Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality?

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Abstract

Food transfers are often hypothesised to have played a role in the evolution of cooperation amongst humans. However, they also occur in non-human primates, though no consensus exists regarding their function(s). We document patterns of begging for food and success rates as well as associated factors that may influence them for wild bonobos at LuiKotale, Democratic Republic of Congo. Our data, collected over 1,074 observation hours, focus on 260 begging events (outside mother-offspring dyads) of which 37% were successful. We find no support for the "reciprocity hypothesis" – that food is exchanged for grooming and/or sexual benefits; and only weak support for the "sharing under pressure" hypothesis – that food is transferred as a result of harassment and pays off in terms of nutritional benefits for the beggar. Instead, our data support the "assessing-relationships" hypothesis, according to which beggars gain information about the status of their social relationship with the possessor of a food item. This seems to hold particularly true for the frequent, albeit unsuccessful begging events by young females (newly immigrated or hierarchically non-established) towards adult females, although it can be observed in other dyadic combinations independent of sex and age.

Introduction

Across the animal kingdom, food availability causes conflict as individuals compete to acquire nutrients needed to survive, grow and reproduce. Still, in various taxa, including primates, food procured by one individual is transferred to conspecifics, even when acquisition was costly. Functional explanations for this behaviour (see reviews in Feistner and McGrew 1989; Brown et al. 2004; Kaplan and Gurven 2005; Jaeggi and van Schaik 2011) have focused on: (a) *kin selection*: typically provisioning of offspring (Feistner and McGrew 1989); (b) *reciprocity*: a possessor trades food against a past or future benefit, such as receiving food him- or herself, or for other currencies such as grooming, alliances or sex (de Waal 1989); (c) *sharing-under-pressure*: "harassment" or "tolerated theft", i.e., beggars will harass the possessor because the resource is more valuable to non-possessors, and the cost of defending the resource outweighs the nutritional benefit it could potentially confer (Blurton Jones 1984); (d) *information gathering*: beggars are not primarily interested in food, but use the possessor's tolerant or agonistic reaction to gain information about his or her personality (van Noordwijk and van Schaik 2009). A related hypothesis views such food sharing as a means to establish or reinforce social bonds (Wittig et al. 2014; Yamamoto 2015). We extend this rationale and develop what we have termed the "*assessing-relationships*" hypothesis, which posits that food beggars explore their own standing with possessors, independent from any nutritional gain.

Our study adds to the growing body of literature on food sharing by exploring social correlates of begging and transfers in wild bonobos (*Pan paniscus*). Studies of these behaviours in bonobos (Kuroda 1984; White 1994; Hohmann and Fruth 1996; Fruth

and Hohmann 2002; Hohmann 2009; Hirata et al. 2010; Yamamoto 2015) are still rare, relative to its congener, the chimpanzee (*Pan troglodytes*) (e.g. de Waal 1989; 1997; Mitani and Watts 2001; Gilby 2006; Gomes and Boesch 2009; Gilby et al. 2010; Pruetz and Linshield 2012; Eppley et al. 2013; Silk et al. 2013; Wittig et al. 2014). Comparing the patterns of food transfer in these two non-human ape species with what is observed in humans can aid our understanding of the evolution of competition and cooperation in hominins (Stanford 2001; Parish and de Waal 2002; Kaplan and Gurven 2005; Kaplan et al. 2009; Jaeggi et al. 2010a; Sommer et al. 2011).

Similar to chimpanzees, wild bonobos – who are restricted to the regions south of the Congo River – consume a diet of mainly fruit with varying proportions of leaves and piths, supplemented by occasional consumption of meat obtained through predation. They form large multi-male, multi-female communities, which, dependent on food availability, split into smaller parties that may later join again or exchange members (fission-fusion). Females tend to emigrate from their natal community upon sexual maturation. As a result, adult males tend to be more closely related than adult females (Gerloff et al. 1999).

