Supplementary material –

Social bonds facilitate cooperative resource sharing in wild chimpanzees

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Food sharing and sharing under pressure

Sharing occurred whenever B received access to food in possession of A (Video S1-S3) [1,2]. By food sharing definition sharing did not include cases of stealing or supplants. We only included cases in which the food source was monopolized by one individual and excluded all cases of co-possession, occurring when two or more individuals gained joint access to the food source, such that there is no clear possessor. This included cases of ant or honey dipping, and feeding in tree holes.

During begging interactions we observed all types of begging behavior formerly described in chimpanzees [1], specifically, close proximity peering, reaching a hand, holding the food or food possessor, and using a hand to cover the mouth of the possessor. The hand to mouth gesture is considered as high degree of harassment [1], but was observed only on a single occasion throughout the study period. To assess measures of begging pressure we investigated complete video recordings of all begging interactions, possessors' responses, and sharing behavior of 38 bouts that involved the sharing of highly divisible food items (i.e., meat and *Treculia africana*). We coded begging interactions as dyadic begging events (n = 255), starting when a beggar was in at least 1m proximity and facing the meat possessor, and ended when begging behavior ceased, either due to accessing food or departure of either the beggar or possessor. As we aim to investigate drivers that influence the occurrence of sharing with certain partners but not with others, we recorded all consecutive begging events until either sharing occurred or begging ended. As the respective analyses aimed at contrasting the properties of events with and without sharing (but not at estimating sharing rates across events), the record of begging events until either sharing occurred or begging ended does not bias the results of the begging analysis. For each event we recorded information on the duration of begging and occurrence of harassment, as well as the number of beggars per food possessor. As interactions that lead to reduced feeding efficiency or increased energy expenditure [1] are considered as harassment, we coded as harassment any begging interactions that interfered with the possessor's feeding behavior or caused the possessor to change posture. Thus, not all interactions involving physical contact were marked as harassment, as they did not necessarily inflicted costs on the possessor [3] (Video S4). Furthermore, physical contact was not a required condition for harassment as some non-contact gestures reduced the possessors feeding ability [3] (Video S5).

Dynamic Dyadic Sociality Index

The Dynamic Dyadic Sociality Index (DDSI) [4,5] was used to calculate two continuous daily measures for grooming and aggression, in which each interaction leads to an update of the dyadic score. Grooming and aggressive interactions were collected during a 4-year period starting beginning of 2012 until the end of 2015. Every grooming interaction (weighted by grooming duration) provided a value added to the dyadic grooming score. The value was then divided by the number of dyads involving the interactants, depending on the group size, and the resulting fraction was subtracted from each of these dyads. Every aggressive interaction (i.e., display, charge, chase, fight) provided a value subtracted from the dyadic agonistic score, and then divided and added to all other dyadic scores involving the interactants, depending on the group size. Similar to the Elo-rating, the impact of the interaction is dependent on predictability, such that positive interactions between individuals with a high value have a weaker impact. Consequently, our method accounts for stability in interactions over months, since individuals have to either regularly groom each other to have consistent high grooming values, or to not engage in aggression in order to have consistent aggression values. During each food sharing event, and for each food possessor and potential partner dyad we assigned two scores representing the respective accumulative grooming or aggression values computed as for the previous day, taking into account all grooming or aggressive interactions until this date. We accounted for the direction of interactions, resulting in a directional score per individual per dyad. This reflected previous interactions directed towards the possessor by the potential sharing partner, to better evaluate coercion ability (resource holding potential) and trade (grooming received). Accordingly, high grooming scores represent individuals that provided more grooming, and high aggression scores represent individuals that directed fewer aggressions, within a dyad. In total, we compiled the scores using 6623 grooming and 1468 aggressive interactions for South group, and 4942 grooming and 1402 aggressive interactions for East group.

