

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

Lucas G. Goldstone^{1,2} · Volker Sommer² · Niina Nurmi^{3,4} · Colleen Stephens⁴ · Barbara Fruth^{1,5,6}

Received: 29 April 2015 / Accepted: 12 February 2016 / Published online: 12 March 2016
© Japan Monkey Centre and Springer Japan 2016

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 1074 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.

Keywords Bonobo · *Pan paniscus* · Food sharing · Reciprocity · Sharing-under-pressure · Assessing relationships

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: (1) *kin selection*: typically provisioning of offspring (Feistner and McGrew 1989); (2) *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); (3) *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); (4) *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

✉ Barbara Fruth
fruth@bio.lmu.de

¹ Department of Biology II, Faculty of Biology, Ludwig Maximilian University of Munich, Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany

² Department of Anthropology, University College London, London, UK

³ Department of Behavioral Ecology, Georg August University Goettingen, Goettingen, Germany

⁴ Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁵ Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium

⁶ Department of Developmental and Comparative Psychology, Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany

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; Pruett and Lindshield 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).

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.

1. *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 3 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).
2. *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

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



subordinates, and who benefit from lower utility costs. Moreover, begging should concentrate on sparser resources which can be monopolized.

3. *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 rain-forest 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.

Definitions

Bonobo parties were followed for 1074 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 ($n = 2148$). 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

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

Individuals				Hierarchy status			Sexual interactions		Food sharing events			
Name (ID)	Sex (F = female, M = male)	Age (years)	Observation time (h)	Dominance rank	Ago- nism given (n)	Ago-nism recei- ved (n)	Homosexual (n)	Heterosexual (n)	Beggings received (n)	Food trans- fers (n)	Begging (n)	Food ob-tained (n)
Paula (Pa)	F	29	320.0	1	30	2	15	1	16	8	12	11
Martha (Ma)	F	36	298.5	2	15	3	39	8	14	5	6	5
Uma (Um)	F	19	427.0	3	38	3	29	1	9	3	5	2
Iris (Ir)	F	29	525.5	4	30	6	47	23	45	22	8	5
Olga (Ol)	F	29	442.0	5	26	5	29	0	19	6	11	8
Camillo (Ca)	M	21	294.5	6	90	28	2	20	23	22	1	1
Ben (Be)	M	19	518.5	7	101	28	1	57	20	9	13	6
Zoe (Zo)	F	29	546.5	8	42	9	43	21	42	17	14	5
Jack (Ja)	M	26	431.5	9	43	41	2	23	3	0	2	0
Rio (Ri)	F	29	184.5	10	10	5	16	0	9	1	1	0
Gwen (Gw)	F	19	212.0	11	7	5	14	1	0	0	4	1
Luna (Lu)	F	14	239.0	12	7	5	7	1	3	2	2	2
Wilma (Wi)	F	14	362.5	13	9	15	37	14	11	2	14	8
Susi (Su)	F	19	629.0	14	28	23	97	40	26	10	36	13
Apollo (Ap)	M	14	340.5	15	26	36	2	27	8	3	12	5
Nina (Na)	F	14	494.5	16	10	41	34	7	10	0	31	10
Djulie (Dj)	F	11	356.5	17	2	20	54	33	5	1	52	17
Polly (Po)	F	11	410.0	18	37	76	55	53	9	0	32	5
Emil (Em)	M	15	442.5	19	14	56	1	25	3	0	3	1
Zed (Ze)	M	11	541.5	20	4	141	2	42	4	0	18	6
Roque (Ro)	M	12	176.5	21	0	21	0	9	0	0	2	1
Mean			390.1		27.1	27.1	25.0	19.3	13.3	5.3	13.3	5.3
Min			176.5		0	2	0	0	0	0	1	0
Max			629.0		101	141	97	57	45	22	52	17

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 ($N_{tot}(i)/T_{tot}(i)$), where $N_{tot}(i)$ = total number of observed begging events for individual i and $T_{tot}(i)$ = 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 3 months prior to and 3 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 and 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 1074 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.