Wild bonobos have regular access to large, high quality fruit (e.g. *Anonidium mannii*, *Treculia africana*), which constitute a significant proportion of their caloric, lipid and protein intake (Hohmann 2009). On occasion, bonobos also prey on mammals such as duikers or monkeys (Fruth and Hohmann 2002; Hohmann and Fruth 2008). Importantly, bonobo habitats often encompass abundant terrestrial herbaceous vegetation (THV), which may reduce female-female competition for food and thus enable greater same-sex tolerance than typically seen amongst chimpanzee females (Wrangham 1980;

Parish 1994; Sommer et al. 2011). In addition, large patch sizes and a relatively low effect of seasonality on fruit availability in bonobo habitats may further reinforce female-female sociality by increasing the time females spend with one another (White and Wrangham 1988; Chapman et al. 1994).

As opposed to chimpanzees, females are typically the primary food possessors in bonobos (Parish 1994; Fruth and Hohmann 2002). Bonobos may show interest in another individual's food by peering from close range at the item or the possessor, often almost touching the possessor's face (Fig. 1) (Furuichi 1989; Idani 1995; Johnson et al. 1999; Stevens et al. 2005); or a beggar may reach for the resource using their hands (Fruth and Hohmann 2002).

< Figure 1 about here>

Actual food transfers appear more contingent upon the intensity of harassment than upon reciprocity, i.e., the possessor appears to passively "tolerate" the beggar's solicitation, as opposed to "active sharing" (Hohmann and Fruth 1996, Fruth and Hohmann 2002). In line with this, some captive studies provide evidence that bonobos tend to eat alone (Parish 1994; Jaeggi et al. 2010b; Bullinger et al. 2013; but see Hare and Kwetuenda 2010; Tan and Hare 2013).

Our study provides the first detailed data on food begging for the site of LuiKotale. We thus enlarge the comparative framework for wild bonobos given that more or less detailed information on food transfer is currently only available for the sites of Lomako (White 1994; Hohmann and Fruth 1996; Fruth and Hohmann 2002; Hohmann 2009) and Wamba (Ihobe 1992; Hirata et al. 2010; Yamamoto 2015).

Leaving aside interactions between mothers and offspring, we test three functional hypotheses for food begging in LuiKotale bonobos.

(a) *Reciprocity:* Food may be used as a commodity to be traded for social benefits, such as grooming. This hypothesis predicts that food transfers will occur more frequently between dyads wherein the possessor and the recipient engage in other prosocial interactions. We restrict our analysis to grooming and sex occurring within three months of a begging event. We did not test food-for-food reciprocity, as not all individuals have equal opportunities to possess resources (Parish 1994; Hohmann and Fruth 1996; Fruth and Hohmann 2002).

(b) *Sharing under pressure:* (e.g. Blurton Jones 1984, for humans; Gilby 2006, for chimpanzees). A food resource may have an increasingly higher value to non-possessors than it does to the possessor, as the possessor becomes satiated over the time during which he or she feeds. The sharing under pressure hypothesis predicts that utility costs incurred by begging (e.g. risk of aggression, time invested that could otherwise be spent acquiring one's own food), are outweighed by the potential nutritional benefits associated with it, and that the more pressure is exerted on the possessors, the more likely they are to allow transfers. Under this hypothesis, food acquisition is the primary goal of begging. We would expect begging to be regularly successful, particularly for dominant individuals who may be able to exert pressure more effectively than subordinates, and who benefit from lower utility costs. Moreover, begging should concentrate on sparser, monopolizable resources.

(c) *Assessing relationships:* (*sensu* van Noordwijk and van Schaik 2009, for orangutans; Yamamoto 2015, for bonobos). Begging may be a means by which individuals assess their relationship to one another. Under this hypothesis, one would expect younger individuals, particularly newly immigrated females to beg more often. In addition, begging should not be limited to sparse resources, but also occur in the context of widely available foods, because the primary aim of begging is not to obtain a nutritional reward.

