The roles of food quality and sex in chimpanzee sharing behavior (*Pan troglodytes*)

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Abstract

Both wild and captive chimpanzees (*Pan troglodytes*) share food with non-relatives. Researchers have proposed several hypotheses to explain this behavior, including 'food for sex', 'food for grooming or agonistic support', and 'sharing under pressure'. We examined food sharing in two captive groups of socially-housed chimpanzees. In contrast to previous captive studies, which only examined transfers of low-quality foods, we conducted seven trials with high-quality food and seven with low-quality food for each group to directly compare transfers of different food qualities. We recorded how male chimpanzees shared food, including active transfers, passive transfers, and co-feeding. We also noted all instances of copulations, female estrous states, benign attempts to access food (termed 'perseverance'), and aggressive attempts (termed 'harassment') to examine whether any of these factors influenced food sharing. Male food possessors shared at the same rate in both food quality conditions, but seemingly for different reasons, indicating that food quality may affect the exchange of social benefits in chimpanzees. In the low-quality condition, there was an interaction with rank and perseverance: while low- and middle-ranking females received more food the more they persevered, high-ranking females received more food without perseverance and gained relatively little benefit from persevering. In the high-quality condition, there was an interaction between copulations and perseverance: females who copulated with the male food possessor received more food during that trial with less perseverance. Non-copulating females received more transfers the more they persevered. This result was only observed in the short-term — copulations over the previous year were not correlated with food transfers. Further, the copulations observed here were unusual for these chimpanzees in that they were not confined to peak fertility, suggesting a non-conceptive function for copulations in chimpanzees. Copulations in this study may have functioned to reduce tension and increase short-term tolerance, allowing females better access to food.

1. Introduction

Unrelated adult chimpanzees (*Pan troglodytes*) share food with each other, including meat obtained from group hunting, at a frequency that is unusual among primates (Goodall, 1963; de Waal, 1989; Feistner & McGrew, 1989; Jaeggi & van Schaik, 2011). Although males are the primary hunters and it has been suggested that meat sharing among males serves to reinforce participation in the hunt (Boesch & Boesch, 1989; Boesch, 1994), male chimpanzees also share meat with females (Nishida, 1970). Indeed, males of all ranks hunt, maintain possession of their kills, and share meat with others (Watts & Mitani, 2002; Muller & Mitani, 2005). In contrast, sharing plant food tends to be quite rare (but see Pruetz & Lindshield, 2012), perhaps because most individuals can access ordinary plant food themselves. However, male chimpanzees at Bossou in Guinea have also been observed to share more food following risky crop raids on human agricultural fields than easily obtainable, uncultivated fruits (Hockings et al., 2007).

Although meat certainly contains valuable fat and protein, chimpanzees do not appear to hunt to make up for a nutritional shortfall (Mitani & Watts, 2001). At Ngogo, chimpanzees hunt more during times of relative plenty when hunting parties can be larger and more successful (Mitani & Watts, 1999). Instead of meeting basic nutritional needs, social benefits may better explain the sharing of high-quality food between non-relatives (Mitani & Watts, 2001). Several reciprocity-based hypotheses suggest putative social benefits of food sharing in chimpanzees: 'food for sex', 'food for grooming' and 'food for support' (Stanford et al., 1994; de Waal, 1997; Mitani & Watts, 2001). Support for these hypotheses varies, possibly in part due to differences between populations since the hypotheses are not mutually exclusive.

The 'food for sex' hypothesis assumes that females are more willing to mate with males who share with her, so males who share food with estrous females may increase their reproductive success. One early study compared interactions over food across the female cycle and found that males gave priority of access to food in their possession to estrous females, particularly those with whom they have recently copulated (Yerkes, 1941). In relation to meat sharing in the wild, the 'food for sex' hypothesis predicts that males hunt more in the presence of estrous females, that they preferentially direct

food transfers to fertile females, and that the transfers correlate with an increase in copulations with those females (reviewed by Gilby et al., 2010).

Early evidence in support of this hypothesis came from Gombe, where males were observed to share more with estrous females (Teleki, 1973). Stanford et al. (1994) argued that the presence of an estrous female was the chief single factor influencing male chimpanzees at Gombe to hunt, but no such relationship was observed at Kanyawara (Gilby et al., 2008). At Bossou male chimpanzees who raided crops shared almost exclusively with females of reproductive age, most often with one cycling female who participated in the majority of consortships (Hockings et al., 2007). However, at Ngogo in Uganda, there was no relationship between the presence of estrous females and hunting or between males sharing meat with females and receiving increased mating opportunities from those females (Mitani & Watts, 2001). Work at Gombe even found a negative correlation between female presence and hunts, supporting a 'meat *or* sex' hypothesis over 'meat *for* sex' (Gilby et al., 2006).

