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Tolerant Food Sharing and Reciprocity Is Precluded by Despotism Among Bonobos But Not Chimpanzees

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KEY WORDS dominance hierarchy; food sharing; *Pan paniscus*; *Pan troglodytes*; prosociality; reciprocal altruism

ABSTRACT Tolerant food sharing among human foragers can largely be explained by reciprocity. In contrast, food sharing among chimpanzees and bonobos may not always reflect reciprocity, which could be explained by different dominance styles: in egalitarian societies reciprocity is expressed freely, while in more despotic groups dominants may hinder reciprocity. We tested the degree of reciprocity and the influence of dominance on food sharing among chimpanzees and bonobos in two captive groups. First, we found that chimpanzees shared more frequently, more tolerantly, and more actively than bonobos. Second, among chimpanzees, food received was the best predictor of food shared, indicating reciprocal exchange, whereas among bonobos transfers were mostly unidirectional. Third, chimpanzees had a shallower and less linear dominance hierarchy, indicating that they were less despotic than

bonobos. This suggests that the tolerant and reciprocal sharing found in chimpanzees, but not bonobos, was made possible by the absence of despotism. To investigate this further, we tested the relationship between despotism and reciprocity in grooming using data from an additional five groups and five different study periods on the main groups. The results showed that i) all chimpanzee groups were less despotic and groomed more reciprocally than bonobo groups, and ii) there was a general negative correlation between despotism and grooming reciprocity across species. This indicates that an egalitarian hierarchy may be more common in chimpanzees, at least in captivity, thus fostering reciprocal exchange. We conclude that a shallow dominance hierarchy was a necessary precondition for the evolution of human-like reciprocal food sharing. *Am J Phys Anthropol* 143:41–51, 2010. © 2010 Wiley-Liss, Inc.

Extensive food sharing is universal among human foragers and has received considerable attention as a model for the evolution of altruistic behavior (Gurven, 2004). Ultimately, food sharing among unrelated humans can be explained by tolerated scrounging (Blurton-Jones, 1984) and/or some form of direct or indirect reciprocity (Alexander, 1987; Trivers, 1971). The relative importance of the two models depends on the degree of control producers have over food distribution: if this control is high, reciprocal sharing patterns are more likely (Gurven, 2004). Proximally, voluntary food sharing reflects high levels of prosociality which have probably co-evolved with reciprocity (Trivers, 1971, 2006). Food sharing is also universal in *Pan*, having been reported from every major study site of both chimpanzees and bonobos (Table 1). How then is food sharing regulated among our closest living relatives?

As for human food sharing, two main hypotheses have been put forward to explain the function of food transfers among nonhuman primates: reciprocal exchange and sharing-under-pressure. Food represents a commodity that can be traded for itself or other commodities such as grooming, sex, or support on a biological market (Noë and Hammerstein, 1994). Such *reciprocal exchange* of food has been reported from a variety of different species including capuchin monkeys (de Waal, 2000) and chimpanzees (de Waal, 1989, 1997; Mitani and Watts, 2001; Mitani, 2006; Gomes and Boesch, 2009), but only limited support has been found in bonobos (Fruth and Hohmann, 2002). Lack of reciprocity may be explained

by transfers being forced rather than tolerated: as Noë and Hammerstein (1994; p. 1) pointed out, “market forces cannot function if it is possible to appropriate desired commodities without the consent of the owner.” In this case, food transfers may be better described as *sharing-under-pressure* (Wrangham, 1975). This hypothesis, which was formalized in a model by Blurton Jones (1984) and later Stevens and Stephens (2002), proposes that food owners may relinquish (part of) their food if the costs of defending it are higher than the benefits of consuming it. This model has been shown to explain food transfers among some groups of chimpanzees and bonobos, as transfers increased with increasing harassment (Fruth and Hohmann, 2002; Gilby, 2006). However, as Stevens and Gilby (2004) and Gilby (2006) have pointed

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TABLE 1. Reported food sharing among adults of well studied chimpanzee and bonobo populations with main references

Species	Study site
Chimpanzees (<i>Pan troglodytes</i>)	Bossou (only plant food) ^a
	Budongo ^b
	Gombe ^c
	Mahale ^d
	Ngogo ^e
	Tai ^f
Bonobos (<i>Pan paniscus</i>)	Lomako ^g
	Lui Kotale ^h
	Wamba (only plant food) ⁱ

^a Hockings et al., 2007.

^b Suzuki, 1971; Reynolds, 2005.

^c van Lawick-Goodall, 1968; Teleki, 1973; Wrangham, 1975; Tutin, 1979; Goodall, 1986; Stanford, 1999; Gilby, 2006; Gilby et al., in press.

^d Nishida, 1970; Suzuki, 1971; Nishida et al., 1992, 1979; Kawana, 1982; Takahata et al., 1984; Hosaka et al., 2001.

^e Mitani and Watts, 2001; Watts and Mitani, 2002; Mitani, 2006.

^f Boesch and Boesch, 1989; Boesch, 1994; Gomes and Boesch, 2009.

^g Hohmann and Fruth, 1993; White, 1994; Fruth and Hohmann, 2002.

^h Hohmann and Fruth, 2008; Surbeck and Hohmann, 2008.

ⁱ Kano, 1980; Kuroda, 1984.

out, the two hypotheses are not mutually exclusive. Reciprocal sharing patterns may still emerge if food owners can retain control over food distribution, despite the costs inflicted by harassment, and selectively relinquish food to particular individuals, e.g. those who relinquished food to them in the past (see also Moore, 1984). Thus, the amount of reciprocal exchange possible is determined by the amount of control owners can exert over food distribution, which depends on the costs of defending food. Here we suggest that these costs, and thus the opportunity for reciprocal exchange, depend on the dominance structure of the population. When dominance hierarchy is steep, dominants can monopolize resources or commodities and there is no reciprocal exchange. In the words of Trivers (1971), "strong dominance hierarchies reduce the extent to which . . . the less dominant individual is capable of performing a benefit for the more dominant *which the more dominant individual could not simply take at will*" (p. 38, emphasis added).