Assessments of the Dynamic Dyadic Sociality Index

As the DDSI is a new approach to evaluate changes in social relationships over time, we provide an assessment of this measure across sex combination and stability over time. The average grooming score for male beggars was 0.73 ± 0.13 with male possessors and 0.51 ± 0.13 with female possessors, and the average grooming score for female beggars was 0.56 ± 0.08 with male possessors and 0.51 ± 0.08 with female possessors. The average aggression score for male beggars was 0.36 ± 0.14 with male possessors and 0.40 ± 0.08 with female possessors, and the average aggression score for female beggars was 0.53 ± 0.02 with male possessors and 0.54 ± 0.02 with female possessors.

We assessed the stability of the DDSI measures for both grooming and aggression scores between the first (October 2013 - May 2014) and the second (September 2014 - May 2015) field periods. To do so we identified dyads with 'high' and 'low' scores by calculating the mean of each score (i.e., grooming and aggression) in the first field period and adding ('high') or subtracting ('low') one standard deviation from the mean for each score. Then, we checked if dyads that had a 'high' or 'low' grooming or aggression scores during the first field period maintained 'high' or 'low' values during the second field period. For grooming, we identified 24 dyads with initial high scores (provided more grooming), and 11 dyads with initial low scores. 'High' grooming scores were stable in 23 out of 24 dyads, with a single male-male dyad having subsequent lower scores, and 'low' grooming scores were stable in 9 out of 11 dyads, with a single male-male and a single female-male dyads having subsequent higher scores. For aggression, we identified 22 dyads with initial 'high' aggression scores (directed fewer aggressions), and 13 dyads with initial 'low' aggression scores. 'High' aggression scores were stable in 18 out of 22 dyads with a single male-male and three female-male dyads having subsequent lower scores, and 'low' aggression scores were stable in 12 out of 13 dyads with a single male-male dyad having subsequent higher scores. The minor changes between 'low' and 'high' scores for both grooming and aggression scores emphasizes that the DDSI measures are fairly stable across time.

Urine Sample Analysis

Before the analysis, we assigned urine samples according to the behavior that occurred within the 15 to 60 minutes time window of oxytocin excretion [6,7]. In order to assure accurate interpretation of the results in relation to the specific control and social events, we did not include samples in which social behaviors other than the ones investigated in the analysis occurred (e.g. grooming, social play). We also excluded 9 samples that produced results outside of the linear range of the assay's standard curve and for which no material was left for re-measurement. Since very low creatinine values may lead to overestimation of urinary oxytocin levels, we only analyzed urine samples with creatinine levels ≤ 0.05 mg/ml. The oxytocin assay standard curve ranged from 15.62 to 1000 pg/ml and assay sensitivity was 15 pg/ml. Oxytocin validations of parallelism and accuracy were conducted and appeared satisfactorily (see [7]). Inter-assay coefficients of variation of low (50 pg/ml) and high (250 pg/ml) value quality controls were 19.4% and 7.6% ($n = 43$), respectively, while intra-assay coefficients of variation of low (50 pg/ml) and high (250 pg/ml) value quality controls were 13% and 8.8%, respectively.

Statistical analysis

We fitted a Generalized Linear Mixed Models (GLMM [8]) to examine the sharing under pressure hypothesis [1] by testing the effect of three measures of begging pressure, that is the number of beggars, begging duration and occurrence of harassment, on sharing likelihood (begging model). We controlled for group identity (East and South), food type (i.e., meat or non-meat), and the sexes of possessor and beggar (as a linear and an interaction term). We included the identity of the bout, possessor, beggar and dyad as random effects to account for variance in specific identities on the likelihood to share. Furthermore, in order to keep type I error rate at the nominal 5%, we included random slopes [9,10] for begging duration within bout and possessor identity, as well as for the number of beggars within possessor identity. Our dataset for the begging model included 255 begging events of 30 beggars and 16 possessors, of 93 dyads from 2 groups and 38 bouts.