Using estrus as a proxy for sex does not directly demonstrate a link between food sharing and increased reproductive success. Furthermore, a review of the 'meat for sex' literature showed that Stanford et al.'s (1994) measurement of estrus counted females who were not yet fully swollen and that Teleki's (1973) numbers were a qualitative estimate, not a quantitative analysis (Gilby et al., 2010). The only quantitative link between food sharing and copulations in chimpanzees is a long-term study by Gomes & Boesch (2009). They found no correlation between sharing and copulations in the immediate context of food sharing, but over the course of 22 months, they found that male–female dyads that shared food at least once also had more copulations than dyads in which sharing did not occur. These results imply that 'food for sex' is a long-term strategy to build relationships that allow for future mating and food-sharing opportunities, not a short-term exchange of food for copulations.

Affiliation is another potential social benefit that may result from a food sharing exchange. The 'food for grooming' hypothesis expects food to be shared in exchange for prior grooming services rendered (de Waal, 1989). In support of this hypothesis, captive chimpanzees were more likely to share browse with others who had groomed them in the two hours before food sharing, than with individuals who had not groomed them (de Waal, 1989, 1997). Chimpanzees that groomed the food possessor prior to the food trial had both higher rates of success at obtaining food and lower rates of aggres-

sion during attempts to get food. Jaeggi et al. (2013), in contrast, found that long-term affiliation patterns explained the sharing of fruits and vegetables in a group of captive chimpanzees, while recent grooming did not. Observations from wild chimpanzees at Ngogo also supported the hypothesis that food sharing reinforces affiliative bonds (Muller & Mitani, 2005). Food sharing as a means of support or reinforcing existing social bonds and coalitions is also well documented (reviewed in Newton-Fisher, 2007). Several studies have shown that males reciprocally share meat in exchange for agonistic or coalitionary support (Nishida et al., 1992; Mitani & Watts, 2001).

It is also possible that food sharing may not provide any tangible social benefits and instead may be used to end harassment by conspecifics interested in the food (Gilby, 2006). The 'sharing under pressure' hypothesis (based on Wrangham, 1975), suggests that there may be costs to maintaining sole possession of a carcass when beset by harassing chimpanzees in the form of a reduced rate of food consumption (Wrangham, 1975; Gilby, 2006). Further, food transfers in response to begging and harassment by non-possessors have been observed in both wild and captive chimpanzees (Stevens, 2004; Gilby, 2006). It is important to carefully distinguish harassment from non-threatening or non-interfering communicative signals (here termed 'perseverance') that do not reduce the rate at which a food possessor consumes the food. These may be important signals to induce prosocial behavior such as food sharing (de Waal, 1989; Horner et al., 2011).

Captive settings provide a unique opportunity to investigate food sharing since many factors, including party size and when sharing occurs can be controlled, and all affiliative relationships are well-documented. Although food sharing appears to be influenced by multiple factors in wild chimpanzees, one variable, food quality, has rarely been manipulated in the study of sharing behavior by captive chimpanzees. Items shared in the wild are typically high-quality and difficult to obtain (Teleki, 1973; Hockings et al., 2007). In contrast, research on food sharing among captive chimpanzees has typically been conducted with low-quality foods or with foods that the chimpanzees receive as a part of their regular diet (Jaeggi et al., 2013). We predict that there may be differences in the behavior of the food possessor and the individuals seeking access to the food due to the differing marginal values of the high-quality and low-quality foods (Winterhalder, 1996). For these reasons we decided to ask whether captive chimpanzees share a rarely encountered low-quality food differently than they share a rarely encountered high-quality food.

We tested only male subjects as food possessors, as males are the primary possessors of high-value, difficult to obtain food in the wild. We observed these males' sharing behaviors when they were given high- and low-quality food items and recorded different types of sharing, begging, and food possessors' responses to begging. We hypothesized that there would be more attempts to gain food by the beggars and more attempts to avoid beggars by the possessor in the high-quality condition. To examine the 'food for sex' hypothesis, we asked whether males would transfer more food to females with whom they copulated than females with whom they did not, and whether males would transfer food to females based on their estrous states. To investigate whether 'food for grooming' or affiliation was taking place, we tested whether long-term affiliative relationships or short-term affiliation (grooming and proximity) prior to the start of the trial influenced transfer rates. Finally, we investigated the effects of rank, perseverance in obtaining the food, and gestural begging on food transfers received by females to test 'sharing under pressure'. Due to the small number of males present for the study, the 'food for agonistic support' hypothesis was not examined. Below we describe the strategies male chimpanzees used to share food and the tactics females used to obtain food in both food quality conditions.