Proximately, the degree of prosociality in food sharing may be measured by the reactions of food owners to approaches and the way in which food is transferred (Jaeggi et al., in review). Thus, positive reactions to approaches and tolerant sharing would reflect more prosociality than negative reactions and forced transfers. Among chimpanzees, food transfers can vary from relatively active to mainly passive, reluctant, or even aggressive (e.g. Teleki, 1973; Boesch and Boesch, 1989; Gilby, 2006), but no formal hypotheses have been put forward to explain differences in sharing patterns between populations. Similar differences probably exist among bonobos although data are scarcer and harder to compare because of different food types being shared (sugar cane (Kuroda, 1984), large fruits (White, 1994), and meat (Fruth and Hohmann, 2002)). In the only study thus far directly comparing food sharing in the two species, de Waal (1992) found that chimpanzees shared more tolerantly, but he did not offer an ultimate explanation.

Following Trivers (1971, 2006), we suggest that the psychological regulations of food sharing may ultimately depend on a history of reciprocity: only if food owners can expect to be reciprocated in some form should they voluntarily give away food. Conversely, more voluntary or active forms of sharing may induce more feelings of gratitude in the recipient, because they reflect genuine altruistic dispositions, and are thus reciprocated better (Trivers, 1971). We therefore hypothesize that both the ultimate and the proximate mechanisms for sharing food will be influenced by the dominance structure of a group. The latter determines the costs of defending food and thus the amount of control owners have over food distribution, which in turn determines how much reciprocal exchange and tolerant sharing is possible.

Dominance hierarchies in primate societies can be characterized as ranging from egalitarian to despotic (van Schaik, 1989) which has been formalized in terms of linearity and steepness of the hierarchy (de Vries, 1995; de Vries et al., 2006). The steepness of the hierarchy is measured by the relative ability of group members to win dyadic conflicts: the steeper the hierarchy, the more easily dominants win conflicts with subordinates. Thus, in a group with a steep hierarchy, the costs of defending food should be high, owners cannot retain control over food distribution and transfers will be forced by dominants, which are unlikely to reciprocate. On the other hand, in a group with a shallow hierarchy, the costs of defending food should be low; owners can retain control over food distribution and selectively tolerate transfers by those individuals who reciprocate. Once reciprocity is established, owners may also share food more actively.

Hierarchy steepness has also been shown to negatively influence reciprocity in *grooming* among captive bonobos (Stevens et al., 2005) and other primates (Schino and Aureli, 2008), mostly because more grooming is directed up the hierarchy in despotic groups. This correlation has so far only been shown within species. To test whether a general relationship between despotism and reciprocity is consistent across the two species studied here, we compared hierarchy steepness and grooming reciprocity in five groups of chimpanzees and eight groups of bonobos.

In sum, we predict that in egalitarian groups, food transfers will be tolerant and reciprocal while in despotic groups, transfers are forced and nonreciprocal. We tested these predictions by recording food interactions in one group of captive chimpanzees and bonobos respectively, and i) describe general food sharing patterns, in particular the relative amount of forced and tolerated transfers, ii) test what factors best explain the observed food transfers, in particular reciprocal exchange, and iii) link the degree of tolerance and reciprocity to the degree of despotism. By studying these aspects in our two closest living relatives we hope to make inferences about the evolution of human food sharing and the proximate mechanisms linked to it.

METHODS

Subjects and housing

The chimpanzees lived at the Abenteuerland Walter Zoo in Gossau SG, Switzerland (indoor enclosures: 2 × 150 m², outdoor enclosures: 2 × 450 m²). The group consisted of 11 adults and 2 infants, a third infant was born in the course of the study and three of the 55 adult

TABLE 2. Details on study period and observers for each group

Species	Study group	Study period	Observers/reference ^a
Chimpanzees	GD a1	Sep 2004–Jan 2005	Peterhans (2006)
	GD a2	Jul–Oct 2006	Ziltener (2007)
	GD b	Sep 2004–Jan 2005	Peterhans (2006)
	GS 1	Feb–May 2007	Ziltener (2007)
	GS 2 ^b	Oct 2007–Feb 2008	This study
Bonobos	A	Feb–Apr 2001	Stevens et al. (2005)
	P 1	1992–1993	Vervaecke et al. (2000)
	P 2	Nov–Dec 1999	Stevens et al. (2005)
	P 3	Nov 2002–Feb 2003	Stevens et al. (2005)
	P 4	Feb–May 2006	Stevens et al. (2007)
	P 5 ^b	Apr–May 2008	This study
	T	Nov–Dec 2001, Feb 2002	Stevens et al. (2005)
	W	Aug–Sep 1999	Stevens et al. (2005)

Capital letters indicate the study site, lower case letters indicate distinct groups at the same site (only GD) and numerical suffixes indicate the same group studied at different times (see Supporting Information Table S1 for details and changes in composition).

^a Main observers were the first authors of the respective reference, except for Stevens et al. (2007), where the second author was the main observer. The methodology (ethogram, observation methods) was the same in all studies. Study sites: GD, Gänserndorf; GS, Gossau; A, Apenheul; P, Planckendael; T, Twycross; W, Wuppertal.

^b Main study groups; others are additional groups only used for hierarchy steepness and grooming reciprocity analyses (Fig. 3).

dyads were maternal relatives (Supporting Information Table S1). None of the females had regular swellings during the study. The bonobos lived at the Dierenpark Planckendael, Belgium (indoor: 88 m², outdoor: 3,000 m²). The group contained six adults and three infants. Three of the 15 adult dyads were maternal relatives (Supporting Information Table S1). All females were lactating and showed no regular swelling cycle. In both groups, only the adults (minimum age 7) were subjects of this study.

