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Supplementary Materials for

Chimpanzees behave prosocially in a group-specific manner

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The PDF file includes:

Other Supplementary Material for this manuscript includes the following:

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Materials and Methods

Experimental Design

The objectives of the study were to assess experimentally whether chimpanzees behave prosocially in a group setting (allowing for temporal autonomy and free partner choice), and whether group-level social climates map onto group-level prosocial expressions in chimpanzees.

Study site and Subjects

The study took place at Chimfunshi Wildlife Orphanage Trust (Chimfunshi), a non-profit sanctuary in the Copperbelt region of Northern Zambia (12°23′ S, 29°32′ E) in miombo woodland forest suitable for chimpanzees (*54*). The study groups comprised the four socially stable groups at the Project Area, totaling 90 chimpanzees. These groups live in forested enclosures measuring between 20 and 77 hectares (see Fig. S1) and consist of chimpanzees that have been rescued from various conditions (e.g., illegal pet trade) as well as of sanctuary-born individuals (see Table S1 for demographic details). The chimpanzees remain in their outdoor habitats overnight and during the day, except for 2 hours midday when they are called inside for additional feeding and medical checkups. During the experiment, all chimpanzees had *ad libitum* access to water from a separate fountain within their enclosures and were not deprived of food in any way.

The Chimfunshi Research Advisory Board (CRAB) approved of the study (case number: C027). CRAB is the ethics committee of Chimfunshi, comprising a team of management and veterinary staff, as well as long-term researchers.

Experimental Setup

Prosociality was tested with an apparatus allowing individuals to provide a valuable food resource (fruit juice) to their group members without being able to benefit themselves (see Movie S1). The apparatus was built inside the chimpanzees' outdoor enclosures. The experimental setup (see Fig. S2) consisted of a retractable button, a fountain with a spout and a tank filled with juice installed on the roof of the feeding building. All three elements were connected with hoses. All hoses inside the enclosure were placed underground and could not be manipulated by the chimpanzees. When the button was pushed down by a chimpanzee, juice was released at the fountain for as long as the individual pushed. The juice flow was

interrupted as soon as the pushing stopped. Button and fountain were installed ~5 meters apart, making it impossible for an individual to simultaneously push the button and drink the juice.

The experimental fountain consisted of a short concrete column with a protruding spout. The spout of the fountain was designed to make it hard to suck on it (due to attached metal strings, preventing the chimpanzees from placing their lips over the spout and creating a vacuum). The experimental fountain was placed in an underground foundation of cement. The button consisted of a pushing device within a hard PVC (polyvinylchloride) box. This box was encased in concrete and placed into the ground such that only the button protruded from the surface. The button could also be accessed from outside the enclosure via a lever that was attached to the button through an underground tube. This enabled the researchers to lift the button out of the box at the beginning of the session and retract it at the end of each session. When retracted, the button could not be pushed by the chimpanzees. Depending on the condition of the session, either the experimental fountain or the control fountain was connected to the button by underground hoses. In control sessions, a portable fountain was installed outside the enclosure at approximately 5 meters from the button (i.e., at the same distance from the button as the experimental fountain). The juice flow from the control fountain was easy to observe, yet entirely unattainable for any of the chimpanzees.

We created pressure in the hose system by placing the juice container on a nearby rooftop. The container was filled with 20 liters of fruit juice. When the container became depleted, we refilled it with another 20 liters of fruit juice. We never had to refill the container more than once per session. The fruit juice was a mixture of fruit syrup and water at the ratio of ±1:4.

The formation of residue of small amounts of juice on the spout and on the ground in front of the fountain after long pushing intervals was inevitable (to reduce puddle formation, we replaced the natural soil by a thick layer of highly permeable gravel under all the experimental fountains). As a consequence, chimpanzees that pushed the button and went to the fountain afterwards were able to obtain some remaining fruit juice. We considered this in our subsequent coding and data analyses (i.e., we labeled pushing acts as "*egoistically motivated*" when the pusher moved over to the experimental fountain after having pushed and ran additional analyses on the subset of data including only pushing acts devoid of this fountain-joining behavior, see main text).