Baseline rates of begging and food transfer

During 1074 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: $\text{Chisq} = 34.5$, $p \leq 0.001$). 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 \pm 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 \pm SE = -0.4 ± 0.2 , LRT = 2.0, $p = 0.15$), nor did the rate of sexual interactions (estimate \pm 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 \pm 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: $\text{Chisq} = 14.9$, $p = 0.3$).

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 \pm SE = -0.3 ± 0.3 , LRT = 1.0, $p = 0.3$; beggar rank: estimate \pm SE = 0.06 ± 0.5 , LRT = 0.03, $p = 0.9$); nor could it be predicted according to possessor age (estimate \pm SE = -0.015 ± 0.3 , LRT = 0.02, $p = 0.9$) or the availability of the resource (estimate \pm SE = 1.1 ± 0.6 , LRT = 3.1, $p = 0.08$). However, a notable difference emerged when investigating

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

Type	Species (if possible)	Total hours fed (h:min)	Number of begging events	Accessibility	
				Open to all	Limited to one
Plant food	<i>Anonidium mannii</i>	05:02	41	y	y
	<i>Cola clamydantha</i>	03:16	16	y	y
	<i>Cynometra alexandrii</i>	11:51	1	y	n
	<i>Dacryodes yangambiensis</i>	01:00	7	y	y
	<i>Dialium</i> sp.	17:37	13	y	y
	<i>Gambeya lacourtiana</i>	02:20	4	y	y
	<i>Grewia oligoneura</i>	04:53	5	y	n
	<i>Haumania</i> sp.	15:00	14	y	n
	<i>Irvingia gabonensis</i>	21:49	19	y	y
	<i>Landolphia owariensis</i>	03:35	12	y	y
	<i>Monopetalanthus microphyllus</i>	07:22	1	y	n
	<i>Nymphaea lotus</i>	04:52	2	y	n
	<i>Palisota</i> sp.	20:56	10	y	n
	<i>Parinari excelsa</i>	01:32	2	y	y
	<i>Treculia africana</i>	08:47	46	y	y
		Bark, stripped from trunk	00:38	2	y
	Leaves, various genera	15:12	18	y	y
Animal food	Bird nestling (unknown genera)	00:11	5	n	y
	<i>Cephalophus</i> sp.	05:32	35	n	y
	Honey of stingless bees (<i>Meliponini</i>)	01:17	3	n	y
Other	Faeces (coprophagy)	00:10	4	n	y

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 \pm SE = -1.3 ± 0.5 , LRT = 6.3, DF = 1, $p = 0.01$, Fig. 2). Furthermore, Fig. 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 \pm SE = -1.3 ± 0.5 , LRT = 6.8, DF = 1, $p = 0.008$), and less likely to receive begging (estimate \pm 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.

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

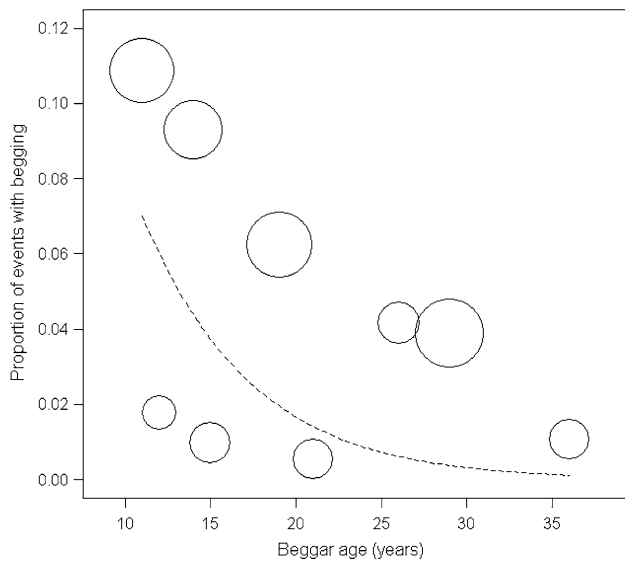


Fig. 2 Influence of age on the likelihood of begging. The centre of each bubble represents the proportion of possession events (Y axis) in which individuals of the given age (X axis) begged; bubble size reflects the number of individuals contributing to each age