For the test predictor variables that revealed significance in the sharing model, we conducted a post-hoc analysis to investigate whether the observed effect on sharing likelihood was influenced by the food type (i.e., individually acquired vs. jointly acquired), by including an interaction of the test predictor with food type into the model, which was otherwise identical to the sharing model. Model constraints restricted inclusion of a four-way interaction between the dominance ranks, sex combinations, and food type.

In the oxytocin model we controlled for sex, dominance rank, sub-group size, and group membership by including them as further fixed effects. We also included the data collection period as a control predictor (with fixed effects) since both chimpanzee groups experienced social changes between the first and second field season periods (specifically, alpha takeover and hierarchical instability in the South group, and elevated rates of intergroup interactions in the East group). We included event and subject identity as random effects with random slopes (see below).

We fitted an additional Linear Mixed Model (LMM; sub-oxytocin model) [8] to investigate whether log-transformed urinary oxytocin levels (pg/mg creatinine) after sharing differ between food donors and recipients, and depending on bonding status (i.e., bond versus non-bond partners). Social bonds were evaluated in the same manner describe for the sharing model. Since in some cases individuals shared with more than one partner, we added the number of sharing partners as a control predictor, and marked whether any of the partners was a bond partner (y/n). In the model we controlled for the type of food shared (meat and non-meat), sub-group size, sex and dominance rank, and group identity by including them as further fixed effects. We as well included the data collection period as a control predictor (with fixed effects) since both chimpanzee groups experienced social changes between the first and second field season periods. We included event, food donor and recipient, and dyad identity as random effects. Our dataset for the sub-oxytocin model included 107 samples from 20 different individuals and 46 dyads from 66 events.

In order to keep type I error rate at the nominal 5%, we included random slopes [9,10] in all fitted models. We included random slopes for begging duration within bout and possessor identity, as well as for the number of beggars within possessor identity in the begging model, and included random slopes for grooming and aggression scores, within all the random effects, as well as for the dominance rank of the possessor within beggar identity, and the dominance rank of the beggar within possessor's and bout identity in the sharing model. We included random slopes for sub-group size, and rank within subject in the oxytocin and sub-oxytocin model, random slopes for event type (after manually dummy coding and centering) in the oxytocin model, and number of partners within subject in the sub-oxytocin model. Note, the random effects of possessor and beggar identity account for certain chimpanzees being the food possessors at some of the bouts and beggars at others.

We fitted the models in R (version 3.3.0 [11]) using the functions lmer or glmer of the R package lme4 [12]. Prior to fitting the models, we checked all predictors and the response for their distribution and, as a consequence, log transformed urinary oxytocin levels to achieve a more symmetrical distribution. We then proceeded by z-transforming the covariates of begging duration, number of beggars, sub-group size, dominance ranks, grooming and aggression scores to a mean of zero and a standard deviation of one [13]. Visual inspection of qqplots and residuals plotted against fitted values did not reveal obvious deviations from the assumptions of normally distributed and homogeneous residuals. We used the "drop1" function in R to test the significance of the interactions and individual fixed effects by systematically dropping them from the model one at a time [14] and comparing the full with the respective reduced model lacking the individual fixed effect. We conducted a post-hoc analysis to test the effect of each of the target behaviors in the oxytocin model in relation to each other. This was done using the function glht of the R package multcomp [15] (Table S1).

We determined model stability for all models by excluding the random effects one at a time. We then compared the estimates derived for these data with those derived for the full data set. This indicated no influential identities to exist. We derived confidence intervals by means of parametric bootstraps (function bootMer of the package lme4). Variance Inflation Factors (VIF), derived using the function vif of the R package car [16], applied to a standard linear model lacking the random effects, did not reveal collinearity problems, as indicated by the largest value [17] (begging model: 2.02; sharing model: 2.37**;** oxytocin model: 1.17; sub-oxytocin model: 1.33).