Experimental Procedure

General outline

The experiment was conducted in each group with two-hour sessions, once a day, alternately in the morning and in the afternoon. During these sessions, the chimpanzees could freely decide if and when they wanted to participate. To ensure that the chimpanzees were aware of the experiment, at the beginning of each session the chimpanzees were called by the researchers and the fountain was flushed with juice for several seconds to draw attention to the setup. Typically, several individuals quickly approached the fountain and were able to drink some of the running juice. After this pre-test flushing, the session started by releasing the button such that it became available for the chimpanzees to push. Every session ended by retracting the button into the ground again, where it could not be manipulated by the chimpanzees any more. This procedure remained constant across sessions with the exception that we flushed the control fountain instead of the test fountain during control sessions. All sessions were video recorded using digital cameras (JVC-Everio) mounted on tripods. Data for analyses were obtained by coding the videos for all relevant behaviors.

Familiarization sessions

First, we conducted familiarization sessions over the course of the first three weeks of the study. During these sessions, the goal was to familiarize the chimpanzees with the mechanism of the apparatus. To achieve this, we positively reinforced any exploration and manipulation of the button by manually releasing juice from the fountain. This was necessary as the chimpanzees in Chimfunshi have had little experience with experimental apparatuses that require the performance of novel actions. Initially, we released juice from the fountain whenever a chimpanzee placed a foot or hand on the button. Subsequently, we restricted the manual juice release to behaviors that resembled accurate pushing, based on individual progress of the chimpanzees. To attract chimpanzees to the apparatus area, the local caretakers sometimes placed food in front of the fence near the apparatus. The keepers then gave the food to the chimpanzees when the sessions were completed. This local enhancement procedure was only done during familiarization sessions.

Groups 1 – 4 received 13, 12, 12, and 8 familiarization sessions, respectively. Group_4 received less familiarization sessions because several of its individuals were sick over the course of one week, during which the familiarization sessions were suspended. After three weeks, in groups 1 – 4, there were 5, 4, 0, and 6 chimpanzees, respectively, who had learned

to use the experimental setup successfully (i.e., this was considered to be the case after three successful pushing events). Subsequently, we decided to proceed to the test sessions in all groups, except for Group_3, as no individual learned the behavior in this group. An additional three familiarization sessions were conducted in Group_3, during which no further pushing behavior was observed. At this point, we decided to exclude Group_3 from the study and performed no further sessions with this group.

Experimental sessions

We conducted 27 test sessions in Group_1 and Group_4, and 26 test sessions in Group_2. Test sessions started and ended as described above (see *General outline*) and lasted two hours. After twenty-one test sessions (twenty for Group_2), we started to conduct control sessions in all three groups. Control sessions were identical to test sessions, except for the location of the fountain (see Fig. S2). The control fountain was placed outside of the chimpanzees' enclosures, thus preventing the chimpanzees from providing the juice to their group members. We repeated blocks of "2 test – 2 control" sessions (AABB) four times in each group, totaling 8 control sessions per group. During control sessions, all researchers and caretakers stayed at least 5 meters away from the control fountain to ensure that the chimpanzees were not pushing for humans. During test sessions, the control fountain was stored out of the chimpanzees' view. Therefore, the presence of the control fountain indicated the execution of a control session to the chimpanzees.

The goal of the control sessions was to test whether pushing behavior was contingent upon juice flow within the chimpanzees' enclosures. As such, we were able to control for alternative motivations for pushing the button, such as enjoyment of the pushing behavior in itself or interest in the resulting juice flow. Chimpanzees' pushing behavior in the blocked test (N=8) and control (N=8) sessions are depicted in Table S2 and visualized, both in terms of frequency and duration, in Figure 3 (*main text*). Due to malfunctioning of the juice dispensing mechanism, in six test and one control session the juice flow was manipulated manually (like in the *familiarization* sessions). This was covertly done from outside the enclosure by one of the researchers releasing juice whenever pushing behavior was observed.

Results

Overall, in groups 1-2-4, we considered 11, 11, and 7 chimpanzees' pushing behavior (i.e., subjects' pushing behavior was considered as of their third successful (i.e., juice-producing) pushing act in order to avoid the inclusion of accidental, non-deliberate events), respectively, whereas all chimpanzees (age ≥3yrs) in the respective groups were considered as possible recipients of the prosocial acts. The corresponding results are reported in the *main text*. Here, we additionally report corroborating analyses on *a*) group differences in preferential pushing for maternal kin (*kinship analysis*), *b*) reciprocity as a possible mechanism underlying the chimpanzees' pushing behavior (*reciprocity analysis*).

