

Perseverance and food sharing among closely affiliated female chimpanzees

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Received: 10 May 2013 / Accepted: 11 July 2013
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Abstract Chimpanzees (*Pan troglodytes*) have been frequently observed to share food with one another, with numerous hypotheses proposed to explain why. These often focus on reciprocity exchanges for social benefits (e.g., food for grooming, food for sex, affiliation, kinship, and dominance rank) as well as sharing based on begging and deterring harassment. Although previous studies have shown that each of these hypotheses has a viable basis, they have only examined situations in which males have preferential access to food whereby females are required to obtain the food from males. For example, studies on male chimpanzee food sharing take advantage of successful crop-raids and/or acquisitions of meat from hunting, situations that only leave females access to food controlled by male food possessors. This begs the question how and with whom might a female chimpanzee in sole possession of a high-quality food item choose to share? In two large captive groups of chimpanzees, we examined each of the hypotheses with female food possessors of a high-quality food item and compared these data to a previous study examining food transfers from male chimpanzees. Our results show that alpha females

shared significantly more with closely affiliated females displaying perseverance, while kinship and dominance rank had no effect. This positive interaction between long-term affiliation and perseverance shows that individuals with whom the female possessor was significantly affiliated received more food while persevering more than those with neutral or avoidant relationships towards her. Furthermore, females with avoidant relationships persevered far less than others, suggesting that this strategy is not equally available to all individuals. In comparison to the mixed-sex trials, females chose to co-feed with other females more than was observed when the alpha male was sharing food. This research indicates that male and female chimpanzees (as possessors of a desired food item) share food in ways influenced by different factors and strategies.

Keywords Food sharing · Chimpanzees · Affiliation · *Pan troglodytes* · Perseverance

Introduction

Food sharing, a term defined as the unresisted transfer of a monopolizable food from a possessor to a recipient (Feistner and McGrew 1989), is common among many animal taxa including non-human primates (Jaeggi and van Schaik 2011). Although food sharing occurs most often between mother and dependent offspring (McGrew 1975; Nishida and Turner 1996; Ueno and Matsuzawa 2004; Jaeggi et al. 2008; Silk et al. 2013), it is of exceptional interest in chimpanzees (*Pan troglodytes*), a species with an unusually high frequency of sharing among unrelated adults (Goodall 1963; Feistner and McGrew 1989). Although many chimpanzee food sharing studies have been

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conducted in the wild, captive populations provide an ideal environment for systematic testing of different hypotheses. In addition, wild studies have tended to focus on the sharing of meat, food that is often the result of hunting by male chimpanzees. This leaves the males in sole possession of the desired food item, allowing distribution of it as they see fit. As such, there is an absence of research on how a female chimpanzee would distribute and share a resource if she were the exclusive possessor. The present study asks how and with whom female food possessors share a desirable, high-quality food item.

Male chimpanzees are known to acquire meat from hunting, and highly desired food items from successful crop raids (Nishida 1970; Hockings et al. 2007), and often maintain possession of the food item until it is fully consumed. As a result, female chimpanzees are often left to persist and possibly beg for pieces of the desired high-quality food item. Sharing often occurs among unrelated individuals, therefore social benefits such as sex, grooming, and reinforcing social bonds are hypothesized to explain this behavior (Teleki 1973; de Waal 1989, 1997; Nishida et al. 1992; Boesch 1994; Mitani and Watts 2001; Watts and Mitani 2002; Hockings et al. 2007; Gomes and Boesch 2009). It may also be that sharing with non-kin promotes popularity and increases status within the group (de Waal 1982; Moore 1984; Nishida et al. 1992).

Relatively little of this research has focused on the types of sharing that occur, whether the transfers of food items were active, passive, collect near, or possibly even co-feeding (definitions adapted from de Waal 1989). While co-feeding, active transfer and passive transfer all require the possessor to have a high tolerance to social proximity, and to make a decision to actively provide another individual with a piece of food, collect near simply requires the possessor to discard pieces of food.

After we conducted a first experiment on the differences between both high- and low-quality food sharing by male chimpanzees (Crick et al. 2013), we repeated the study with only the high-quality food item after the males had been removed from each of two social groups for management purposes. The removal of male chimpanzees allowed us to see how females would share a high-quality food item without the risk of male interference. We only utilized high-quality food items as this is what chimpanzees typically share in the wild (Slocombe and Newton-Fisher 2005; Hockings et al. 2007). We ask, with only female chimpanzees remaining in the social group and no males to monopolize the high-quality food item, with whom and how would high-ranking females choose to share? In addition, we use the male food sharing data to draw direct comparisons on how and why the types of food transfer differ depending on whether a male or female chimpanzee was in possession.