Relatedness

Maternal kinship was reliably known for East and South group individuals using pedigree data and confirmed by genetic data extracted from fecal samples [18]. As described in Schubert et al., [18], kinship was assessed with a well-established likelihood-based parentage analysis using 19 autosomal loci [18]. We identified three mother-son dyads and one close maternal kin dyad (brother-sister), representing 0.02% of dyads. We took neither paternal siblings nor father-offspring relations into account due to limited evidence for recognition or social preference for paternal kin [19]. Due to limitations of the genetic analysis, all possible female sibling relationships that were not observed from birth, and accordingly were not known to have the same mother were assigned as unrelated. The rationale behind this is based both on the typical male-philopatry female-dispersal biology of chimpanzee societies, but as well on evidence showing that the vast majority of female-female dyads within a group are not maternal siblings [19]. Owing to our methodological limitations, we might have underestimated the degree of female-female relatedness in the East group chimpanzees.

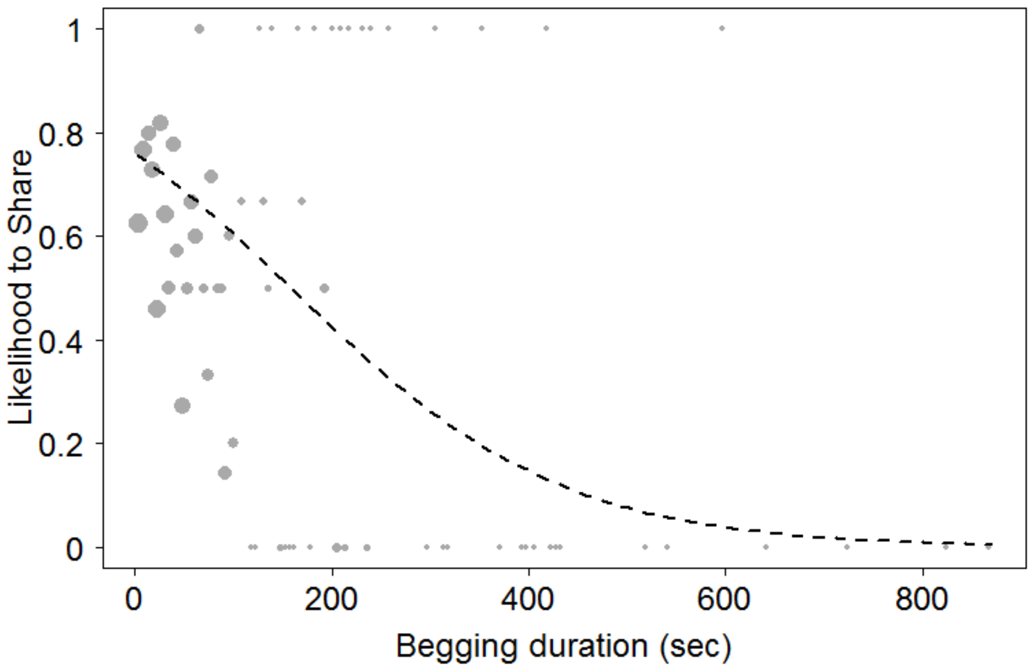

Figure S1. Effect of begging duration (second) on the likelihood to share. Shown in grey are the observed probabilities to share (larger point areas denote a larger number of observations) as well as the fitted model (dashed lines)