2. Methods

The study was conducted with two groups of socially housed chimpanzees ($N = 11$ in each group) at the Yerkes National Primate Research Center Field Station. The first group (FS1) consisted of one adult male (age 27) and 10 unrelated adult females (ages 15–48), while the second group (FS2) consisted of two adult males (ages 18 and 22) and eight unrelated adult females (ages 12–44) and the alpha male's mother (age 37). Outdoor enclosures are grassy areas with climbing structures and enrichment toys connected to indoor areas containing sleeping platforms, nesting materials and swings, and are 711 m^2 and 528 m^2, respectively. Testing took place in the outdoor enclosures at 0900 h, and the chimpanzees were locked outside for the duration of testing so that the observer could have visual access to all transfers. Chimpanzees were not given access to the indoor areas until after each trial. The individuals that did not voluntarily go outside in the morning were excluded from the trial on that particular day.

Seven trials were conducted for each of the high-quality and low-quality food conditions with each of the two chimpanzee groups, resulting in a total

of 28 trials in May–August 2011. The chimpanzees were locked out for the duration of testing, but not all females elected to be locked out and, therefore, did not participate in all trials. With 19 females and 7 trials per condition per group, a total of 133 attendances were possible for each food quality condition. Eight females missed a cumulative 26 high-quality food trials out of a possible 133, and 10 females were absent 21 times out of a possible 133 attendances in the low-quality condition. These absences are accounted for as the analyses are done by trial.

Trials alternated by group and by food quality such that a low-quality trial in FS1 on one day was followed by a high-quality trial in FS2 on the next day. Thus, each group was only tested every other day and only received a trial of each food quality once every four days. Trials were conducted in this manner to accommodate each stage in individual female reproductive cycles across trials of both food qualities.

The high-quality food item was a cylindrical block of ice roughly 6 cm deep and 15 cm across containing five bananas that had been sliced into 2 cm thick cross-sections. Banana (*Musa* sp.) sections were uniformly distributed throughout the ice block and held in place with paper straws as the block froze overnight. The low-quality food item was a large, leafy branch of sweet gum (*Liquidambar styraciflua*) approximately 1.5 m in length, cut shortly before each food trial began. Although the starting size of each item was quite different, both items were easily monopolized by one individual but without inhibiting sharing: the banana block could be broken into pieces as it melted and leaves could be removed from the branch of browse. Prior to testing trials, chimpanzees were assessed for their food item preference. Each individual was offered a slice of banana or sweet gum leaf 10 times, and their choices were recorded. The side on which each food was presented was switched from trial to trial to avoid documenting a side bias instead of the chimpanzees' preference.

Data collection began with a 30-min observation of any social interactions with the alpha male before the test began. These data were used to examine the role of short-term affiliation on subsequent food transfers. Since testing took place before morning husbandry and feeding, 30 min was the maximum period of time we could allow for pre-trial observations. The food item was brought to the observation tower at the conclusion of this 30-min period to ensure that the chimpanzees could not see which food it was before the trial began. The food item was then delivered to the alpha male. On two occasions

in the FS2 low-quality food trials, the alpha male exhibited no interest in the food item, and the beta male took the food instead. Since we did not collect baseline social interaction data of group members in relation to the beta male, beta-male data were excluded from the analysis of sharing strategies but included in the descriptive statistics regarding overall transfer rates (see below). Data collection continued for at least 30 min or until the food was entirely consumed, whichever was longer.

Scan samples were collected every minute for each group members' proximity to the food possessors and were categorized on two levels: close proximity (sitting in contact or within arm's reach) or not nearby. This allowed us to calculate the proportion of time each female was in proximity to the alpha male prior to and during the trial. All copulations were also recorded. Estrous states of the females were recorded based on an index of their anogenital swelling: none, medium, or maximally swollen (Dahl et al., 1991). All of the females except one in the study sample were cycling normally; FS1 was not on any form of birth control and the females in FS2 all had intra-uterine devices. One female in FS1 was on Depo-Provera for non-contraceptive reasons. All data were collected by one observer (J.C.).

Different types of food sharing behaviors, including active transfer, passive transfer and co-feeding; collect near; and begging were recorded (adapted from de Waal, 1989; Table 1). Transfers for this study were defined as any piece of food leaving the male's possession and entering a female's possession which totaled one leaf or greater for the low-quality food and any chunk of ice and/or banana greater than 2 cm^2 for the high-quality food. Only food sharing behaviors (active transfer, passive transfer and co-feeding) were analyzed. Begging was defined as placing a hand out with an open, upturned palm. Perseverance was scored as any occurrence of waiting in close proximity (closer than arm's reach) to the possessor or repositioning to have better access to the food. Those behaviors that interfered with food consumption, including attempting to steal food and removing food from the possessor's mouth, were defined as harassment (Gilby, 2006). Data collection ceased for the food possessor whenever he finished eating or abandoned the food.