Data collection

The chimpanzees were observed from October 2007 until February 2008 (Table 2). All occurrence observations on the whole group (Altmann, 1974) took place between approximately 9 a.m. and 4 p.m. on average 2 days a week, totaling 82 h of observation on all individuals. The bonobos were observed from 3rd of March to 5th of May 2008 on 5–6 days a week between approximately 9 a.m. and 5 p.m., totaling 125 h of observation on all individuals (Table 2). Observations on both groups included all occurrences of social interactions, i.e. all grooming bouts (in seconds), affiliative contact, dominance-, agonistic-, and sexual interactions. In addition, proximity scans recording each individual's distance to each other individual were taken every 5 min if the animals were not moving or feeding. The ethograms used were based on van Hooff (1973) for the chimpanzees and on Vervaecke et al. (2000) for the bonobos. Behaviors in both groups were recorded by AJ on paper or using live coding on InterAct 8.4.1.

Food-sharing experiments

Following de Waal (1989, 1997), we used monopolizable food sources to induce food interactions. We used paper shopping bags filled with part of the apes' regular diet, mostly vegetables. In the chimpanzee group, food-sharing experiments were conducted once a day, around 1–2 p.m. ($N = 30$). In the bonobo group, experiments were conducted once or twice a day, in the morning, around 9–10 a.m. ($N = 28$) and/or in the early afternoon, around 1–2 p.m. ($N = 25$). For both species, the paper bags were either put in the indoor enclosure before the

apes were let in, or thrown to specific individuals in the outdoor enclosure. In addition, spontaneous food interactions during normal feedings were recorded. All experiments were video-taped, and all food interactions were subsequently coded by AJ with InterAct 8.4.1. To test for interobserver comparability of our food transfer definitions, JS also coded a sequence including different types of transfers among the chimpanzees, resulting in substantial agreement ($K = 0.63$).

Food interactions. The food owner's reaction to each approach was classified as either *positive*, i.e. conducive to food transfer (give food to approacher, drop food in approacher's reach or hold food toward approacher), *negative*, i.e. impeding food transfer (protest vocally, hold on to food, hold away food, turn away, leave, flee, push away approacher's hand, attack approacher), or *neutral*, i.e. neither conducive to nor impeding food transfer (ignore approacher, other behavior). We defined food transfers like van Noordwijk and van Schaik (2009) as transfers out of the owner's hand. Following de Waal (1989, 1992), we distinguished between types of *nontolerated transfers* and *tolerated transfers* (Table 4 for operational definitions). Contrary to de Waal (1989, 1992), we did not observe *co-feeding* (due to the different food types) and did not include *collect near* in the analyses as this was never protested by food owners and ownership was thus not claimed. *Food-getting success* was defined as the proportion of approaches that led to food transfer.

On average (\pm SD), individual chimpanzees were first owner 2.8 ± 2.6 times (range 0–8) and bonobos 8.8 ± 5.6 (2–17) times. 564 and 640 approaches respectively were recorded and each possible owner-approacher dyad interacted on average (\pm SD) 6.3 ± 13.2 (0–100)/ 22 ± 28.7 (0–121) times.

Additional groups

To compare general patterns of reciprocity and dominance across different groups of chimpanzees and bonobos, we included data from an additional five groups (one of which studied twice) and five different study periods on the main groups resulting in five and eight samples per species (see Supporting Information Table S1 and Table 2 for details on composition as well as

TABLE 3. Dependent variables included in the generalized linear mixed models to explain food transfers and hypotheses associated with them

Dependent variable	A shares with B because...	Hypothesis	Supported? ^a
(Tolerated) Transfers received	B shares with A	Reciprocity (food for food)	Chimpanzees yes, bonobos no
Relationship quality ^b , affiliative relationship ^c	A and B are friends	Interchange (food for other services)/ expression of tolerance	Yes
Political relationship ^c	A and B are allies	Interchange (food for support)	No
David's score difference	B is "stronger" ^d	Sharing under pressure/harassment	Yes
Relatedness	A and B are maternal relatives ^e	Kin selection	Chimpanzees yes, bonobos no
Sex combination	B is from the same/opposite sex	Interchange (δ - δ : food for sex, δ - δ / δ - δ : food for support); sharing under pressure (chimpanzees: δ - δ , bonobos: δ - δ)	No

^a See Table 5 for effect sizes (parameter estimates).

^b Only chimpanzees.

^c Only bonobos.

^d i.e. on average more likely to win dyadic conflicts with A.

^e i.e. mother-daughter and mother-son pairs, with most transfers going from mothers to (adult) offspring. The maternal brother pair among the bonobos never shared food. We did not include paternal relatives since there was no evidence that individuals preferentially associated, groomed, supported or shared food with paternal kin (unpublished analyses).

observation periods and observers). To be included in this analysis, the data had to fulfill two criteria: i) the hierarchy steepness estimate had to be significant, which was tested with a randomization test using 2000 repeats (de Vries et al., 2006) and ii) the grooming matrix correlation coefficient for any group of n individuals had to be based on at least $2n(n-1)$ grooming bouts, thus allowing for each dyad to reciprocate at least once.

Statistical analyses

To test the influence of various factors on food transfers, we used generalized linear mixed effects models (GLMM: Bolker et al., 2009), including the identities of owner and approacher as random factors. For an overview and definitions of fixed factors see Table 3 and below. GLMM's were fitted with lme4 (Bates and Maechler, 2009) in R 2.9.0 (R Development Core Team, 2009) with binomial error distribution. We first constructed a full model, including all possible factors and tested the overall significance of the full model against a null model, including only the intercept and the random factors (Johnson and Omland, 2004). We then used the corrected Akaike's Information Criterion (AICc: Hurvich and Tsai, 1989) to select the most parsimonious model with the best fit to the data (Johnson and Omland, 2004). Factors were excluded only if this improved the model fit by >2 AICc units. This approach avoids the danger of increased type II errors with repeated significance testing (Mundry and Nunn, 2009). We used likelihood ratio tests to test whether a full model or a factor of interest explained a significant amount of the variance compared to the null model or a reduced model without the factor of interest, respectively. Since likelihood ratio tests against a Chi-square distribution tend to overestimate effect size (Faraway, 2006), we used parametric bootstrapping with 1,000 Monte Carlo simulations to generate a distribution of likelihood ratios (LR) from the fitted parameter estimates and tested the observed LR against this distribution (Faraway, 2006). In the case of borderline P values (0.05–0.1) we ran 10,000 simulations. Row-wise matrix correlations in MatMan (de Vries, 1993) yielded very similar results, but since matrix correlations cannot handle multiple factors simultaneously we only report the results of the GLMMs.