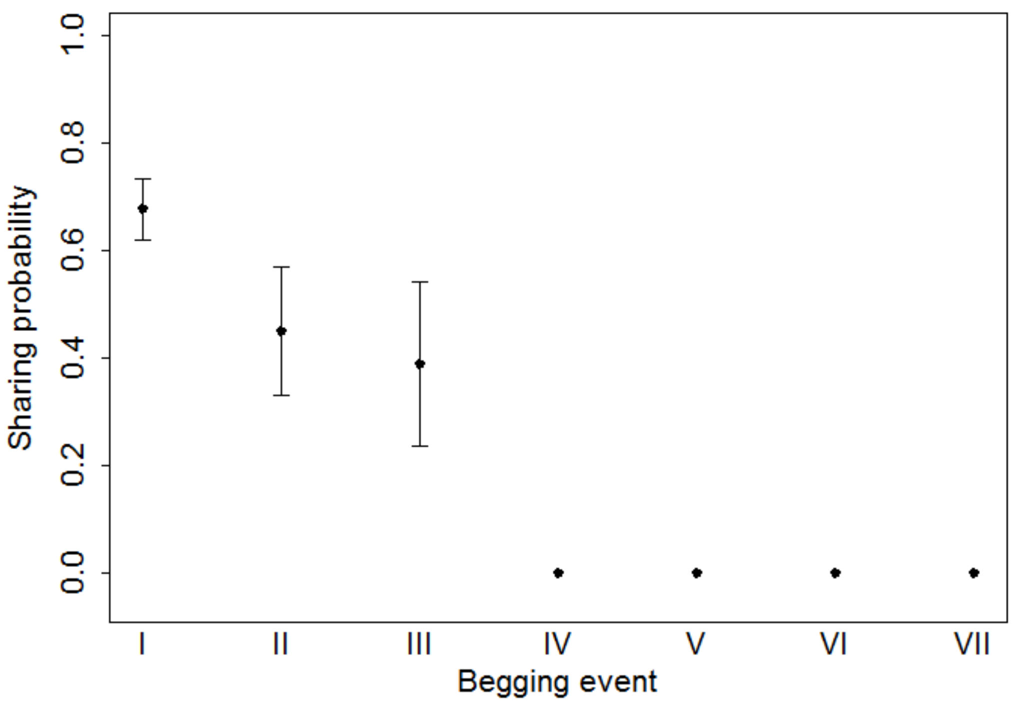

Figure S2. Effect of begging event order on the likelihood to share. Shown are the mean ± SE.

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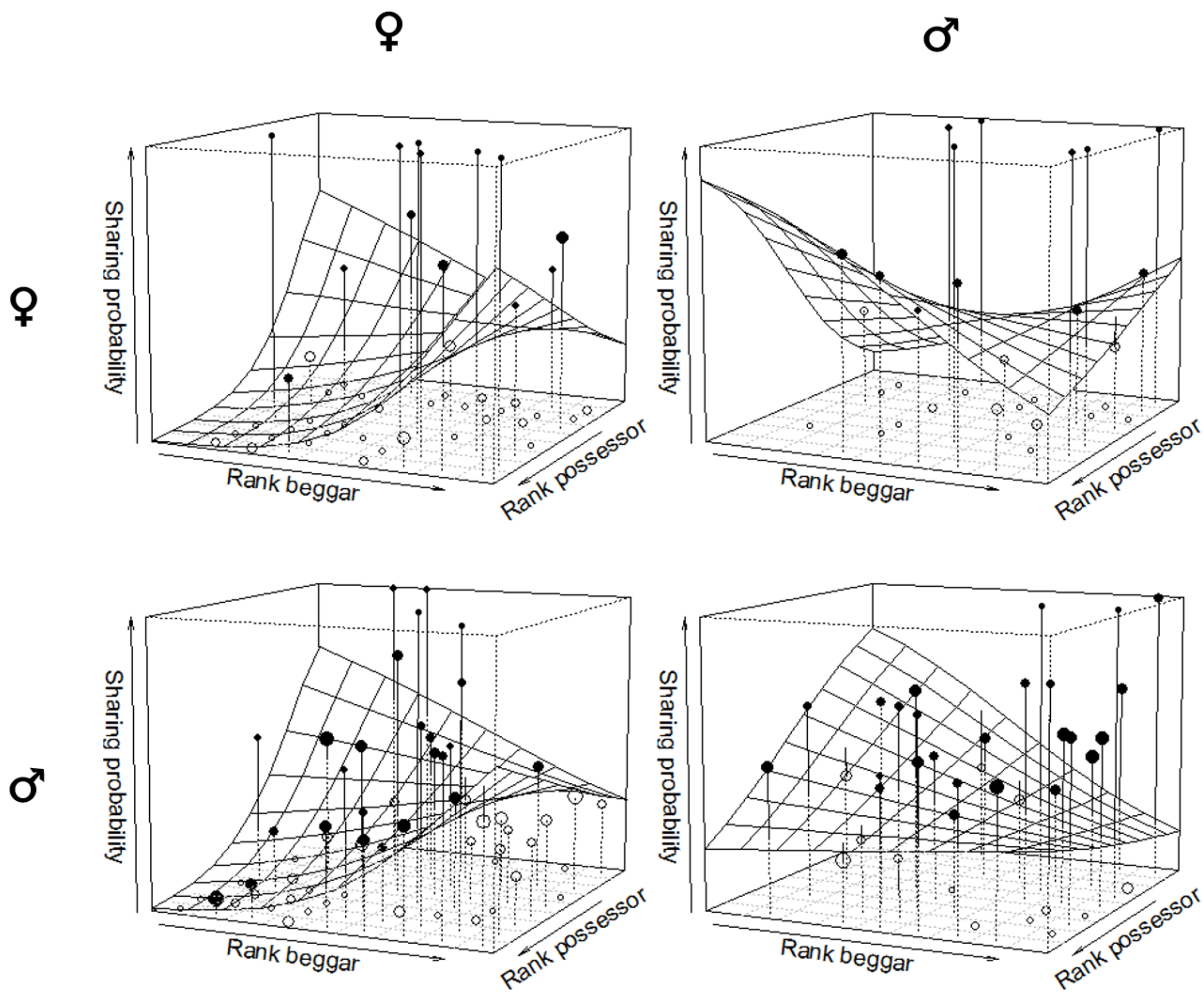