In addition to data collected during the trial, two other measures were used in the analysis: rank and long-term affiliation. Dominance ranks were calculated using pant-grunts, a submissive vocalization, collected ad libitum from 2010–2011. Among the 19 females there were three pairs that reciprocally pant-grunted to each other during that time period, which resulted in the lack

Table 1.
Food sharing ethogram (adapted from de Waal (1989)).

Sharing behaviors	
Active transfer	Obviously directed transfer of food from the possessor to another chimpanzee, e.g., food placed in an outstretched hand, spitting food into an outstretched hand, etc.
Co-feeding	The possessor allows other chimps to eat from the ice block or browse branch while he is eating. The recipient must remain near the food item while eating.
Passive transfer	The possessor allows other chimps to eat from the ice block or browse branch while he is in possession of the food, but not actively eating. The recipient can break off a piece and move away, requiring less tolerance on behalf of the food-possessor than co-feeding.
Non-sharing food transfers	
Collect near	A non-possessor acquires food that the possessor has discarded (e.g., scrounging).
Begging behavior	
Begging	The beggar extends a hand, palm up and flat, towards the food or the possessor.
Perseverance behaviors	
Waiting	The beggar waits within arm's reach of the food possessor, with his or her attention fixated on the food or the possessor.
Repositioning	The beggar repositions him or herself to be closer/have better access to the food.
Harassment behaviors	
Attempted stealing	A contested attempt to gain possession of the food.
Hand near mouth	The beggar places a hand in front of the possessor's mouth or under it to catch falling pieces of food.
Avoidance behaviors	
Leave	The food possessor walks away from the approach of an individual or beggar.
Shielding/repositioning	The food possessor shields the food with his body or repositions to make it harder for a beggar to access the food.

of a perfect linear hierarchy in one group (FS1 Directional Consistency Index (DCI) = 0.74; FS2 DCI = 1.0). For this study individuals with ties were assigned to the same rank and all subjects were evenly grouped into three rank classes to facilitate analysis (high, middle and low; Vogel, 2005).

Long-term affiliation was calculated from routine observations taken between 2010 and 2011 (FS1 = 5220 min, FS2 = 4860 min). Every 10 min scan samples were taken for affiliation data: grooming, close proximity (contact sitting or within arm's reach), and play. These scans were used to construct a sociometric matrix from which an adjusted residual or closeness coefficient was calculated (Everitt, 1977). These values range from significantly negative (significantly avoidant) to significantly positive (significantly affiliative). Each female's closeness coefficient in relation to the alpha male was used for long-term affiliation in the current study.

To determine which strategies influenced food sharing from male to female chimpanzees, for each food quality we ran a linear mixed model (LMM) with the number of food transfers in a given trial as a continuous dependent variable. Long-term affiliation, short-term proximity before trials, whether or not the female copulated during that trial, the swelling level of the female, rank, begging, and perseverance were included as fixed terms in various combinations. Models were constructed with combinations of the variables that best represented each sharing hypothesis (e.g., one model to test the 'sharing under pressure hypothesis' had rank, begging, and perseverance). Then, because the background literature suggests that these hypotheses might not be mutually exclusive (e.g., Teleki (1973) found the females with larger swellings were more persistent), we tested the interactions between rank, sex, and swelling with the other independent variables. We also ran a null model (random effects only) and a full model (including all fixed effects). For the low-quality condition, this resulted in 10 different models representing different food sharing strategies or combinations of strategies. As begging only occurred during the high-quality food condition, it was added as a fixed term for those analyses only, resulting in 14 models being compared in the high-quality food condition. Male identity, female identity and trial number were included as random effects to control for repeated sampling and interdependence between dyads. We used an ANOVA to determine which model had the most explanatory power by comparing the Akaike's information criterion (AIC) values for all of the possible models. Once the best model was identified, a Markov chain Monte Carlo simulation of 10 000 interactions was used to obtain significance values.

3. Results

3.1. *Food preference and transfer types between food conditions*

The preference test showed that all chimpanzees strongly preferred banana slices to sweet gum leaves, with all individuals picking the banana slice over the sweet gum 10 out of 10 times, except one female who chose banana 9 out of 10 times (mean $\pm$ SEM choice for banana $= 99.55 \pm 0.21\%$, Wilcoxon signed-rank test: $Z = -4.60$, $p < 0.0001$, $N = 22$). To compare whether this preference translated into behavioral differences between the food trials, we calculated rates of food sharing by dividing the number of food transfers received by the number of minutes that the trial lasted. This compensates for the fact that the ice block typically took longer to consume than the browse. In FS1, the alpha male was in possession of the high-quality item for 153 min and the low-quality item for 89 min. In FS2, the alpha male possessed the ice block for 392 min and browse for 52 min. The beta male in FS2 obtained the food item on two occasions, totaling 149 min of food possession and reducing the time the alpha male in FS2 possessed the browse. Sharing occurred at approximately the same rate in both food conditions, with an average of 0.30 transfers/min in the high-quality food trials and 0.28 transfers/min in the low-quality trials.

