was no longer involved. However, the same pattern was also present in the nonsocial control conditions: When no partner was present, subjects preferred not to open the door when food was present, but opened the door more readily to the empty compartment as soon as food was no longer involved. This shows that the subjects were not generally unwilling/unable to open a door, but rather that they were refraining from this behaviour if food was present, largely regardless of whether a partner was present or not.

In the baseline (NFNP), subjects of all species often opened the door (46.2%). This can be explained by subjects' curiosity to explore and look for interesting items where there is nothing else to do. The only condition in which subjects opened the door more often than in the baseline was in the NFP condition (52%), although this was not true for the marmosets (−18%). Having opened the door, marmosets rarely sought proximity to their partner, but instead moved restlessly through the rooms. Being close to a group member apparently was not motivating for them. Probably they were motivated by a desire to increase the area of accessible space or to open the door per se, a desire suppressed by the presence of food. The apes in contrast at first sought to interact with the conspecific in the majority of the trials (59%). Apes' opening the door in this NFP condition thus suggests a motivation to be together or at least shows that the subjects do not mind having the partner around them if no food is present.

In relation to the baseline, chimpanzees (−88%) and marmosets (−92%) opened the door significantly less often in the food conditions suggesting that the presence of food has an influence on subjects' preferences to engage in other behaviour such as opening doors. Opening the door in the FNP condition rarely happened (2.5%), as subjects were basically busy eating. Subjects who did open the door usually returned immediately to the food, suggesting that it was just a brief diversion from the task at hand. Opening the

door in the FP condition also rarely occurred (6.3%). These results do not support the hypothesis that the more tolerant species, bonobos and marmosets, overall seek co-feeding. We tried to increase the potential for co-feeding for all species by pairing together highly tolerant subjects, that is, ensuring prior to the test phase that pairs were able to co-feed without any aggression or attempts to monopolize the food if externally constrained to be in the same room with food. Even though we supplied more food than one individual could eat within the given time interval, subjects did not open the door for their conspecific and also did not increase doing so across trials after realizing that food was abundant. Despite the fact that opening the door would have benefited the partner at little cost (in terms of loss of food) to themselves, subjects preferred to stay alone when feeding. Other studies that do not involve food sharing support this finding, showing that subjects do not deliver food to others at no cost to themselves (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008; Cronin et al. 2009). For chimpanzees at least, this is true not only for contexts in which they can deliver benefits to others when acting alone, but also, as another study establishes (Bullinger et al. 2011a), in a collaborative context. Experiment 1, using a different method, supports these findings for the marmosets, showing that they were indeed indifferent as to whether they fed alone or together with a tolerant partner. So, at least for marmosets and chimpanzees two different methods showed that they do not seek company to feed/collaborate unless this company is associated with higher payoffs (at least for the chimpanzees).

One could argue, similar to findings on chimpanzees' instrumental helping behaviour (e.g. Warneken et al. 2007; Yamamoto et al. 2009, 2012; Melis et al. 2011b), that in the presence of the food subjects were so preoccupied obtaining their selfish goals that they forgot about others' needs. The partners in the current study, however, were unmistakably signalling their preference to join in 58% of the trials. While such overt signalling of their needs and goals had a positive effect on chimpanzees' behaviour in instrumental helping tasks, our study showed a negative effect on subject's willingness to open the door. Similar results were obtained in studies focusing on other-regarding preferences showing that begging and reaching attempts either had no or a negative effect on prosocial behaviour (Burkart et al. 2007; Vonk et al. 2008; Cronin et al. 2009; Horner et al. 2011; but see Takimoto et al. 2010). Another explanation for less frequently opening the door in this condition could of course be the threat of competition for food, even if pairs were tolerant. In the few cases in which subjects chose to open the door, their goal was not always to co-feed: chimpanzees played rather than co-fed in 50% of the trials, suggesting that they rather opened the door for company (as if they were in NFP trials) and marmoset subjects stopped eating and let the partner have the rest of the food in 75% of the trials, suggesting that they were no longer interested in the food (see Appendix for details). In the few co-feeding instances, however, we observed tension reduction behaviour beforehand, that is, copulation/genito-genital rubbing in bonobos and submissive greeting in chimpanzees.