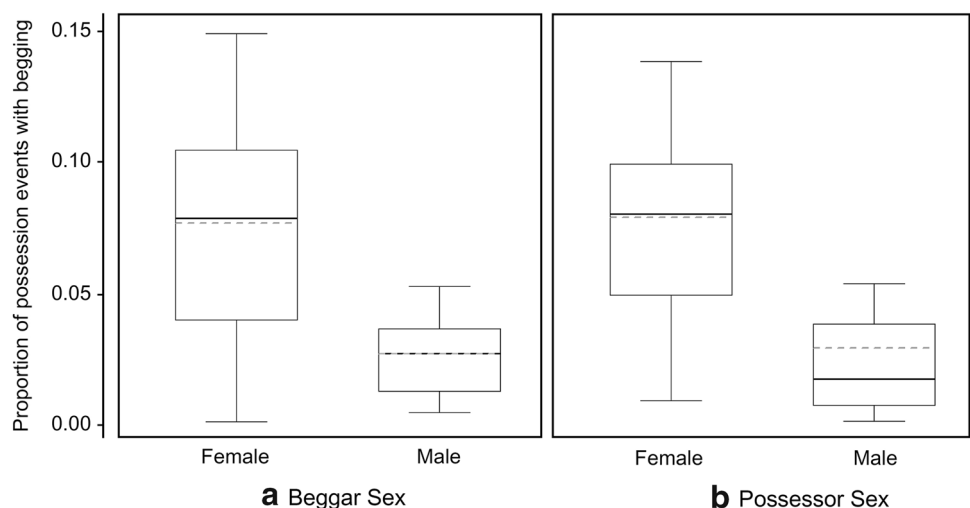
food, it does not suggest that food is exchanged for sexual interactions. Rather, the sex itself appears only to be related to the begging event, and may be a part of the begging behaviour itself (Hohmann and Fruth 2000; Fruth and Hohmann 2006).

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.

Fig. 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)



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 Figs. 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 better understanding of 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).

Acknowledgments The Institut Congolaise pour la Conservation de la Nature (ICCN) kindly granted permission to conduct fieldwork in the Salonga National Park buffer zone. Villagers of Lompole allowed research to be carried out in their communal forest, and staff at LuiKotale field station provided assistance. BF and LG appreciate the support of Gottfried Hohmann, Benedikt Grothe, and Michael Tomasello. Heidi Douglas, Robyn Thiessen-Bock, and Martin Surbeck provided help in the field, Roger Mundry provided statistical support. Core-funding for fieldwork at LuiKotale came from the Max Planck Society, the Federal Ministry for Education and Research (BMBF), the Royal Zoological Society of Antwerp (KMDA), and private donors. The collection of observational data adhered to animal welfare concerns as well as ICCN requirements and fulfilled the legal requirements of the host country, the République Démocratique du Congo.

References

- Altmann J (1974) Observational study of behaviour: sampling methods. *Behav* 49:227–267
- Bates D, Maechler M, Bolker B, Walker S (2015) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8
- Blurton Jones NG (1984) A selfish origin for human food sharing: tolerated theft. *Ethol Sociobiol* 5:1–3
- Bowles S, Gintis H (2004) The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theo Popul Biol* 65:17–28
- Brown G, Almond R, van Bergen Y (2004) Begging, stealing and offering: food transfer in non-human primates. *Adv Study Behav* 34:265–295
- Bullinger AF, Burkart JM, Melis AP, Tomasello M (2013) Bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, prefer to feed alone. *Anim Behav* 85:51–60
- Chapman CA, White FJ, Wrangham RW (1994) Party size in chimpanzees and bonobos: a reevaluation of theory based on two