Methods

Research was conducted with two groups of socially-housed chimpanzees at the Yerkes National Primate Research Center Field Station, Lawrenceville, GA, USA. Originally, the first group (FS1) consisted of one adult male and ten adult female chimpanzees and the second group (FS2) of two adult males and nine adult females. As part of a previous study (Crick et al. 2013), we conducted seven experimental sessions from June to July 2011, collecting data on how male chimpanzees share high-quality food items in their mixed-sex group. Approximately 6 months after these sessions, all of the males were removed from each group for management reasons while the females remained. We then conducted another seven sessions within these all-female groups from January–February 2012 following the same procedures as the previous study.

Food sharing sessions took place in the chimpanzees' outdoor enclosures and they did not have access to the indoor areas during the session. Outdoor enclosures for FS1 and FS2 consist of 711 and 528 m² grassy areas, respectively, with climbing structures and enrichment toys connected to indoor areas containing sleeping platforms, nesting materials and swings. Each group was provided with a single, high-quality food consisting of 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 sections were uniformly distributed throughout the ice block and held in place with paper straws as the block froze overnight (Crick et al. 2013).

Data collection began 30 min before the delivery of the food item; we recorded short-term proximity via scan samples (categorized as: in proximity, which included close contact and within arm's reach, and not nearby) every minute, for each individual relative to the eventual food possessor (the alpha female). All occurrences of grooming and agonistic behavior were also recorded. At the conclusion of 30 min, the food item was brought to the observation tower and delivered to the alpha female, ensuring that the chimpanzees could not see the food item beforehand. Data, including food sharing, begging, and perseverance, were recorded until the food was entirely consumed, or abandoned by the original possessor. Sexual cycles of the females were recorded as none, medium or maximal swelling based on a tumescent index of each female's anogenital swelling (Dahl et al. 1991).

Food sharing behaviors included active transfer, passive transfer and co-feeding; relaxed claim or scrounging; and begging, defined in Crick et al. (2013; adapted from de Waal 1989). As with the previous study, transfers were defined as any piece of food, e.g., any chunk of ice or banana ≥ 2 cm², leaving the alpha female's possession and entering another's possession. Waiting in close proximity

(closer than arm's reach) to the possessor and/or repositioning to have better access to the food was regarded as perseverance, whereas begging was defined as holding out a hand with an upturned palm, gesturing for food. Perseverance and begging differ from harassment in that these behaviors, while indicating an interest in the food, do not interfere with the possessor's consumption. Behaviors that interfered with food consumption, e.g., attempting to steal food, temper tantrums, and removing food from the possessor's mouth, were defined as harassment (Gilby 2006). Avoidance behaviors were recorded when the possessor repositioned herself, shielded the food with her body to impede other's access to the food, or when she left another individual's immediate proximity. Data collection ceased for the food possessor whenever she finished eating or relinquished control of the remaining food.

In addition to data collected during the session, three other measures were used in the analysis: dominance rank, long-term affiliation, and kinship. Since individual dominance rank among female chimpanzees is often not perfectly linear, a three-tiered hierarchical ranking was established (Vogel 2005) within both groups via pant-grunts, a submissive vocalization that we recorded ad libitum prior to and throughout the study period that offers the most reliable measure of dominance (Noë et al. 1980). Long-term affiliation was calculated from routine observations of each dyad's overall proximity to one another (via 10-min scan sampling of grooming, contact sitting, being within arm's reach, and play) taken between 2010 and 2011 (FS1 = 5,220 min of observation, FS2 = 4,860 min). An adjusted residual or closeness coefficient was then generated from these scans to construct a sociometric matrix (Everitt 1977), with values ranging from significantly negative (avoidant) to significantly positive (affiliative). Each

female's closeness coefficient in relation to the alpha female was used for long-term affiliation in the current study. Lastly, since these chimpanzees were members of the same long-established groups, kinship was known (Table 1).