Dependent variables. We used two different measurements of food getting success as dependent variables. *Transfers given*¹: Proportion of approaches that led to food transfer, both tolerated and forced, for a given owner-approacher dyad. *Tolerated transfers given*: Proportion of approaches that led to tolerated food transfer for a given owner-approacher dyad. Both measurements were weighted by the total number of approaches per dyad. Reciprocal exchange is mainly expected for tolerated transfers but may also occur over all transfers, if forced transfers are rare. The more common forced transfers, the weaker the signal of reciprocity over all transfers.

Independent variables. We tested the influence of several explanatory variables on food sharing (Table 3). *(Tolerated) transfers received*¹: The proportion of approaches of the current owner to the current approacher that led to (tolerated) transfer when the latter was food owner. *Relationship quality*: Numerical. Following Fraser et al. (2008), we performed a principal components analysis (PCA) on the variables *grooming given* (proportion of scans approacher groomed owner), *support given* (agonistic support given by approacher to owner as proportion of all support given to others), and *proximity* (proportion of scans approacher and owner rested within arm's reach, excluding grooming). A minimum eigenvalue of 1.0 was used to determine the number of components extracted from the PCA (Tabachnik and Fidell, 2007). For the chimpanzees, we thus extracted one component, explaining 50.4% of the variance. It had a high positive load of grooming, support, and proximity and is thus largely equivalent to Fraser et al.'s (2008) *relationship value* component. For the bonobos, two components were extracted, explaining 45.2% and 34.4%, respectively. The first component had a high loading of grooming and proximity but negative loading of support, whereas the second one had a high loading of support, minor loading of proximity and negative loading of grooming. Thus, we called the first component *affiliative relationship* and the second one *political relationship*. *David's score difference*: Numerical factor

¹"Given" and "received" are only used to indicate the direction of transfers, from owner to approacher or vice versa, but do not imply intention or voluntariness.

TABLE 4. Types of food transfers and their occurrence among chimpanzees and bonobos

	Definition	Chimpanzees	Bonobos
<i>N</i>		228	73
Offering ^a	O ^b initiates transfer without request by A ^c	0.9%	0%
Active sharing ^a	O actively transfers food to A	5.7%	0%
Facilitated taking ^a	O makes movements conducive to transfer but A takes the food	18%	0%
Relaxed claim ^a	O allows A to take food	61.4%	39.7%
Forced claim ^d	A takes food despite resistance by O	13.2%	57.5%
Stealing ^d	A snatches food by surprise, preventing resistance by O	0.9%	2.7%

^a Tolerated transfers.

^b O, owner.

^c A, approacher.

^d Nontolerated transfers.

indicating the relative ability of two individuals to win dyadic conflicts, calculated as normalized David's score (de Vries et al., 2006) of the owner minus normalized David's score of the approacher, i.e. the factor is positive for dominant food owners and negative for subordinate ones. We initially included formal ranks of owners and formal rank differences as factors, but found high collinearity in these factors and thus had to consider them redundant. *Relatedness*: Binary factor indicating whether owner and approacher are maternal relatives. *Sex combination*: Factor with four levels, female–female, male–male, female–male, male–female.

Dominance style and reciprocity. Dominance hierarchies were calculated with MatMan 1.1 (de Vries, 1995; de Vries et al., 1993) on the basis of pant-grunts for the chimpanzees (Noë et al., 1980) and fleeing upon aggression in dyadic conflicts for the bonobos (Vervaecke et al., 2000). The steepness of dominance hierarchies was calculated as the slope of a linear regression line through the ranked normalized David's scores, based on the outcome of dyadic agonistic interactions (de Vries et al., 2006). While a shallow slope represents an egalitarian dominance hierarchy in which rank differences are small, a steep slope represents a despotic hierarchy with large rank differences (van Schaik, 1989; de Vries et al., 2006; Stevens et al., 2007b). Following Stevens et al. (2005), we included only individuals over 7 years of age, when they become socially and sexually mature, and in captivity have been shown to reproduce (chimpanzees: Carlsen, 2007; bonobos: Pereboom and Stevens, 2008).

Grooming reciprocity was calculated using rowwise matrix correlations in MatMan1.1. (de Vries, 1993; de Vries et al., 1993). The units of analysis were grooming bouts given and received. To compare mean hierarchy steepness and mean grooming reciprocity between the species, we first calculated a mean for the repeatedly sampled groups (Table 2) before calculating the mean among independent groups. To analyze the influence of hierarchy steepness on grooming reciprocity, we used linear mixed effects models (Pinheiro and Bates, 2000), fitted with nlme (Pinheiro et al., 2008) in R 2.9.0 (R Development Core Team, 2009). Since we were interested in the general influence of dominance structure on reciprocity, *hierarchy steepness*, ranging from 0 to 1, was set as the only explanatory variable. *Species* (binary: chimpanzees/bonobos) and *group identity* were set as random factors. Other factors potentially influencing hierarchy steepness and reciprocity, namely *total group size* (numerical) and *sex ratio* (the proportion of males) were also included as random factors.

RESULTS

General patterns of food sharing

In total, we recorded 228 transfers among the chimpanzees and 73 transfers among the bonobos. Chimpanzees were on average food owner during 42.4 min (± 43.5), whereas bonobos were food owner during 124 min (± 78.3). Thus, chimpanzees on average transferred food almost 10 times more frequently than bonobos (21.4 vs. 2.6 transfers per hour of being food owner, $t_{14} = 3.02$, $P < 0.01$).

Food acquisition. In both species, food owners never approached non-owners and never initiated food transfers, except for one instance among the chimpanzees (Table 4). Food was virtually only shared if non-owners approached food owners and actively tried to acquire food by begging or by taking. Peering at a food owner without begging or taking never led to transfer.