Of the 45 browse transfers, the majority were passive transfers (48.28%), followed by co-feeding (37.21%), then collect near (15.52%). Active transfers only accounted for 2.3% of the transfers observed. The pattern was a bit different for the 165 ice block transfers, with the majority of transfers being collect near (44.24%), followed by co-feeding (27.27%), passive transfer (18.07%). Active transfers accounted for 10.30% of the high-quality transfers, although the difference in sharing types between the two conditions was not significant ($\chi^2 = 2.17$, df $= 2$, $p = 0.33$). It is important to note that the type of transfer may have been constrained by physical characteristics of the food; for example, it was initially easier to break a piece off of the browse (as would occur during a passive transfer) than the ice block.

3.2. *Perseverance behaviors and food quality*

Female behavior did differ between the two conditions. The average rate of perseverance behaviors per minute from the females was 0.63 ± 0.82 (mean $\pm$ SD) during the high-quality trials and 0.07 ± 0.14 (mean $\pm$ SD) during the low-quality food trials (Wilcoxon signed-rank test: $Z = 3.22$,
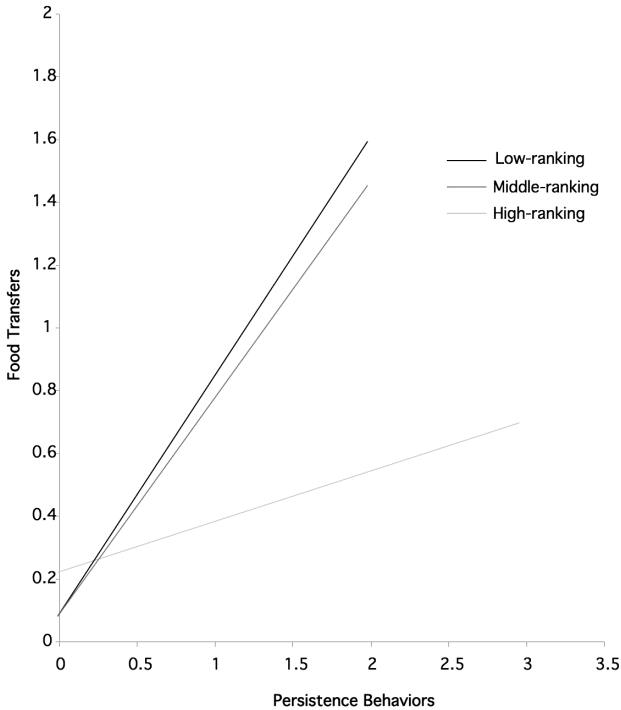
Figure 1. The effect of rank and perseverance on food transfers. High-ranking females received more food without perseverance than middle- and low-ranking females. Increasing perseverance did not result in much added benefit for high-ranking females. In contrast, the more a low- or middle-ranking female persevered, the more food she obtained. The lines are trends based on the raw data.

$p = 0.001$, $N = 19$). Perseverance by the females correlated with avoidance behavior by the males only in the high-quality food condition (Spearman's correlation: high-quality: $\rho = 0.61$, $p = 0.021$, $N = 19$; low-quality: $\rho = 0.09$, $p = 0.77$, $N = 19$). No harassment behaviors occurred in either food quality condition. Additionally, the average number of individuals in proximity to the food possessor was 0.85 ± 0.94 (mean $\pm$ SD) in the low-quality and 1.17 ± 1.39 (mean $\pm$ SD) in the high-quality condition. Begging gestures were only observed in the high-quality food condition. Finally, the high-quality condition seemed to elicit copulations more than the low-quality condition as out of 10 copulations observed, 9 of them were during the high-quality trials (binomial test, $p = 0.01$, $N = 10$ copulations). Further raw data for perseverance behaviors, copulations, and transfers by individual are provided in Table 2.

Table 2.
Raw data for perseverance behaviors, copulations and transfers by individual.

Female ID	High-quality food					Low-quality food				
	No. of trials present	No. of transfers	Copulations (session numbers)	Perseverance	No. of sessions fully swollen (session numbers)	No. of trials present	No. of transfers	Copulations (session number)	Perseverance	No. of sessions fully swollen (session numbers)
FS1 group										
GG	7	12	0	5	0	7	5	0	0	0
RN	7	18	0	6	1 (7)	7	1	0	2	2 (6, 7)
BO	4	0	0	0	0	5	3	0	0	0
MA	7	8	0	6	1 (2)	7	5	0	1	0
KT	7	15	0	3	0	7	1	0	0	0
AJ	2	8	1 (1)	2	1 (1)	4	1	0	0	0
RI	3	2	0	1	1 (3)	4	0	0	0	0
DN	4	0	0	0	0	7	3	0	0	0
TA	7	9	1 (4)	3	1 (4)	7	6	0	2	2 (4, 5)
MS	7	4	0	4	0	7	5	0	0	0

Table 2.
(Continued.)