Methods

Study site and subjects

Data were collected on the wild, fully habituated bonobos of the Bompusa community at LuiKotale, a lowland rainforest study site near Salonga National Park, DRC (02° 45.610', 20° 22.723') (Hohmann and Fruth 2003a). During the 9-month study period (August 2012 – April 2013; data collection: LG), the community consisted of 21 individually identifiable adult and subadult individuals, including 12 adult parous females, 2 subadult females (one a recent immigrant, and one a natal female), 5 adult males and 2 subadult males (Table 1). Infants were not included in our analyses.

< Table 1 about here>

Definitions

Bonobo parties were followed for 1,074 observation hours during the morning, the afternoon, or all day, adhering to a random rota of focal animals, which included all 21 study bonobos.

Party composition scans ran across successive half-hour segments, noting which individuals were present at any point during a 30-min period (n = 2,148). Within this schedule, individuals were observed for an average of 390 h each (range 177–629 h). Times at which individuals entered and exited feeding patches were recorded on a continuous basis. Socio-sexual and agonistic behaviours were documented *ad libitum* (Altmann 1974). Food resources were defined as being of *"*limited access*"* if they were scarce enough that individuals besides the possessor(s) could not access any other undefended item of the same species, and "accessible*"* if there were items available to non-possessors (e.g. THV, stands of small fruit dispersed across branches).

Food begging occurred when bonobos showed interest in an item possessed by another individual within arm's reach. This included peering, reaching for the food or the mouth of the possessor, or attempting to take a portion of food. When begging was observed, the full duration during which the resource was consumed was considered a "possession event". The duration of possession events were used to compare the frequency of begging for resources in given age and sex classes.

Begging was considered successful when food transfer(s) occurred, whether tolerated or resisted by the owner, and unsuccessful if not. Begging or transfers across the same dyad during the same possession event were considered as a single event.

Agonistic interactions, used for the determination of the dominance hierarchy, were defined as one individual moving out of the way of a conspecific's trajectory, either

as anticipatory movement, or as a result of a chase, charge or contact aggression. For 569 agonistic interactions recorded across the study period, a matrix was constructed with displacers on the vertical axis and displacees on the horizontal axis. The matrix was re-ordered using Matman© (Noldus 1998), which minimised the number of reversals to 7.2%. An improved linearity test revealed a significant linearity (although not necessarily steep), which allowed us to assign individual dominance values from 1 to 21 ($h' = 0.51$, $P < 0.01$) (Table 1). As a general rule, adult females occupied the first third of the hierarchy (average rank 8.2, range 1–18, $n = 12$), adult males the second third (average rank 11.6, range 7–17, $n = 5$), and subadults the bottom third (subadult females, average rank 17, range 15–19, $n = 2$; subadult males, average rank 20.5, range 20–21, $n = 2$).

Baseline begging frequency was calculated for each individual using the formula (Ntot(i)/Ttot(i)), where Ntot(i) = total number of observed begging events for individual i and Ttot(i) = total observation time for individual i. The average of these values was used as the baseline frequency of begging events across the community.

Sexual interactions included homosexual female–female encounters (genito-genital rubbing, $n = 258$), homosexual male–male encounters (mounts; $n = 5$) and heterosexual sex (copulations; $n = 203$).

Statistics: To analyze which factors predicted begging (response variable: whether or not begging occurred within a dyad at each opportunity) and success (response variable: whether or not food transfer occurred within a begging event), we ran generalized linear mixed models (GLMMs) with binomial error structure. Our test predictors were possessor and beggar ranks, possessor and beggar ages, possessor and beggar sexes, whether or not the food resource was defensible, as well as three interaction

terms between possessor and beggar rank, possessor and beggar age, and possessor and beggar sex. The begging model contained an additional interaction between defensibility and beggar rank. The control predictors for both models were grooming rate, and rate of sexual interactions, covering both three months prior to and three months after the begging event. In addition we added the short-term perspective investigating whether or not there was a sexual interaction during the feeding event. Random effects and slopes were also included as control predictors for both models. The random effects were beggar ID, possessor ID, dyad ID, and food item. Random slopes were included where possible. Time of possession and number of begs in the begging event were included as offset terms in the begging and success models, respectively. Ranks, ages, and rates of interactions were z-transformed prior to running the models. To establish the significance of the test predictors, we used likelihood ratio tests (Dobson 2002), comparing each full model with its null model, which lacked all test predictors.