Donor–recipient combinations. Among the chimpanzees, 67.2% of all transfers were from dominants to subordinates and 32.8% from subordinates to dominants. Furthermore, 90.4% were among non-kin and 9.6% among kin. Finally, 45.5% of all transfers were from males to females, 27% were among females, 16.9% from females to males, and 10.7% among males. Among the bonobos, 61.2% of all transfers were from subordinates to dominants and 38.2% from dominants to subordinates; 84.3% were among non-kin and 15.7% among kin; 41% of all transfers were among females, 41% from males to females, 16.7% from females to males and 1.2% among males. Whether dominance, kinship, or specific sex combinations had an influence on success rates was evaluated in the models below.

Reactions to food approaches. In both species reactions to approaches were mostly negative (chimpanzees: mean \pm SD: 49.5% \pm 31.5%; bonobos: 53.4% \pm 24.1%) or passive (47.9% \pm 29.9%; 45.9% \pm 24.6%). Positive reactions were rare (2.6 \pm 4.7%; 0.7 \pm 1.2%). In both species, low-ranking food owners showed significantly more negative reactions (Spearman correlation of negative reactions with rank: chimpanzees: $\rho = 0.62$, $N = 10$, $P = 0.05$; bonobos: $\rho = 0.83$, $N = 6$, $P < 0.05$).

Food-getting success. Average food-getting success (\pm SD) was significantly higher for chimpanzees (33% \pm 9%) than for bonobos (19% \pm 11%, $t_{15} = 2.97$, $P = 0.01$).

Sociosexual behavior. Bonobo approachers presented sexually to the food owner 23 times (3.5% of approaches) which led to sexual interactions 12 times (1.9% of approaches). In two cases, food was transferred after

sexual intercourse. Hence, food getting success was not significantly different with or without sexual interactions (16.7% vs. 19%; $X^2 = 0.01$, $df = 1$, $P = 0.9$). Chimpanzees never used sociosexual behavior in food acquisition.

Types of transfers. Contrary to bonobos, chimpanzees fairly often transferred food actively to approachers (Table 4). Active forms of transfers (active sharing and facilitated taking) were thus significantly more common among chimpanzees (mean \pm SD = 13.1% \pm 13.7% vs. 0 \pm 0%; $t_{14} = 2.3$, $P < 0.05$). Overall tolerated transfers were also significantly more common among chimpanzees (mean \pm SD = 71.8% \pm 32.7% vs. 36.4% \pm 26.3%, $t_{14} = 2.33$, $P < 0.05$, Fig. 1).

In sum, both species rarely responded positively to approachers and low-ranking food owners were more likely to respond negatively. Among chimpanzees most transfers were from dominants to subordinates, while the opposite was true for the bonobos. Chimpanzee food owners allowed higher food-getting success and more tolerated taking and also transferred food more actively than bonobos. The latter only rarely engaged in sexual interactions during sharing without any effect on success.

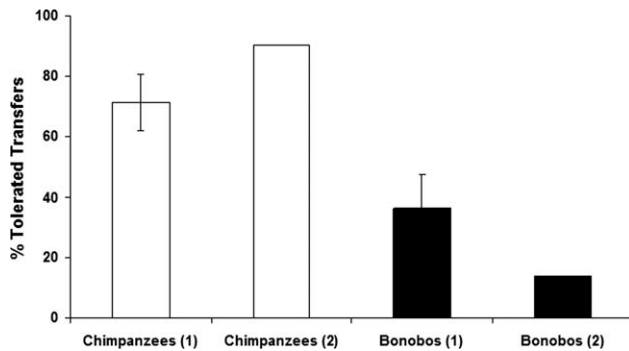


Fig. 1. The average percentage (\pm SEM) of tolerated food transfers for chimpanzees and bonobos as observed (1) in this study and (2) by de Waal (1992). In both studies, chimpanzees shared food more tolerantly than bonobos.

Mechanisms of food sharing

Chimpanzees. For tolerated transfers given, the full model explained significantly more variance in the data than the null model (LR = 37.16, $df = 7$, $P < 0.001$). The parameter estimates of the most parsimonious model are given in Table 5. Relatedness explained most of the variance in that model (LR = 5.42, $df = 1$, $P < 0.05$), followed by tolerated transfers received (LR = 3.78, $df = 1$, $P < 0.05$) and, to a lesser extent, David's score difference (LR = 8.36, $df = 1$, $P = 0.09$) and relationship value (LR = 1.39, $df = 1$, $P = 0.26$), the former of which had a negative influence. This indicates that reciprocity explained most of the food transfers among non-kin. While closely affiliated dyads also shared more, dominant food owners were less likely to tolerate food taking than subordinate ones.

For all transfers given, the full model also explained significantly more variance than the null model (LR = 25.95, $df = 7$, $P < 0.01$). The parameter estimates of the most parsimonious model are given in Table 5. Transfers received (LR = 10.29, $df = 1$, $P < 0.001$) and relatedness (LR = 8.31, $df = 1$, $P < 0.01$) best explained transfers given. This indicates that reciprocity and kin benefits best explain overall food transfers.

Bonobos. For tolerated transfers given, the full model did not explain significantly more variance than the null model (LR = 14.75, $df = 8$, $P = 0.34$). The most parsimonious model (Table 5) only approached significance (LR = 10.9, $df = 2$, $P = 0.08$) and included affiliative relationship (LR = 4.57, $df = 1$, $P = 0.23$) and, with negative influence, David's score difference as factors (LR = 1.76, $df = 1$, $P = 0.19$), none of which explained a significant amount of the variance. This indicates that bonobos tolerated transfers more by closely affiliated approachers but less by subordinate ones.