The current results conflict with those of Hare & Kwetuenda (2010), who found that bonobos preferred to open a door for a partner in order to feed together. One possible explanation is that the subjects in Hare & Kwetuenda's study lived in a sanctuary. Maybe they are less used to being separated from other group members inside the holding facility and felt much less comfortable when being alone (independently of feeding or not), leading to much higher door-opening levels. Hare & Kwetuenda's finding on high levels of social interaction before finishing the food (67.6%) supports this idea. So maybe what Hare & Kwetuenda found was not bonobos' preference to feed together, but rather their preference to be together, a result that is in line with our findings.

Unfortunately our sample size for the bonobos was too small to establish whether or not this is a significant effect in the NFP condition (see Appendix for further possible explanations).

Overall, this study shows that all tested species regardless of their social organization and associated levels of tolerance readily open the door for a partner as long as no food is involved, but stop doing so when food is available. However, since the same pattern of door opening was present in the complete absence of a partner, two alternatives have to be considered. The first is that the effect is purely nonsocial, and that the availability of food reduces their tendency to open the door by default, since they are busy feeding. The second is that they do not voluntarily seek the presence of conspecifics during feeding bouts. Both explanations might suggest that cases of food sharing observed in the wild do not reflect intrinsically motivated behaviour of the food owner, but are rather externally enforced either by fairly moderate means in the case of solicitation behaviour, or more aggressive means in the case of harassment. Even though bonobos' and marmosets' natural behaviour appears to be more tolerant than chimpanzees' behaviour (but see Jaeggi et al. 2010b), their level of tolerance does not suffice to give rise to voluntary co-feeding. Perhaps the behaviour of the 'more tolerant species' is not really more tolerant, but it is their passive strategy to cope with socially tense situations. In contrast such situations escalate in the 'more competitive species' to severe aggression or avoidance behaviour. Studies on increased hormonal stress levels in the *Pan* species during feeding bouts support this idea (Hohmann et al. 2009; Wobber et al. 2010b), showing that both bonobos and chimpanzees have increased levels of steroids when confronted with restricted food access in a social context. While bonobos show an increase in cortisol, a hormone that helps to cope with stress, chimpanzees show an increase in testosterone, a hormone connected to high aggression potentials. Additionally, bonobos and chimpanzees are averse to food loss and try to avoid such losses (Heilbronner et al. 2008; Wobber et al. 2010a).

It is of course possible that the current results are confined to the species studied and/or to the captive situations in which they were studied. Also, the door-opening paradigm might be less straightforward than it may look for testing primates' preferences to be/feed together. Maybe the costs of opening the door are too high to pay for the potential benefits. Additionally, the specific task setting seems important, as the marmosets were the same individuals as in the study by Burkart et al. (2007), in which they showed other-regarding preferences. Future research should target a wider range of species and contexts to determine whether, under what circumstances and to what degree the various primate species seek out conspecific companionship.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2012.10.006.

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Appendix

Design and Materials

The subject within the pair being tested first had to complete an entire set of 16 trials, before the same pair was tested in reverse. Bonobos and chimpanzees were tested with several partners, whereas marmosets were tested with only one. Bonobos were paired with up to four different partners (13 dyads in total; no mother–offspring dyads; only one pair with related subjects [half-siblings]) and chimpanzees were paired with three different partners (four mother–offspring, one siblings, two father–offspring, seven half-siblings, seven unrelated). Subject–partner order was assigned randomly.

The subject's room measured 260 × 250 cm and 250 cm high for the apes and 72 × 55 cm and 33 cm high for the monkeys, that is, they had the same relationship of average body size to room size. The sliding door measured 60 × 80 cm for the apes and 15 × 20 cm

for the monkeys. The platform for the food piles measured 160 cm for the apes and 40 cm for the monkeys.