We determined Variance Inflation Factors (VIFs) of our predictors to assess co-linearity and found no problem (maximum VIF = 3.07). To test the individual predictors in the begging model, we used likelihood ratio tests (R function drop1 with the argument 'test' set to "Chisq"). Model stability was assessed by removing each possessor ID, beggar ID, dyad ID and food item one by one from the data and re-running the full models. The estimates of these models did not vary problematically compared to the estimates from the original models.

The GLMMs were run in R (version 3.2.1; R Core Team, 2015) using the function glmer of the package lme4 (Bates et al. 2015). Variance Inflation Factors were calculated using the package car (Fox & Weisberg 2011).

Results

Food Items

Table 2 shows the items that individuals of the Bompusa-community at LuiKotale begged for and/or shared during the 9-month study period, as well as their general accessibility. A total of 23% of the 1,074 h of observation time were spent feeding on these items. Of these, 97.12% were dedicated to plant food, 2.81% to animal food, and 0.07% to other items.

< Table 2 about here>

Baseline rates of begging and food transfer

During 1,074 h of observation time, begging events were recorded between 76 of the 213 potential dyads of bonobos. Begging was observed in 53% of 91 female–female dyads, 26% of 94 female–male dyads and 14% of 28 male–male dyads.

The total number of begging events was 279. Excluding begging within dyads known to be related, this was reduced to 260 events, which translates into an average baseline frequency of 3.0 events / 100 h / individual. Of all begging events between non-related individuals, 144 (55.4%) were related to food resources with limited access (total feeding time = 23.1 h, begging rate = 580 events / 100 h), and 110 (42.3%) to accessible food (total feeding time = 436.8 h, begging rate = 25 events / 100 h). Unidentified food resources, for which the availability could not be estimated, elicited 6 begging events (2.3%).

Hypotheses tested

In sum, the predictors clearly influenced the response in the begging model (full model comparison: Chisq = 34.5, p = <0.001). Specifically, the higher a beggar's age, the less frequently he or she begged. Overall, males were less frequently beggars, and less frequently the recipients of begging, than were females. Begging was not obviously related to possessor or beggar ranks; nor could it be accurately predicted according to possessor age. The availability of resources did not have a significant effect on the likelihood of begging (estimate±SE = 1.1±0.6, LRT = 3.1, p = 0.08), though there was a trend for defensible resources (e.g. those not accessible to all individuals) to be more frequent targets of begging than for non-defensible resources (odds ratio = 3.0). None of our predictors had any impact on the likelihood of success. With respect to our above-mentioned hypotheses and predictions, detailed results are as follows:

Investigating the *Reciprocity hypothesis.* The rate of grooming in a dyad within 3 months prior or after the begging event did not affect the likelihood of begging (estimate±SE = -0.4±0.2, LRT = 2.0, p = 0.15), nor did the rate of sexual interactions (estimate±SE = -0.2±0.2, LRT = 0.6, p = 0.43). The occurrence of a sexual interaction *within the same feeding event* did increase the likelihood of begging to occur (estimate±SE = 2.7±1.0, LRT = 5.3, p = 0.02). None of our predictors had any impact on the likelihood of success (full model comparison: Chisq = 14.9, p = 0.3)

Investigating the *Sharing under pressure-hypothesis*. Food was transferred in 97 of 260 cases of begging, constituting a 37.3% success rate. Begging was not obviously

related to possessor or beggar absolute ranks (possessor rank: estimate±SE = -0.3±0.3, LRT = 1.0, p = 0.3; beggar rank: estimate±SE = 0.06±0.5, LRT = 0.03, p = 0.9); nor could it be predicted according to possessor age (estimate±SE = -0.015±0.3, LRT = 0.02, p = 0.9) or the availability of the resource (estimate±SE = 1.1±0.6, LRT = 3.1, p = 0.08). However, a notable difference emerged when investigating relative dominance rank; dominant individuals begging to subordinate individuals (begging "down the hierarchy") succeeded in 56% of cases, whereas subordinate individuals begging to higher ranking individuals (begging "up the hierarchy") succeeded in only 25% of begging events.