Female ID	High-quality food					Low-quality food				
	No. of trials present	No. of transfers	Copulations (session numbers)	Perseverance	No. of sessions fully swollen (session numbers)	No. of trials present	No. of transfers	Copulations (session number)	Perseverance	No. of sessions fully swollen (session numbers)
FS2 group										
ER	4	15	1 (4)	15	1 (4)	6	2	0	1	1 (3)
CY	4	0	0	0	0	5	2	0	0	0
VV	7	1	0	4	1 (2)	7	2	0	0	1 (2)
TI	3	0	0	0	0	5	3	0	0	0
BB	7	16	0	2	1 (1)	6	2	0	0	0
VR	7	27	1 (2)	5	2 (1, 2)	7	5	1 (1)	0	1 (1)
JL	7	21	5 (1, 3, 5, 6, 7)	6	0	7	7	0	0	0
DA	6	3	0	1	2 (5, 6)	6	0	0	3	1 (5)
WA	7	6	0	3	2 (3, 4)	7	0	0	0	1 (3)

The number of trials present is out of a maximum of 7 trials. Transfers received, copulations observed and perseverance behaviors are raw totals for all trials in the study; however, analyses presented in the Results section were conducted by trial, and male and female identity was controlled for.

3.3. *Food sharing strategies by food quality condition*

We ran a linear mixed model to determine which of the food sharing strategies (or which combination of food sharing strategies) was most predictive of obtaining a food transfer. During the low-quality trials, the model with the best explanatory power included rank, perseverance, and a rank by perseverance interaction (AIC $= 152.0$, $\chi^2 = 46.46$, df $= 0$, $p < 0.001$). Of the fixed effects, only the interaction between rank and perseverance was significant (Table 3). Higher-ranking females received more food transfers with less perseverance than lower-ranking females (Figure 1). Lower- and middle-ranking females tended to get more food with increased perseverance.

To analyze the high-quality trials, we tested the same models as in the low-quality condition except for the addition of begging as a fixed effect. Since begging and perseverance were correlated ($r = -0.77$), they could not be added into the same model. There were no other correlations between fixed effects. For the high-quality condition, the model with the best explanatory power included copulations, perseverance, and a copulation by perseverance interaction (AIC $= 377.8$, $\chi^2 = 9.84$, df $= 0$, $p < 0.001$). For this model there was a trend towards copulations as a significant factor; perseverance and the interaction between copulations and perseverance were highly significant (Table 4). The results of the full model, which was not the optimal model, also supported the idea that that perseverance plays a larger role than

Table 3.
Results of the LMM analyses for the best model in the low-quality food condition.

Variable	β	SE	95% CI	t	p
Fixed effects					
Intercept	0.23	0.15	$-1.02 - 1.47$	1.54	0.13
Rank	-0.06	0.05	$-0.16 - 0.05$	-1.04	0.30
Perseverance	-0.08	0.16	$-0.41 - 0.22$	-0.54	0.59
Rank × perseverance	0.27	0.07	$0.13 - 0.41$	3.83	0.002*
Random effects					
Male	Variance	0.05			
Female	Variance	0.01			
Trial	Variance	0.05			

The highest ranking category was represented as 1 in analyses, and the lowest category as 3 (e.g., high-ranking females with high rates of perseverance received less food). SE, standard error; CI, confidence interval.
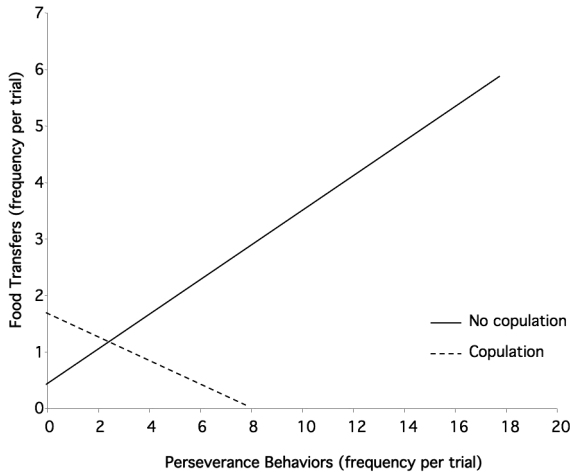* Factor significant at $p < 0.05$.