194 **Figure S3.** Effect of the interaction between the rank of the possessor, rank of beggar and the sex
195 combination from the perspective of the food possessor on the likelihood to share. Sex symbols
196 on the top and left side represent beggars and possessors, respectively. Shown are the observed
197 probabilities to share food (larger point volumes denote a larger number of observations), as well
198 as the model results (surface).

Table S1. Effect of begging duration, harassment occurrence and number of beggars on sharing likelihood.

Term[*]	**Coded level**	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	**χ^2**	**df**	**P**
Intercept		0.402	0.934	-1.387	2.335	--		--
Test predictor levels								
Begging duration[a]		-0.855	0.287	-1.258	-0.299	9.267		0.002
Number of beggars[b]		-0.749	0.214	-1.256	-0.294	9.687		0.002
Harassment (yes)	no	0.506	0.497	-0.502	1.739	0.795	1	0.373
Control predictors								
Group (East)	South	-1.903	0.803	-3.989	-0.624	6.729	1	0.009
Sex Possessor (female)	male	0.320	0.698			--		--
Sex beggar (female)	male	1.401	0.993			--		--
Food type (meat)	Treculia	0.343	0.537	-0.750	1.398	0.128	1	0.720
Sex possessor*Sex beggar (female-female)	male- male	-1.163	0.991	-4.212	0.606	1.524	3	0.217

[*]Reference categories of factors are indicated in parenthesis. [a-b]z-transformed, mean ± SD of the original variables: [a]97.56 ± 133.31 (range 2-870 sec), [b]4.5 ± 2.5 (range 1-11).

Table S2. Effect of social bonds, rank, and past grooming and agonistic experience on the likelihood to share (0/1).