Investigating the *Assessing relationships-hypothesis*. Younger individuals begged significantly more than older individuals when they were near possession events (estimate±SE = -1.3±0.5, LRT = 6.3, DF = 1, p = 0.01, Figure 2). Furthermore, figure 3 a&b shows that females begged much more frequently than males during an event in which females rather than males were the possessors, while the predicted values for the likelihood of begging were lower than observed for both sexes. In sum, males were less likely to beg (estimate±SE = -1.3±0.5, LRT = 6.8, DF = 1, p = 0.008), and less likely to receive begging (estimate±SE = -1.4±0.6, LRT = 4.7, DF = 1, p = 0.03) than were females. As illustrated in Table 2 and shown in our results mentioned above, begging could not be accurately predicted by the availability of the resource, as it also occurred in the context of widely available foods.

<Figure 2 about here>

< Figure 3 a&b about here>

Discussion

For a community of wild bonobos at LuiKotale, DRC, we quantified the influence of age-sex class, dominance rank, and affiliatory behaviour relationships on the likelihood of begging for food and associated sharing. With these data, we assessed three major hypotheses regarding the function of food begging.

Hypothesis 1: Reciprocity

We focused on the idea that bonobos might exchange food for grooming or sex (both heterosexual copulations and homosexual genito-genital rubbing amongst females). Our data do not support the predictions of this hypothesis. Neither the rate of sexual interactions nor grooming had any effect on the likelihood of receiving food following begging.

It is interesting to note that in the short term, the occurrence of a sexual interaction during a feeding bout did have an effect on the likelihood of immediate begging. However, as it did not increase the likelihood of receiving food, it does not suggest that food is exchanged for sexual interactions. Rather, the sex itself appears only to be related to the begging event, and may be a part of the begging behaviour itself (Hohmann and Fruth 2000; Fruth and Hohmann 2006).

Hypothesis 2: Sharing under pressure

This hypothesis assumes that the main goal in begging is nutritional gain. Our results did not provide strong support for this hypothesis, although it may be applicable in certain circumstances.

First, under this assumption, begging should often lead to food transfer. However, when viewed all together, begging events only lead to food transfers in 37% of cases. Nevertheless, a notable difference emerged with respect to relative dominance rank; in cases where dominant individuals begged to relatively subordinate individuals (begging "down the hierarchy"), they succeeded 56% of the time, whereas only 25% of begging events "up the hierarchy", where subordinate individuals beg higher ranking individuals, were successful. Dominant individuals are able to exert pressure more effectively than are subordinates, and are less likely to incur utility costs such as aggression as a result of their action. There appears to be a rank-dependent difference in the *function* of begging (despite the fact that rank does not affect *frequency* of begging): higher-ranking individuals are more likely to beg as a means of food acquisition, whereas lower-ranking individuals likely have another motive.

Secondly, if the primary motive for begging is food acquisition, we expected begging to occur primarily for resources with limited access. Although less accessible resources were indeed begged for slightly more frequently than were widely available foods, this effect was not significant. Even resources that were available to all members of a party, including THV such as *Palisota* and *Haumania* species, were begged for (see table 2).

Hypothesis 3: Assessing relationships

An alternative hypothesis postulates that begging is used to gain information regarding his or her relationship with the possessor. Begging may in this way help to gauge the status of a social dyad. The relatively low aggression rates in bonobos (Furuichi 2011), as well as the potential lack of discernable formal signals of dominance and subordination (Stevens et al. 2005), mean that bonobos need this sort of tool to assess their social relationships.

The extreme physical proximity associated with begging, particularly the commonly observed peering at a possessor from close range, appears to be a suitable yardstick. A tolerant reaction of the possessor (which potentially also translates into access to food) would signal a positive relationship, while an intolerant reaction would signify a less relaxed or antagonistic relationship.