- similarly forested sites. In: Wrangham RW, McGrew WC, deWaal FBM, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 41–58
- Core Team R (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- de Waal FBM (1989) Food sharing and reciprocal obligations among chimpanzees. *J Hum Evol* 18(433):459
- de Waal FBM (1997) The chimpanzee's service economy: food for grooming. *Evol Hum Behav* 18:375–386
- Dobson AJ (2002) An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton
- Eppley TM, Suchak M, Crick J, de Waal FBM (2013) Perseverance and food sharing among closely affiliated female chimpanzees. *Primates* 54:319–324
- Feistner ATC, McGrew WD (1989) Food-sharing in primates: a critical review. In: Seth PK, Seth S (eds) Perspectives in primate biology, vol 3. Today and Tomorrow's, New Delhi, pp 21–36
- Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks
- Fruth B (2015) Un pouvoir au féminin. *Pour la Sci* No 86:64–68
- Fruth B, Hohmann G (2002) How bonobos handle hunts and harvests: why share food? In: Boesch C, Hohmann G, Marchant L (eds) Behavioral diversity in chimpanzees and bonobos. Cambridge Univ Press, Cambridge, pp 231–243
- Fruth B, Hohmann G (2006) Social grease for females? Same-sex genital contacts in wild bonobos. In: Sommer V, Vasey P (eds) Homosexual behaviour in animals: evolutionary perspectives. Cambridge Univ Press, Cambridge, pp 294–315
- Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *Int J Primat* 10:173–197
- Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. *Evol Anthropol* 20:131–142
- Furuichi T, Idani G, Ihobe H, Hashimoto H, Tashiro Y, Sakamaki T, Mulavwa MN, Yangozene K, Kuroda S (2012) Long-term studies on wild bonobos at Wamba, Luo Scientific Reserve, D.R. Congo: towards the understanding of female life history in a male-philopatric species. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin, pp 143–433
- Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (1999) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc R Soc B* 266:1189–1195
- Gilby IC (2006) Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim Behav* 71:953–963
- Gilby IC, Emery Thompson M, Ruane JD, Wrangham RW (2010) No evidence of short-term exchange of meat for sex among chimpanzees. *J Hum Evol* 59:44–53
- Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One* 4:e5116
- Hare B, Kwetuenda S (2010) Bonobos voluntarily share their own food with others. *Curr Biol* 20:R230–R231
- Hashimoto C, Furuichi T, Takenaka O (1996) Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): sequencing the D-loop region of mitochondrial DNA. *Primates* 37:305–318
- Hirata S, Yamamoto S, Takemoto H, Matsuzawa T (2010) A case report of meat and fruit sharing in a pair of wild bonobos. *Pan Afr News* 17:21–23
- Hohmann G (2009) The diets of non-human primates: frugivory, food processing and food sharing. In: Hublin JJ, Richard MP (eds) The evolution of hominin diets: integrating approaches to the study of paleolithic subsistence. Springer, Berlin, pp 1–14
- Hohmann G, Fruth B (1996) Food sharing in status in unprovisioned bonobos. In: Wiessner P, Schiefenhövel W (eds) Food and the status quest: an interdisciplinary perspective. Berghahn, New York, pp 47–67
- Hohmann G, Fruth B (2000) Use and function of genital contacts among female bonobos. *Anim Behav* 60:107–120
- Hohmann G, Fruth B (2003a) Lui Kotal—a new site for field research on bonobos in the Salonga National Park. *Pan Afr News* 10:25–27
- Hohmann G, Fruth B (2003b) Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour* 140:1389–1413
- Hohmann G, Fruth B (2008) New records on prey capture and meat eating by bonobos at LuiKotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatol* 79:103–110
- Hohmann G, Fruth B (2011) Is blood thicker than water? In: Robbins MM, Boesch C (eds) Among African apes: stories and photos from the field. University of California Press, Berkeley, pp 61–76
- Hohmann G, Gerloff U, Tautz D, Fruth B (1999) Social bonds and genetic ties: kinship association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour* 136(9):1219–1235
- Idani G (1991) Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol* 57:83–95
- Idani G (1995) Function of peering behavior among bonobos (*Pan paniscus*) at Wamba, Zaire. *Primates* 36:377–383
- Ihobe H (1992) Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. *Primates* 33:163–179
- Jaeggi AV, van Schaik CP (2011) The evolution of food sharing in primates. *Behav Ecol Sociobiol* 65:2125–2140
- Jaeggi AV, Burkart VM, van Schaik CP (2010a) On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Phil Trans R Soc Lond B* 365:2723–2735
- Jaeggi AV, Stevens JMG, van Schaik CP (2010b) Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *Am J Phys Anthropol* 143:41–51
- Johnson CM, Frank RE, Flynn D (1999) Peering in mature, captive bonobos (*Pan paniscus*). *Primates* 40:397–407
- Kaplan H, Gurven M (2005) A natural history of human food sharing and cooperation: a review and a new multi-individual approach to the negotiation of norms. In: Gintis H, Bowles S, Boyd R, Fehr E (eds) Moral sentiments and material interests. MIT Press, Cambridge, pp 75–115
- Kaplan H, Hooper P, Gurven M (2009) The evolutionary and ecological roots of human social organisation. *Phil Trans R Soc Lond B* 364:3289–3299
- Kuroda S (1984) Interaction over food among pygmy chimpanzees. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and behaviour. Plenum, New York, pp 301–324
- Mitani JC, Watts D (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924
- Noldus (1998) Matman. Noldus, Wageningen
- Parish AR (1994) Sex and food control in the “uncommon chimpanzee”: how bonobo females overcome a phylogenetic legacy of male dominance. *Ethol Sociobiol* 15:157–179
- Parish AR, de Waal FB (2002) The other “closest living relative”. How bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Ann N Y Acad Sci* 907:97–113
- Pruetz JD, Lindshield S (2012) Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates* 53:133–145
- Reichert KE, Heistermann M, Hodges JK, Boesch C, Hohmann G (2002) What females tell males about their reproductive status: are morphological and behavioural cues reliable signals of ovulation in bonobos (*Pan paniscus*). *Ethol* 108:583–600
- Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro S (2013) Chimpanzees share food for many reasons: the role of kinship,