Figure 2. The effect of sex and perseverance on food transfers. Females who had sex received more food transfers without perseverance than females who did not copulate. Females who did not copulate during the trial received more food the more they persevered. The lines are trends based on the raw data.

other social factors. Nine copulations were observed in the high-quality conditions, from five females. One female (JL) copulated with the alpha male a total of five times occurring in five different sessions, which is accounted for by the treatment of female identity as a random effect in analyses. The interaction shows that females who copulated during a given trial were more

Table 4.
Results of the LMM analyses for the best model in the high-quality food condition.

Variable	β	SE	95% CI	t	P
Fixed effects					
Intercept	0.25	0.24	$-3.27 - 4.16$	1.05	0.30
Copulations	1.27	0.66	$0.12 - 2.80$	1.90	0.06
Perseverance	0.33	0.05	$0.23 - 0.41$	7.22	<0.001*
Copulations × perseverance	-0.50	0.16	$-0.81 - -0.20$	-3.16	0.002*
Random effects					
Male	Variance	<0.001			
Female	Variance	<0.001			
Trial	Variance	0.19			

SE, standard error; CI, confidence interval.
* Factor significant at $p < 0.05$.

likely to get food with less perseverance than females who did not copulate during that trial (Figure 2). Females who did not copulate obtained more food transfers with increasing perseverance.

Copulations and swelling were not correlated and models including both copulations and swelling or swelling independent of copulations did not have more explanatory power than ones including copulations alone. These copulations contrast with those observed during regular observations from 2010–2011. Out of 27 copulations occurring during this time period (14 in FS1, 13 in FS2), 26 of them occurred with a maximally swollen female. Thus, nearly all copulations outside of the experimental context were restricted to the chimpanzees' fertile periods.

We asked if the increased food transfers received by females who copulated may have been the product of these females being favored for copulations by the males in general. As a follow-up test, we compared long-term sexual interactions between the males and females, but found that whether an individual female had copulated with the male food possessor during routine observations conducted from 2010–2011 did not correlate with food transfers received in this study (Spearman's correlation: $\rho = 0.18$, $p = 0.46$, $N = 19$), indicating that copulations in the short-term had an effect that long-term sexual interactions do not.

4. Discussion

Alpha male chimpanzees share both high- and low-quality foods non-randomly with females, and both males and females change their behavior based on food quality. The food items in this study were different sizes, and the high-quality food (an ice block) was not as divisible as the low-quality food (browse) until it began to melt. However, chimpanzees used the different transfer types (active transfer, co-feeding, passive transfer, and collect near) with the same frequency in both conditions, indicating that the physical differences between the food items were not so great as to impede the males' sharing decisions. The food conditions instead differed in who received food and in support provided for the 'food for sex' hypothesis.

In the high-quality trials, we found statistical support for the 'food for sex' hypothesis, despite having only two alpha males to study. These male food possessors copulated more when they possessed the high-quality food item than when they had the low-quality one, and females who copulated with

the male food possessor received more transfers without any perseverance than females who did not copulate. Interestingly, perseverance by females who copulated correlated with fewer food transfers within those trials, while females who did not copulate received more food the more they persevered.

The effect of perseverance was relatively larger than the effect produced by copulations, perhaps due to the many instances of perseverance in this study dwarfing the few copulations we observed. Additionally, the role of perseverance was the only significant factor noted in the full model (which contained all of the fixed effects without interactions). Critically, though, the best fit models reported here demonstrate that perseverance was being modulated by other social factors for both food quality conditions. Even with so many fewer data points for copulations than for perseverance, we were able to observe an interaction between the two: either copulations or perseverance may result in receiving more food, but doing both in the same trial results in less food for reasons that remain unclear. While we never saw high rates of perseverance from females who copulated during the trials in which they copulated, these females did exhibit varying levels of perseverance in those trials, indicating that perseverance and copulations were not used as mutually exclusive strategies by the females. Although five of the copulations came from one female, the perseverance by copulation interaction was significant when controlling for female identity. Other females may have been using this strategy less frequently, while some did not use copulations as a tactic at all.

The positive association between copulations and food transfers was a short-term one and applied only to copulations occurring during trials. Although we found an effect of copulations in the short-term, this effect was independent of female estrous state. If there was a significant interaction between swelling and perseverance, it did not predict food transfers as well as the interaction between copulations and perseverance. There was also no association over the long-term between the frequency of copulations occurring in the previous year and the rate of food transfer. The males in this study did not seem to be attempting to influence long-term female mate choice with food sharing. Because one group had only one male (i.e., no choice) and the other group had a very subordinate beta male for whom we did not observe any copulations in the previous year, this apparent lack of effort on the part of the alpha males is unsurprising.