The notion that sharing may have a social function recently found considerable support in a study of wild bonobos at Wamba, DRC, also asserting that food sharing has a social rather than primarily nutritional function (Yamamoto 2015), although peering was excluded from begging gestures in that analysis. Our own data on the LuiKotale bonobos put emphasis on the begging component, independent from actual success, and thus provide further corroborating evidence for the social aspect.

Under this hypothesis, we expected that individuals with a less established position in the hierarchy, i.e. younger, recently immigrated females, would beg more. Indeed, as shown in Figures 2 and 3, younger individuals and females were more likely to beg. As males form a clear linear hierarchy deriving from agonistic interactions (Surbeck et al. 2011), they may not necessitate another measure to determine relationship quality.

Female hierarchies, on the other hand, are less linear and more complicated (Stevens et al. 2007), and may thus benefit from additional measures such as begging.

Secondly, we expected that begging would not be limited to less accessible resources. In support of this hypothesis, we found that the accessibility of a food resource had no significant effect on the likelihood of begging, meaning individuals were not more likely to beg for a resource to which they had limited access. Begging events therefore cannot be fully explained as a means to gain access to food.

Implications

The current study clearly supports the hypothesis that begging has a social aspect, as elaborated upon by Yamamoto (2015). Nevertheless, begging can also have straightforward nutritional benefits as it results at least sometimes in the transfer of high quality food (Hohmann and Fruth 1996, Fruth and Hohmann 2002, Hohmann 2009). In chimpanzees, nutritional acquisition is likely to be the primary function of soliciting for food, and accordingly, only high quality foods (e.g. meat) are begged for or transferred. However, a rise in oxytocin levels among food-sharing chimpanzees also hints at a social dimension of this behaviour (Wittig et al. 2014). Although this endocrinological component has not been investigated in our study bonobos, the role of food sharing as a "social tool" is evident because begging is not limited to high quality or defensible foods, and is often not successful. The function of begging may therefore be rank-dependent. Higher-ranking bonobos can bank on a reasonable chance to actually obtain food when they beg, or they may use begging and food transfers as a reinforcement of social ties.

Low ranking bonobos, on the other hand, beg more commonly for social information and reinforcement, with the possible, albeit infrequent, added benefit of food acquisition.

Comparisons of food sharing patterns across species or within species and across study sites are currently hampered by a lack of standardised methodology. Nevertheless, identifying factors that influence food transfers in our closest living relatives can aid to better understand patterns of cooperation and competition in humans. Our study suggests that begging can function as more than a means to acquire inaccessible nutritional resources. Furthermore, patterns of food transfer in bonobos appear different from those of chimpanzees. Thus the evolution of food sharing in hominins turns out to be more complex than traditionally acknowledged, a fact that adds to the importance of food sharing as a major factor in the evolution of human sociality (Bowles and Gintis 2004; Kaplan et al. 2009).

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adhered to animal welfare concerns as well as ICCN requirements and fulfilled the legal requirements of the host country, the République Démocratique du Congo.

Captions

Table 1. Bonobo individuals of the Bompusa community at LuiKotale specifying age, sex, observation time and rank, as well as sexual interactions, begging and food sharing events for each individual.

Table 2. Food resources begged for and / or transferred by bonobos at LuiKotale. Accessibility y = yes; n = no.

Figure 1. Typical scenes of food begging amongst bonobos at LuiKotale / DRC. (a) Immature female Solea (left) peers closely at a piece of duiker meat possessed by adult female Susi (Photo © LKBP/ LG, 2012). (b) Immature male Kebo (left) peers closely at a stem of Palisota sp. 395 possessed by adult male Dango (right) (Photo © LKBP / BF, 2015).

Figure 2. The center of each bubble represents the proportion of possession events (Y-axis)in which individuals of the given age (X-axis) begged. ; bubble size reflects the number of individuals contributing to each age.

Figure 3. Effects of (a) beggar and (b) possessor sex on the proportion of possession events in which individuals begged. The predicted values (dashed lines) were calculated using the mean of the relevant fitted values. Horizontal bar in box indicates median, length of box corresponds to interquartile range. Bars outside boxes indicate percentiles (97.5 above; 2.5 below).

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