- reciprocity, social bonds and harassment on food transfers. *Anim Behav* 85:941–947
- Sommer V, Bauer J, Fowler A, Ortmann S (2011) Patriarchal chimpanzees, matriarchal bonobos: potential ecological causes of a *Pan* dichotomy. In: Sommer V, Ross C (eds) *Primates of Gashaka: socioecology and conservation in Nigeria's biodiversity hotspot*. Springer, New York, pp 375–407
- Stanford CB (2001) The ape's gift: meat-eating, meat-sharing, and human evolution. In: de Waal FBM (ed) *Tree of origin: what primate behavior can tell us about human social evolution*. Harvard Univ Press, Cambridge, pp 97–117
- Stevens JR, Vervaecke H, de Vries H, van Elsacker L (2005) Peering is not a formal indicator of subordination in bonobos (*Pan paniscus*). *Am J Primatol* 65:255–267
- Stevens JR, Vervaecke H, de Vries H, van Elsacker L (2007) Sex differences in the steepness of dominance hierarchies in captive bonobo groups. *Int J Primatol* 28:1417–1430
- Surbeck M, Mundry R, Hohmann G (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc R Soc B* 278:590–598
- Tan J, Hare B (2013) Bonobos share with strangers. *PLoS One* 8:e51922
- Trivers R (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man: 1871–1971*. Aldine, Chicago, pp 137–179
- van Noordwijk MA, van Schaik CP (2009) Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behav Ecol Sociobiol* 63:883–890
- White FJ (1994) Food sharing in wild pygmy chimpanzees, *Pan paniscus*. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N (eds) *Current primatology*, vol II., Social development, learning, and behaviour. Université Louis Pasteur, Strasbourg, pp 1–10
- White FJ, Wrangham RW (1988) Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behav* 105:148–164
- Wittig RM, Crockford C, Deschner T, Langergraber KE, Ziegler TE, Zuberbühler K (2014) Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Phil Trans R Soc Lond B* 281:20133096
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behav* 75:262–300
- Yamamoto S (2015) Non-reciprocal but peaceful fruit sharing in wild bonobos in Wamba. *Behav* 152:335–357