Term*	Coded level	Estimate	SE	CI_{lower}	CI_{upper}	χ^2	df	P
Intercept		1.618	0.820	-0.167	3.191	--		--
Test predictor levels								
Directed grooming [a]		0.288	0.178	-0.093	0.675	2.615	1	0.106
Directed aggression [b]		-0.013	0.233	-0.469	0.450	0.017	1	0.896
Social bonds (no)	**bond**	**1.076**	**0.473**	**0.203**	**2.127**	**4.705**	**1**	**0.030**
Rank possessor [c]		-0.354	0.336	-1.143	0.341	--		--
Rank partner [d]		0.885	0.386	0.140	1.838	--		--
Sex combination (female-female)	female-male	0.352	0.379	-0.436	1.276	--		--
	male-female	1.127	0.589	-0.037	2.508	--		--
	male-male	0.303	0.607	-0.892	1.689	--		--
Rank possessor [c]: rank partner [d]		0.773	0.392	-0.024	1.703	--		--
Rank possessor [c] : sex combination (female-female)	female-male	-0.127	0.383	-0.921	0.761	--		--
	male-female	0.673	0.465	-0.230	1.870	--		--
	male-female	0.173	0.393	-0.651	1.069	--		--
Rank partner [d] : sex combination (female-female)	female-male	-0.321	0.339	-1.360	0.440	--		--
	male-female	-1.231	0.541	-2.477	-0.311	--		--
	male-female	-1.156	0.471	-2.297	-0.326	--		--
Rank possessor [c]: rank partner [d]: sex combination (female-female)	**female-male**	**-0.140**	**0.430**	**-1.125**	**0.757**			
	male-female	**-1.245**	**0.517**	**-2.477**	**-0.252**	**9.201**	**3**	**0.027**
	male-male	**-0.409**	**0.459**	**-1.470**	**0.546**			
Control predictors								
Sexual swelling status (non-cycling)	fully-tumescent	-0.136	0.458	-1.063	0.736	0.104	1	0.747
Group (East)	South	-0.458	0.336	-1.218	0.196	1.886	1	0.170
Kinship (kin)	non-kin	-0.066	0.635	-1.449	1.303	0.059	1	0.809
Food type (meat)	**non-meat**	**-1.117**	**0.239**	**-1.631**	**-0.650**	**23.126**	**1**	**< 0.001**

Statistically significant results ($P \leq 0.05$) appear in bold. *Reference categories of factors are indicated in parenthesis. [a-f]z-transformed, mean ± SD of the original variables: [a]0.60 ± 0.14 (range 0.31-0.92), [b]0.47 ± 0.11 (range 0.04-0.6), [c]0.68 ± 0.25, [d]0.62 ± 0.26 (range 0-1 with 1 being the highest social rank).

Table S3. Post-hoc analysis of the effect of hunting, food and meat sharing on urinary oxytocin levels (log transformed)

Term	Estimate	SE	z-value	P
Sharing meat vs. hunt	-0.155	0.200	-0.778	0.436
Sharing non-meat vs. hunt	0.112	0.211	0.532	0.594
Sharing non-meat vs. sharing meat	0.268	0.171	1.565	0.118

Table S4. Effects of donating or receiving food and social bonds on urinary oxytocin levels (log transformed).

Term*	Coded level	Estimate	SE	χ^2	P
Intercept		3.761	0.204	--	--
Test predictor levels					
Social bond (yes)	no	0.033	0.164	0.031	0.859
Role (recipient)	donor	0.104	0.143	0.401	0.526
Control predictors					
Food type (meat)	non-meat	0.199	0.174	0.994	0.319
Number of partners		0.020	0.076	0.061	0.804
Group (East)	South	-0.164	0.167	0.649	0.420
Sex (female)	male	-0.160	0.157	0.876	0.349
Dominance Rank		0.180	0.071	3.527	0.060
Sub-group size		-0.041	0.083	0.233	0.630
Data collection period (First)	Second	1.400	0.176	43.578	< 0.001

*Reference categories of factors are indicated in parenthesis.

Dataset S1 – All data used to fit the models

Video S1. Active honey sharing in the Taï chimpanzees

Video S2. Active meat sharing in the Taï chimpanzees

Video S3. Chimpanzees passively sharing meat with some individuals while excluding others

Video S4. Chimpanzee begging gestures with physical contact that do not interfere with the possessors' feeding behavior

Video S5. Chimpanzees begging gestures without physical contact considered as harassment as they interfere with the possessors' feeding behavior

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