Comparisons between the male and female food possessor trials were calculated as proportional rates (food transfers per minute), due to the differing total consumption times between the two studies. Although the full consumption of the ice block during the male–female trials (M–F) took an average of 53.2 ± 16.6 min in June–July, the female–female trials (F–F) lasted an average of 30.7 ± 5.9 min in January–February. Data were combined from both chimpanzee groups as there were no significant differences across groups. A re-analysis of the data from the previous study (Crick et al. 2013) allows us to examine the differences in how an alpha male shared a high-quality food item versus how an alpha female shared. As in Crick et al. (2013), we tested which strategies influenced food sharing among female chimpanzees using a linear mixed model (LMM) with the frequency of food transfers in a given trial as a continuous dependent variable. Food transfers included active transfer, passive transfer and co-feeding, but did not include collect near (scrounging). Long-term affiliation, short-term proximity before trials, kinship, dominance rank, anogenital swelling index, begging, and perseverance were included as fixed terms in various combinations. Models were constructed with combinations of the variables best representing each sharing hypothesis, resulting in nine models being compared. The session number, group, and the identities of the recipient female and possessor were included as random effects to control for repeated sampling and interdependence between dyads. The LMM generates an Akaike's information criterion (AIC) for each model; the model that offered the greatest predictive power was determined using an ANOVA that compared the AIC for all of the possible models, after which a Markov chain Monte Carlo simulation of 10,000 permutations was performed to obtain significance values for the best fit model.

Table 1 All-female chimpanzee social groups

FS1 Georgia	Long-term affiliation	Transfer rate (per trial)	FS2 Ericka	Long-term affiliation	Transfer rate (per trial)
Reinette	+	10.71	Cynthia	–	2.71
Borie ^a	o	0.14	Vivienne	–	0.00
Mai	–	0.57	Tai	+	1.86
Katie ^a	+	11.71	Barbie	o	1.86
Anja	+	7.40	Virginia ^a	+	10.43
Rita ^a	o	0.71	Julianne	o	4.43
Donna	o	7.86	Daisy	o	0.14
Tara ^a	o	5.00	Waga	–	0.71
Missy	o	4.43			

All information is relative to the alpha female within each respective social group. Individuals listed in a linear dominance hierarchical order, with kinship denoted by ^a

Long-term affiliation: +, affiliative; o, neutral; –, avoidant

Results

We compared data from the previous and the current study on the rate of food sharing. Accounting for differences in duration of food possession, female chimpanzees received significantly more food from female possessors than from male possessors (Paired *t*-test: $t_{16} = -3.83$, $P = 0.001$). F–F food sharing occurred at a rate of 1.37 ± 0.66 (M \pm SD) transfers per minute whereas M–F sharing in the previous study had been 0.30 ± 0.19 (M \pm SD) transfers/min. In addition, female chimpanzees differed in the type

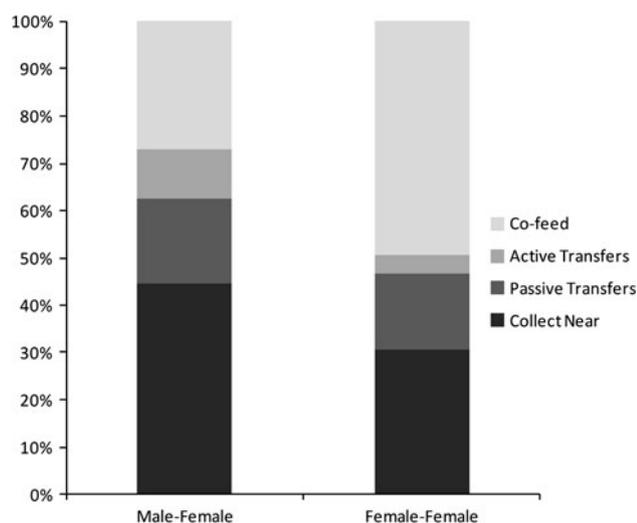


Fig. 1 Comparison of male and female chimpanzee food sharing as provided by a percentage of each transfer type by the total overall food transfers

Table 2 Results of the LMM analyses for the best model predicting F–F food sharing