Results

Preliminary analyses, for the 2 min trials, of chimpanzees' and bonobos' opening the door across all four conditions revealed that different partners had no effect on subjects' behaviour (bonobos: $F_{2,4} = 0.615$, $P = 0.477$, $\eta^2 = 0.133$; chimpanzees: $F_{2,26} = 0.138$, $P = 0.872$, $\eta^2 = 0.011$). Kinship in chimpanzees also had no effect (independent-sample *t* test: $t_{40} = 1.123$, $P = 0.268$). Furthermore, it did not matter whether trials lasted 1 or 2 min. A 2×2 repeated measures ANOVA (food × partner) separately for each species revealed a main effect of food for both species (bonobos: $F_{1,4} = 16.000$; $P = 0.016$, $\eta^2 = 0.8$; chimpanzees: $F_{1,13} = 18.118$; $P = 0.001$, $\eta^2 = 0.582$). There was no main effect of partner and no interaction between the two factors. Bonobos opened the door on average 31 s after entering the subject's room, in the majority of trials (82%) before 1 min had passed. Chimpanzees opened the door on average 28 s after entering the subject's room, in the majority of the trials (85%) before 1 min had passed.

Across the three species we could observe directed behaviour of the partners towards the subject's room to various extents across the partner conditions. Bonobos showed directed behaviour in 90.0% of the trials. Partners either waited silently at the door (20.0%, range 0–50%) or employed audible behaviours by manipulating the door or vocalizing (70.0%, range 50–88%). Chimpanzees showed directed behaviour in 75.0% of the trials. Partners either waited silently at the door (24.1%, range 0–88%) or employed audible behaviours by manipulating the door (50.9%, range 0–100%). Marmosets showed directed behaviour in only 52.1% of the trials; all of these were audible behaviours by manipulating the door (range 25–75%). While silently waiting at the door had no influence on the subject's choice in any species (paired *t* tests: bonobos: $t_4 = 0.387$, $P = 0.718$; chimpanzees: $t_{13} = 0.739$, $P = 0.473$), audible behaviours did in all species (paired *t* tests: bonobos: $t_4 = 3.846$, $P = 0.018$; chimpanzees: $t_{13} = 4.077$, $P = 0.001$; marmosets: $t_{11} = 2.966$, $P = 0.013$), such that subjects opened the door less if partners manipulated the door or vocalized (Fig. 3). The partners' behaviour did not differ between conditions (paired *t* tests: (a) silent behaviour: bonobos: $t_4 = 2.359$, $P = 0.078$; chimpanzees: $t_{13} = 1.242$, $P = 0.236$; (b) audible behaviour: bonobos: $t_4 = 1.969$,

$P = 0.120$; chimpanzees: $t_{13} = 1.194$, $P = 0.254$; marmosets: $t_{11} = 2.128$, $P = 0.057$).

Discussion

In the few cases of the FP condition in which subjects had chosen to open the door, subjects did not open the door to co-feed. In half of the trials in which chimpanzees opened the door, individuals played rather than co-fed, so the subject rather opened the door for company. Playing could also be a means to reduce tension and increase tolerance around food (Palagi et al. 2004). In the majority of the trials in which marmosets opened the door (75%), only one individual fed while the other stayed away from the food. It is important to note, though, that in these trials no aggressive behaviour or attempts to monopolize the food between the tested pair was observed, so that both individuals could have approached the food.

The conflict between the current results and those of Hare & Kwetuenda (2010) could have various other reasons: Motivations to co-feed might also relate to acquaintance between individuals or age. Subjects in Hare & Kwetuenda's study who opened the door for a partner were mainly juveniles and opened the door for a stranger and not for a groupmate, which also supports the interpretation that they could have opened the door out of curiosity or other social reasons, but not necessarily to share food. Relationship between bonobos in our study did not have an influence on the behavioural pattern, despite the fact that two bonobos participating in the study were 'strangers' to the group having just been introduced (opening door for stranger: 21%; opening door for groupmate: 19%). For analysing effects of age, the sample size was too small in our study, but from the raw data there was no hint that this factor consistently characterized the behavioural patterns. Another possible explanation is the different methodology employed by the two studies. In their study, subjects could choose to open two doors and the researchers coded whether they preferred to open the door for the conspecific rather than to an empty room. In that sense, our study used a simplified version that should have resulted in an overall higher degree of door opening, which is not what we found. Another possible explanation is that there was a difference in the amount and type of food the different studies used. Maybe subjects in our study were much more motivated to eat the food provided.