For all transfers given, the full model explained significantly more variance than the null model (LR = 30.47, $df = 8$, $P < 0.01$). Transfers received when not an owner was a significant factor in the full model ($\beta \pm$ SE = -4.04 ± 1.09 , $P < 0.001$) and had a significant but negative influence on transfers given (LR = 15.1, $df = 1$, $P < 0.01$). In the most parsimonious model (Table 5), transfers given was strongly negatively influenced by transfers received (LR = 11.55, $df = 1$, $P < 0.01$) and

TABLE 5. The parameter estimates for the most parsimonious GLMM explaining (tolerated) food transfers given by chimpanzees and bonobos

Food sharing measure	Chimpanzees		Bonobos	
	Factor	$\beta \pm$ SE ^a	Factor	$\beta \pm$ SE ^a
Tolerated transfers given	Intercept	-2.23 \pm 0.28***	Intercept	-3.49 \pm 0.52***
	Tolerated transfers received	1.53 \pm 0.78*	Affiliative relationship	0.71 \pm 0.28*
	Relationship value	0.16 \pm 0.13 ^{NS}	David's score difference	-0.37 \pm 0.27 ^{NS}
	Relatedness	1.49 \pm 0.63*		
	David's score difference	-0.51 \pm 0.15**		
All transfers given	Intercept	-1.89 \pm 0.31***	Intercept	-1.41 \pm 0.43***
	Transfers received	1.53 \pm 0.47**	Transfers received	-3.14 \pm 1**
	Relatedness	1.48 \pm 0.52**	Affiliative relationship	0.8 \pm 0.24***
			David's score difference	-0.4 \pm 0.23 ^{NS}

For both measurements of food sharing there is a reciprocal relationship among the chimpanzees but not the bonobos.

^{NS} $P > 0.1$,

* $P < 0.05$,

** $P < 0.01$,

*** $P < 0.001$.

^a Coefficients (\pm SE) of the factors retained in the most parsimonious model based on AICc.

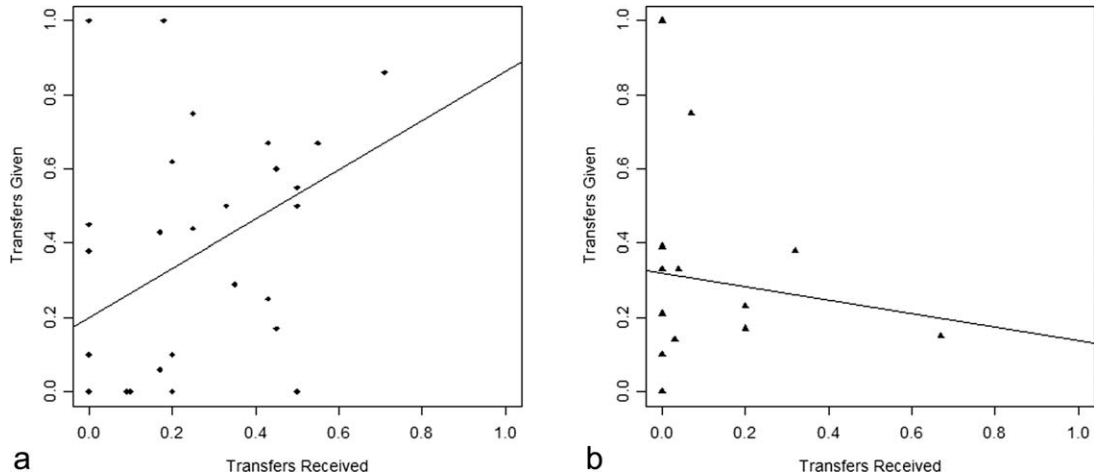


Fig. 2. The relation between food transfers received (as the proportion of successful approaches) and food transfers given for (a) chimpanzees (squares) and (b) bonobos (triangles). There was a significant positive influence of food received on food given among the chimpanzees, indicating reciprocity, but a significant negative one among the bonobos, indicating mainly unidirectional transfers.

mildly positively influenced by affiliative relationship ($LR = 9.63$, $df = 1$, $P = 0.09$). David's score difference shows the main direction of transfers, to individuals likely to win conflicts, but did not explain a significant amount of the variance ($LR = 3.18$, $df = 1$, $P = 0.19$). This indicates that food transfers among bonobos were unidirectional, from subordinates to dominants especially if they were closely affiliated.

In sum, both measurements of food transfers given were significantly explained by food transfers received for the chimpanzees, thus indicating reciprocal exchange (Fig. 2). Relatedness and relationship value also had positive influences on food transfers given. The fact that relationship value was only an important factor for tolerated transfers but not all transfers shows that owners may share with preferred individuals if they have a choice, which was restricted when transfers were forced. No model could significantly explain tolerated transfers given by bonobos, although affiliative relationship tended to influence it. Transfers received had a significant and *negative* effect on transfers among the bonobos, thus strongly indicating that transfers were mainly unidirectional. Hence, food sharing seemed to be reciprocal among chimpanzees but not among bonobos.

Dominance and reciprocity

The chimpanzees in this study had a shallower and less linear dominance hierarchy than the bonobos (slope: chimpanzees, 0.18; bonobos, 0.54, linearity: 0.44; 0.6) and can thus be called more egalitarian. Across all sampled groups, chimpanzees had shallower hierarchy steepness (three independent groups; mean \pm SD = 0.16 ± 0.02) than bonobos (four independent groups; 0.73 ± 0.07 ; $t_5 = 14.12$, $P < 0.001$) and higher grooming reciprocity coefficients (0.82 ± 0.1 vs. 0.29 ± 0.26 ; $t_5 = 3.3$, $P < 0.05$). In a linear mixed effects model including species and group identity as random factors, hierarchy steepness had a significant negative influence on grooming reciprocity ($AICc = 12.16$, $\beta \pm SE = -0.81 \pm 0.19$, $t_5 = -4.24$, $P < 0.01$, Fig. 3). Even after including group size and sex ratio as additional random factors, hierarchy steepness still tended to negatively influence groom-