a) Kinship analysis

Based on kin selection models predicting nepotism as the driver for the evolution of cooperation and prosociality (*58*, *59*) and their application to the study of chimpanzees (*60–62*), in the current study, we investigated whether chimpanzees in groups with multiple family units (i.e., Group_1 and 2) exhibited preferential prosociality directed at maternal kin (paternity relations are unknown to date). We used generalized linear mixed models (GLMM; (*63*)) with binomial error distribution and logit link function in the R statistical environment v3.5.2 (*64*). As response variable, we operationalized "pushing for kin" (at least one kin-member in fountain group: yes/no); as fixed predictors we included group, session, rank, sex, and age; to control for obvious confounds we included the number of chimpanzees benefitting from the prosocial pushing event and the proportion of maternal kin present in the group as offset terms (log-transformed); as random intercept effects we included focal and session; as random slope effects we included session (in focal) and sex, age, and rank (in session) (*65*).

Group_1 comprised 7 pushing subjects with maternal kin in their group (3 family units; kin present in group in proportion: range 0.143-0.190); group_2 comprised 11 pushing subjects with maternal kin in their group (7 family units; kin present in group in proportion: range 0.024-0.098). Group_4 was not included in the analysis given that this group comprised only one family unit (3 individuals) of which only 2 members participated in the study. Model stability was reasonable as indicated by the range of estimates obtained when excluding individuals one at a time (Fig. S9). The models consistently estimated pushing for kin to be lower in group_2 (the group higher in social tolerance). In light of the focus of the

paper, we refrain from interpreting the estimates of the control variables (all other variables than "group"), but provide them in Table S4.

b) Reciprocity analysis

Based on models predicting reciprocity as the driver for the evolution of cooperation and prosociality (*59*, *66*) and their application to the study of chimpanzees (*52*, *67*), in the current study, we checked for possible reciprocity within the same currency (i.e., prosocial pushing) by assessing the correlation between given and received benefits (i.e., juice) for all possible dyads. Neither across the groups (Pearson's correlation coefficient $r = -0.187$, df = 73, $P = 0.108$), nor in any group separately (Group_1: $r = -0.227$, df = 36, $P = 0.170$; Group_2: $r = -0.164$, df = 32, $P = 0.354$; Group_4: $r = -0.055$, df = 35, $P = 0.748$) did the chimpanzees show evidence of reciprocity-based prosociality. Given the tangential character of this analysis to our main focus (i.e., group differences in prosociality) and the fact that our setup did not allow for encompassing reciprocity tests (i.e., no targeted observations on for instance grooming and food-sharing were done), we refrain from further investigation of reciprocity as a possible mechanism underlying the here reported prosociality in chimpanzees.