Variable	β	SE	95 % CI	t	P
Fixed effects					
Intercept	0.62	1.07	–5.33 to 6.73	0.58	0.56
Affiliation	0.07	0.12	–0.18 to 0.22	0.58	0.56
Perseverance	0.31	0.06	0.20 to 0.44	5.39	0.000
Beg	0.43	0.33	–0.13 to 1.23	1.33	0.19
Affiliation*Perseverance	0.03	0.01	0.01 to 0.06	2.87	0.005
Affiliation*Beg	–0.04	0.06	–0.17 to 0.07	–0.63	0.53
Random effects					
Female	Variance	1.62			
Session	Variance	0.30			
Possessor	Variance	0.95			
Group	Variance	0.95			
Residual	Variance	1.97			

Fixed effects that were not part of the best fit model (kinship, dominance, rank, proximity, anogenital swelling index) are not included in this table

Bold indicates factors significant at $P < 0.05$

SE standard error, CI confidence interval

of food transfer most commonly observed, which was tested by comparing the overall frequencies of four transfer types between F–F and M–F sharing ($\chi^2 = 29.07$, $df = 3$, $P < 0.001$; Fig. 1), with significantly more occurrences of co-feeding in F–F food sharing.

We ran a LMM to determine which of the food sharing strategies (or which combination of food sharing strategies) was most predictive of obtaining a food transfer from the

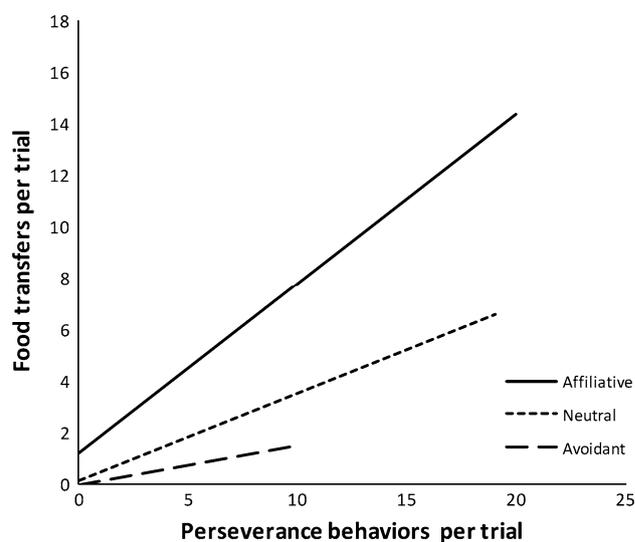


Fig. 2 The effect of affiliation and perseverance on food transfers. Perseverance increased food transfers for all females; however, neutral and avoidant females received far fewer food transfers compared to those that were closely affiliated with the alpha female. For the purposes of displaying these data, females were grouped into three categories (affiliative, neutral, and avoidant) based on the significance level of the adjusted residual, whereas raw adjusted residual levels were used in the LMM. Trend lines are based on the raw data

female food possessor. The model with the best explanatory power included long-term affiliation, perseverance, begging, long-term affiliation by perseverance interaction, and long-term affiliation by begging interaction ($AIC = 559.5$, $\chi^2 = 10.72$, $df = 0$, $P < 0.001$). For this model perseverance was a significant predictor of receiving a share of the food item, as was the interaction between long-term affiliation and perseverance (Table 2). Those females that were significantly affiliated with the food possessor were more likely to receive food with more perseverance, while females that were significantly avoidant persevered less and received fewer food transfers (Fig. 2). Neither long-term affiliation alone nor begging had a significant impact on the amount of food received from the possessor.

Discussion

Many hypotheses seek to explain why chimpanzees share food with one another, ranging from reciprocity of social benefits to buying-off persistent non-possessors. There appear to be, however, a range of differences between how males and females share food with others in their group. Research supports male chimpanzees exchanging resources for grooming (de Waal 1997) or for coalition support and sex (Nishida et al. 1992; Hockings et al. 2007; Gomes and Boesch 2009; Crick et al. 2013), while female sharing may

aim at maintaining close affiliations within the group, not necessarily with kin.