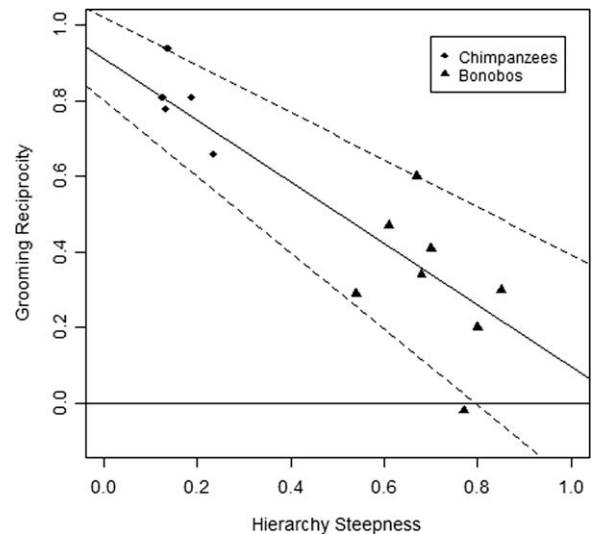


Fig. 3. The influence of hierarchy steepness on grooming reciprocity among different groups of chimpanzees (squares) and bonobos (triangles). The full line is the predicted curve fitted with a linear mixed effect model, controlling for species and repeated measures of the same groups. The dotted lines represent the standard errors of the fitted curve. Hierarchy steepness had a significant negative influence on grooming reciprocity ($P < 0.01$).

ing reciprocity ($AICc = 41.46$, $\beta \pm SE = -0.64 \pm 0.26$, $t_3 = -2.42$, $P = 0.09$), but the $AICc$ of this model was significantly higher, indicating that these factors did not help explain more variance in the data.

DISCUSSION

We hypothesized that both the ultimate and the proximate mechanisms for sharing food are influenced by the dominance structure of a group. In this study, individuals of neither species tended to encourage food transfers but most often ignored approaches or made movements impeding food transfer, especially if low-ranking. This indicates that low rankers had to avoid forced transfers

more than high rankers, i.e. did not enjoy a “respect for possession” (Kummer and Cords, 1991). Chimpanzees were significantly more successful in acquiring food from others than bonobos. Sexual interactions were only rarely observed among bonobos and did not alter food-getting success. Chimpanzees also shared food more actively and tolerantly, while bonobos often forced transfers. Thus, chimpanzees were more prosocial (Table 4).

We predicted that reciprocal exchange was more likely if transfers are tolerated rather than forced. Among chimpanzees, forced transfers were rare and the results of both models strongly indicate that food transfers were reciprocated. Among bonobos, forced transfers were common and the overall model indicated that food transfers were unidirectional. If only tolerated transfers were considered, bonobos tended to share more with closely affiliated individuals; however, this model could not explain a significant amount of the variance in the data. Thus, chimpanzees reciprocated food transfers but bonobos did not (Fig. 2). General relationship components included in the model never explained a significant amount of the variance, suggesting that food was, if at all, traded for itself rather than for grooming, support or shared proximity. Similarly, Gurven et al. (2000) found that meat received was the best predictor for meat given. However, other studies did find reciprocal exchange of food with other currencies (cf. Nishida et al., 1992; Mitani, 2006; Gomes and Boesch, 2009) and we also found some interchange with grooming and support among the chimpanzees using matrix correlations (unpubl. analyses), hence these differences may partly be due to the choice of statistical method.

From our results, we cannot make inferences about the proximate regulations of reciprocal exchange. The observed patterns are consistent with symmetry-based, attitudinal- or calculated reciprocity (Brosnan and de Waal, 2002). However, it is most parsimonious to assume symmetry-based reciprocity, especially since analyses on short-term contingency of exchange (i.e. within hours, cf. de Waal, 1997) were not significant in our study groups (Jaeggi et al., in prep.). Thus, over the whole study period, food exchanges were on average reciprocal within dyads, but giving was not necessarily contingent on receiving, since the latter may have happened before or after the former.

We found differences in dominance style that were consistent with the observed patterns of food sharing and reciprocity. The chimpanzee group was more egalitarian and was thus expected to share more tolerantly and more reciprocally. The bonobos were more despotic, which can explain why transfers were mainly forced and unidirectional, from subordinates to dominants. In a comparison of several groups of chimpanzees and bonobos, the latter were more despotic and hierarchy steepness was a significant negative predictor of reciprocity in grooming (Fig. 3), thus confirming the pattern found in food sharing. A model including other factors potentially influencing both grooming reciprocity and hierarchy steepness, namely total group size and sex ratio, explained less variance in the data. Thus, hierarchy steepness seems to be a robust predictor of reciprocity in grooming across different populations of chimpanzees and bonobos; whether this effect also holds for patterns in food sharing remains to be tested.

Although the food type most commonly shared among wild chimpanzees and hunter-gatherers is meat (Table 1; Gurven, 2004), we used plant food (fruits or vegetables).

Could this affect sharing patterns? Moore (1984) noted two characteristics of meat which make it prone to sharing: First, meat is easily carried and shielded and thus highly defensible. The same is true for the large fruits commonly shared by wild bonobos (*Treculia africana* and *Anonidium mannii*: White, 1994; Fruth and Hohmann, 2002) and chimpanzees (cultivated fruits: Hockings et al., 2007), the bundles of browse used by de Waal (1989, 1992, 1997) and the paper bags used in this study (as long as they were not torn, which happened only rarely). Second, meat is only infrequently available and of high quality, making it highly attractive. While this is again true to some extent for the large fruits cited earlier, it applies less to the food sources in this study since they consisted of parts of the apes' daily diet. However, in both groups the individuals were always highly motivated to acquire food, despite the relatively low attractiveness. Furthermore, de Waal (1989, 1997) already showed that reciprocal sharing patterns may emerge from relatively low-quality food. Finally, bonobos in the wild also regularly hunt and share meat (Fruth and Hohmann, 2002; Hohmann and Fruth, 1993, 2008; Surbeck and Hohmann, 2008) with a frequency that may well have been underestimated in the past (Stanford, 1998). Hence, even though meat may be shared more actively than large fruits within the same population (Watts, pers. comm.), there is no a priori reason to relate interspecies differences in sharing patterns or psychology to resource type.