Instead, copulations may be a mechanism for increasing tolerance in high excitement or tense social situations. This use of copulations has been observed in bonobos (de Waal & van Roosmalen, 1979; de Waal, 1987), and Parish (1994) showed that female bonobos use socio-sexual contact to reduce tension in female–female food sharing situations. Jaeggi et al. (2013) found that bonobos used grooming and socio-sexual contact more in the tension caused by a monopolizable food item, but did not find similar tactics with chimpanzees. This non-reproductive function of sex is further suggested by the fact that males in this study mated with females outside of estrus, whereas wild chimpanzees prefer to mate with females at their peak swelling periods, which have the highest likelihood of fertility (Deschner et al., 2004). The captive chimpanzees included in this study have also historically confined copulations to periods of maximal swelling. If males had been acting purely under the assumptions of the 'food for sex' hypothesis narrowly defined, we should have only seen copulations targeted towards females with the highest chances of conception. However, in the high-quality condition only, the chimpanzees exhibited copulations at various points in their cycles. The observation of copulations at both maximal and non-maximal swellings may suggest additional non-reproductive motives and explain swellings' inability to explain food transfers as well as copulations did.

It is important to note that of the nine copulations in this study, only two occurred in the FS2 group. This observation still fits the tolerance hypothesis however, because the male in FS1 shared and avoided non-significantly more than the male in FS2. Thus, there may have been differences between the two groups' initial tolerance levels. Copulations may have been a relatively more important or useful strategy for females in the group with higher tension caused by an alpha male who was initially less inclined to share. Even so, the effect of copulations in the high-quality condition was not group-driven, since we controlled for group/male in our analyses. More research into the tolerance-building function of sex in chimpanzees could clarify the issue.

In the low-quality condition, high-ranking females received similar amounts of food regardless of how much they persevered, suggesting that perseverance may not be an effective strategy for high-ranking females to obtain food. In contrast, low- and middle-ranking females received more food during trials in which they persevered more. Thus, high-ranking females received more food without persevering, but perseverance was a much

more beneficial strategy for low- and middle-ranking females trying to obtain food. While social factors may play a role in the way in which females obtain food, food sharing in exchange for social benefits was not supported in the low-quality food condition. The 'sharing under pressure' hypothesis is also not supported because none of these perseverance behaviors impeded the alpha male's ability to consume the food item at his regular pace.

Other individual attributes, such as long-term affiliation, did not appear to influence which females the males shared with in either condition. Additionally, harassment was not observed in this study and could not be examined. One possibility for the lack of harassment could be the sex ratio of the groups: no males who would provide a serious challenge to complete possession of the food may have obviated relatively aggressive behaviors. Neither proximity to the male before the trial had begun nor proximity to the male once the food trial started had an effect on food transfers received, indicating that short-term affiliation was not predictive of food transfers. There were also no discernible effects of dominance rank on females' success at obtaining food, only on the way in which they obtained food in the low-quality condition. Long-term affiliation between males and females similarly had no effect on food sharing in this study, which is consistent with the findings of de Waal (1989). Prior work, including Nishida et al. (1992) and Mitani & Watts (2001), has shown that long-term male–male relationships influence sharing in the wild. Since male–female relationships do not usually involve hunting or coalitions to obtain rank, they may have little bearing on who receives food, perhaps suggesting that these more immediate factors — copulations and perseverance — may influence food sharing between male and female chimpanzees.

Gomes & Boesch (2009) observed a long-term correlation between copulations and food transfer in the Taï forest, where females have many males to choose from and meat may be used to bias future mate choice. Our results show that long-term mate choice biasing is not the sole function of 'food for sex' and that short-term function also plays a role. This role does not appear to be enhancing the current reproductive success of the male because short-term sharing was not biased toward females at peak estrus and copulations in these groups actually differed from their normal sexual behavior, in which copulations almost exclusively occurred with females at peak swelling. Short-term 'food for sex' may instead function to reduce tension, to enhance the male's tolerance of individual females' presence near the food,

and to enable females who copulated with the food possessor to obtain food without persevering.

The interaction between copulations and perseverance in the high-quality condition implies that these are alternative strategies to gain access to food. Females who had not obtained the alpha male's tolerance through copulation received more food the more they persevered in the high-quality condition. Assuming that the high-quality food item does induce more excitement and tension in the chimpanzees than the low-quality item, the relative lack of tension induced in the low-quality condition could explain why there were fewer instances of copulations in our low-quality condition and why the 'sex for tolerance' strategy by non-possessors has not been observed in captive studies of chimpanzees until now. Without such tension, access to food by non-possessors may already be fairly well tolerated, and perseverance may become the behavior of choice for obtaining food. Because we did not anticipate this short-term function for copulations, we did not study anxiety behaviors before and after copulations, which would be a logical test of this hypothetical tolerance-building function. Nonetheless, our results imply that humans and bonobos are not the only apes that use copulations for the non-conceptive purposes of reducing tension and enhancing tolerance (de Waal, 1995).

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