Long-term affiliation and perseverance had little effect on whom males shared with (Crick et al. 2013), but were significant predictors for whom female chimpanzees chose to share with. Our data do not support the notion that placing pressure on the food possessor can explain all sharing, however, because clearly this strategy is not equally available to all individuals. In order to utilize this strategy, individuals need to be socially close to the food possessor, suggesting that the ultimate cause of higher sharing rates is the social relationship rather than the pressure put on the female possessor. This could be the product of female chimpanzees tending to be more nurturing towards close affiliates and offspring. Within both groups the female food possessors (FS1 = Georgia; FS2 = Ericka) shared most frequently to their independent adult daughters, Katie (an average of 11.71 transfers/trial) and Virginia (10.43 transfers/trial), respectively, with each acquiring the highest individual transfer rates within their respective groups. These females, however, also maintained close affiliations with their mothers, whereas the remaining kin displayed neutral affiliations towards the food possessors, leading kinship by itself to have no effect on with whom the females shared. Furthermore, Ericka and Virginia would on occasion take turns licking or biting the banana block, with Ericka holding out the food item for her daughter to eat from but always remaining in possession. Co-feeding bouts such as this were often very well tolerated by the females, whereas the males were much more resistant to female individuals crowding them, potentially explaining the differences in the overall amount of sharing that occurred.

Consistent with the findings of Silk et al. (2013), social rank did not affect with whom the food possessor shared. In a recent study, Horner et al. (2011) showed that high-ranking female chimpanzees were spontaneously more prosocial to others within their group regardless of the rank of the recipient chimpanzee, suggesting perhaps that high-ranking individuals may use generosity to emphasize their dominance (Massen et al. 2010; King et al. 2011).

Although begging was not found to have a significant influence on food transfers, individuals would often resort to begging as the food item broke into multiple pieces and the possessor became satiated, a theoretical circumstance in which the cost of defending the food outweighs the benefits of keeping it (Blurton Jones 1984; Stevens 2004). This result has received empirical support, including a study on jackdaw (*Corvus monedula*) food sharing (de Kort et al. 2006). Unlike the persistent harassment attempts described in Gilby (2006), none of our observed occurrences of begging included any agonistic patterns (i.e., pilo-erection, swaying, screaming, etc.), possibly due to the desired food

item being possessed by the alpha within each respective group.

Alpha female chimpanzees shared more food when in sole possession than their male counterparts, while both sexes transferred food to those individuals that displayed more perseverance. The female possessors, however, frequently shared food with their close affiliates (who persevered more often compared to avoidant individuals), whereas this was not observed among the males. This may be more of a reflection on their natural social relationships, as females tend to spend the most time with individuals of significant affiliation (Langergraber et al. 2009) while males are more flexible in whom they socialize with (Mitani et al. 2010). Although we did observe the females sharing a high proportion with certain kin, they only did so when these individuals maintained a close affiliation with them (see Table 1). Furthermore, food sharing appears to parallel other cooperative behaviors, e.g., where males may form short-term coalitions in exchange for social benefits and females may form long-term alliances based on affiliation (de Waal 1993).

Although seasonal temperature differences between the two studies may account for some of the food sharing differences between the M-F and F-F trials, the results suggest this is unlikely. Considerably more time was spent consuming the ice block in the summer by the male possessor than in the winter by the female possessor. Had these differences been due to the contrasting seasonal temperatures, we would have observed the opposite effect. The quick consumption time of the females also suggests that the food was highly desirable, even in the lower temperatures. Furthermore, alpha females only relinquished the remaining piece(s) of the desirable food item on six of the 14 trials, which again suggests that they found the food highly desirable. In contrast, the alpha males relinquished the food on 12 of the 14 trials. The lack of willingness to relinquish the food indicates that it was highly desirable to the alpha female food possessor.

Although field research observations are often limited to the reality of males acquiring the desirable food(s), experimental food sharing designs can manipulate the situation so as to assist in our understanding of female social relationships and/or strategies.

Acknowledgments We would like to thank Julia Watzek, Zanna Clay, and Noah Snyder-Mackler for assistance with analyses, and Matthew W. Campbell and Katie Hall for helpful comments throughout the study. We are thankful to the animal care, behavioral and colony management, and veterinary staff of the Yerkes National Primate Research Center Field Station for their support throughout this project. The Yerkes NPRC is fully accredited by the American Association for Accreditation for Laboratory Animal Care. This research was supported by the base grant to the YNPRC by the National Center for Research Resources P51RR165, currently supported by the Office of Research Infrastructure Programs/OD

P51OD11132. It was also supported by Emory's PRISM program (NSF GK12 Award # DGE0536941), SURE program (Howard Hughes Medical Institute Grants number 52006923 and 52005873), and the Living Links Center. The experimental conditions, food presented, and subjects included in this study were all approved by the Institutional Animal Care and Use Committee (IACUC) of Emory University.

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