It is noteworthy that the four studies directly comparing chimpanzees and bonobos in similar competition situation, namely monopolizable food sources, did find conflicting results concerning tolerance (de Waal, 1992; Hare et al., 2007; Wobber et al., 2010; this study). However, this could be due to the fact that tolerance was measured differently: While Hare et al. (2007) and Wobber et al. (2010) measured the tendency to *monopolize* food, de Waal (1992) and our study measured the tendency to *share* food (once monopolized). Given this difference, direct comparison between these studies is difficult. However, a greater tendency both to monopolize *and* to share in chimpanzees would be consistent with evolutionary models emphasizing both the benefits of being food owner per se and of selective sharing (e.g. Moore, 1984). In fact, if sharing has direct benefits, individuals are expected to seize every possible opportunity for sharing. This is consistent with the commonly observed scramble for ownership after hunts, followed by relatively peaceful sharing (e.g. Nishida et al., 1979, 1992). Hence, the two tendencies might even be psychologically linked.

Our interspecific analysis of hierarchy steepness and grooming reciprocity (Fig. 3), along with intraspecific correlations (Stevens et al., 2005; Schino and Aureli, 2008), suggests that hierarchy steepness could be a valuable predictor of reciprocity expected in other species or at least other populations of chimpanzees and bonobos. The fact that Schino and Aureli (2008) did not find an effect across species may be because their data set lacked relatively egalitarian species for comparison. This relation could easily be tested with data from other populations of chimpanzees and bonobos.

Some studies on food sharing in chimpanzees or bonobos report reciprocal exchange (de Waal, 1989, 1997; Mitani and Watts, 2001; Mitani, 2006), while others found more support for sharing-under-pressure (Fruth and Hohmann, 2002; Gilby, 2006). In our study, reciprocal exchange was found among the chimpanzees but not

among the bonobos, where sharing-under-pressure better explained food transfers. As Stevens and Gilby (2004) and Gilby (2006) have pointed out, the two hypotheses are not mutually exclusive. Rather, there may be a behavioral continuum between the possibility for reciprocal exchange, when the costs of defending food are low and owners can selectively share with particular individuals, and sharing-under-pressure, when the costs of defending food are high and transfers are mainly from subordinates to dominants (see also Moore, 1984). The steepness of the dominance hierarchy may determine the position of groups on this continuum and could thus be helpful in predicting the patterns of food sharing in different populations.

Similarly, at the proximate level, food transfers among chimpanzees and bonobos can range from highly tolerant and active to reluctant or forced (Teleki, 1973; Kuroda, 1984; Boesch and Boesch, 1989; Nishida et al., 1992; Fruth and Hohmann, 2002; Gilby, 2006; Surbeck and Hohmann, 2008). The amount of active sharing (active giving and facilitated taking) among the chimpanzees in this study was relatively high compared to other populations (this study: ~24%; Tai: ~7% (Boesch and Boesch, 1989); Gombe: 1.2% (Teleki, 1973); Yerkes: 0.5% (de Waal, 1989)), suggesting higher degrees of prosociality. However, these differences could also be due to different food types and group compositions. Among wild bonobos, food sharing seems to be largely tolerant (Kuroda, 1984; White, 1994; Fruth and Hohmann, 2002), but in captivity, food transfers were found to be more tolerant among chimpanzees than among bonobos (de Waal, 1992; this study). While general discrepancies between captivity and the wild, e.g. the lack of fission–fusion dynamics might explain some of these differences, our results suggest that they may also be related to the steepness of the dominance hierarchy in a given population (within a captivity or wild context). Pending formal attempts to explain differences in reciprocity or tolerance in food sharing within or between species (Mitani, 2009), more data on hierarchy steepness from other populations of chimpanzees and bonobos could provide a valuable test of our hypothesis.

The fact that in this study bonobos were less tolerant and more despotic than chimpanzees may seem unexpected, given that although chimpanzees can be characterized as relatively egalitarian (Boehm, 1999) bonobos have often been described as more tolerant and egalitarian (de Waal and Lanting, 1997; Hare et al., 2007). However, this strict dichotomy has recently been questioned. First, Stanford (1998) suggested that reported behavioral differences may be due to the relative paucity of data on wild bonobos and the different research focus in the two species. Second, comparisons of various wild populations indicated that levels of sociality, which depend on food availability and the resulting feeding competition, may lie on a continuum for the two species rather than representing a dichotomy (Hohmann and Fruth, 2002; Stumpf, 2007). Finally, various captive groups of bonobos were shown to exhibit high rates of (serious) aggression and consistently steep hierarchies, resulting in “semi-despotic” societies (Stevens et al., 2008), which may be a response to increased contest competition under captive conditions (cf. Gore, 1993). In general, it is difficult to maintain clear species differences as expressed levels of sociality, dominance relationships, aggression and playfulness in *both* species may well lie on a continuum dictated by the levels of feeding competition (van Schaik,

1989; Stanford, 1998; Stumpf, 2007) and space availability (Aureli and de Waal, 1997; Sannen et al., 2004; Tacconi and Palagi, 2009).

Human foragers are characterized as relatively egalitarian (Woodburn, 1982) and group-wide sharing of meat is universal, largely voluntary and often reciprocal (Gurven, 2004). In fact, all studies statistically testing reciprocal exchange found significant evidence for it (Gurven, 2004) and in a multivariate analysis similar to ours, Gurven et al. (2000) also found that food received was the best predictor of food given. Our results indicate that a relatively egalitarian hierarchy may have favored such reciprocal exchange because of increased control of owners over food distribution. During evolutionary (and ontogenetic) history, food owners should become more tolerant to requests by those likely to reciprocate. They may also start to share more actively, which could reflect genuine altruistic dispositions and thus induce greater feelings of gratitude in the recipient, resulting in even better reciprocation (Trivers, 1971).

In sum, we suggested that a shallow dominance hierarchy allows food owners to selectively tolerate requests by those individuals who reciprocate. We found that chimpanzees were more egalitarian than bonobos and shared more tolerantly and reciprocally. A cross-species analysis of the influence of despotism on grooming reciprocity confirmed this pattern. We conclude that a relatively shallow dominance hierarchy was an important precondition for the evolution of extensive food sharing in humans and the prosocial predispositions related to it.

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