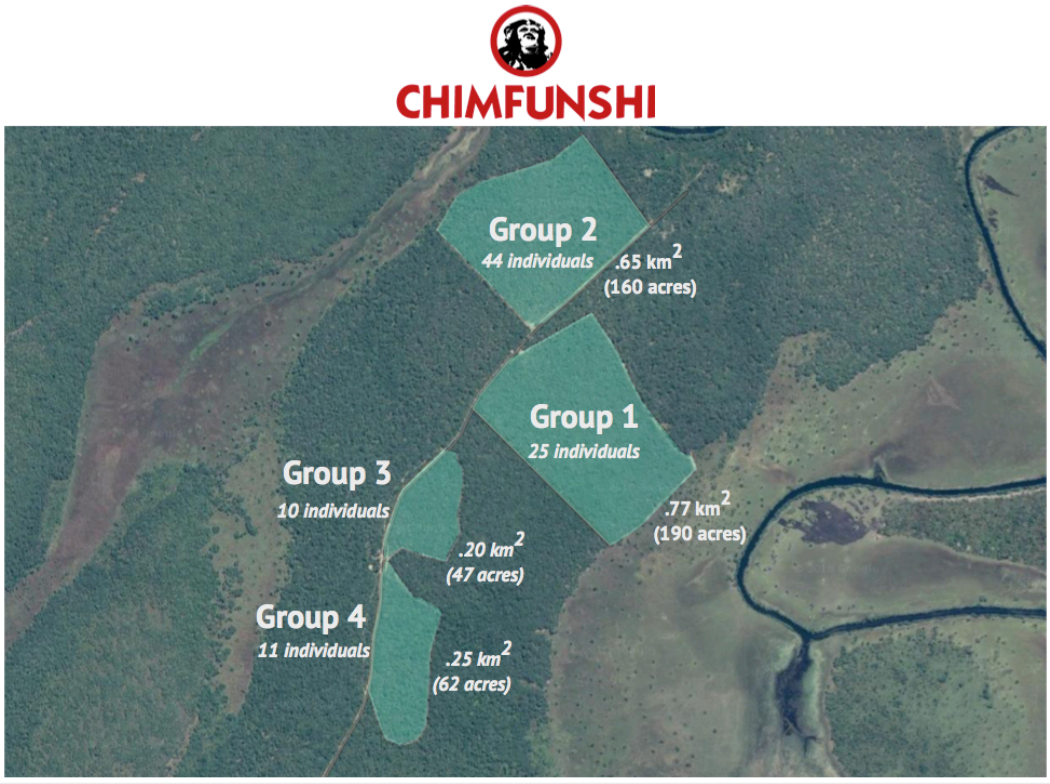

Fig. S1 Aerial view of semi-free ranging groups of chimpanzees at Chimfunshi Wildlife Orphanage Trust. Depicted (in light green) are the fenced-off enclosures; included is information on their sizes (in km^2 and acres) and the number of chimpanzees per group. Photo Credit: Google Maps.

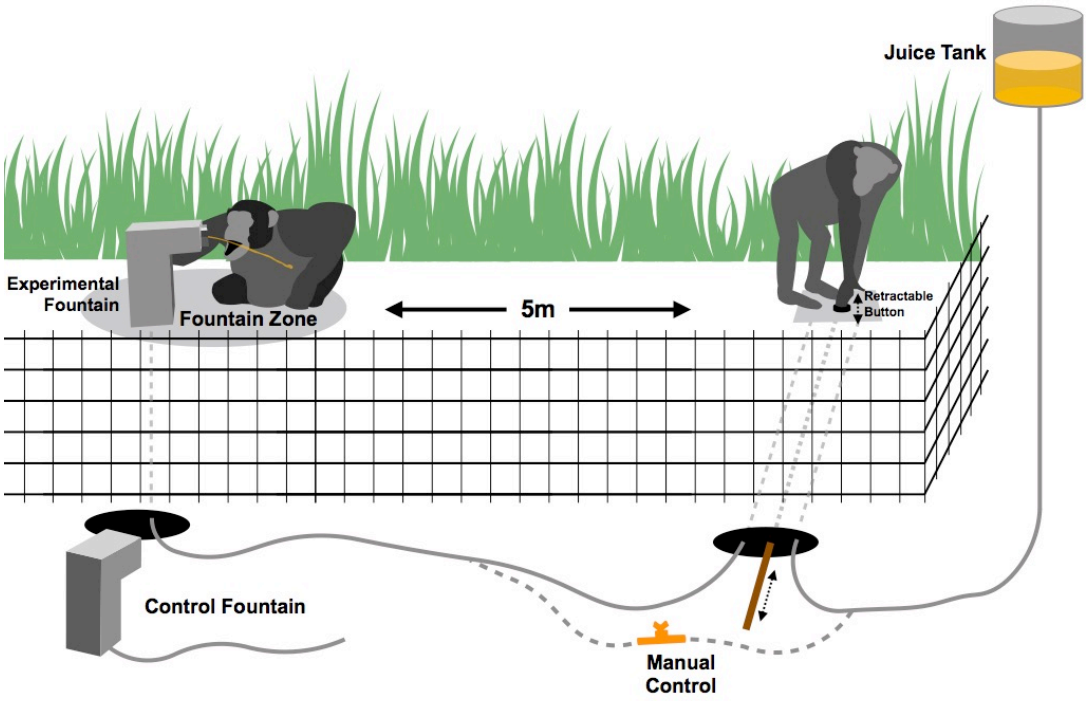

Fig. S2 Depiction of the experimental setup used to test prosocial behavior in chimpanzees. The Juice Tank was placed on top of the roof of a nearby building, thereby providing the pressure needed for the juice to run through the hose system. When the hose was connected to the Retractable Button and the button was made available for pushing by lifting it from outside the enclosure with a custom-made stick, the chimpanzees could push the button upon which juice would flow from the Experimental Fountain (as depicted – this represents the *test* condition). When the hose was connected to the Manual Control, the experimenters could control the juice flow from the fountain, which was used during the familiarization phase. When the hose was connected to the Control Fountain (which was only present during *control* sessions) and the button was made available for pushing, the chimpanzees could push the button upon which juice would flow from the Control Fountain, outside the reach of all chimpanzees (this represents the *control* condition).

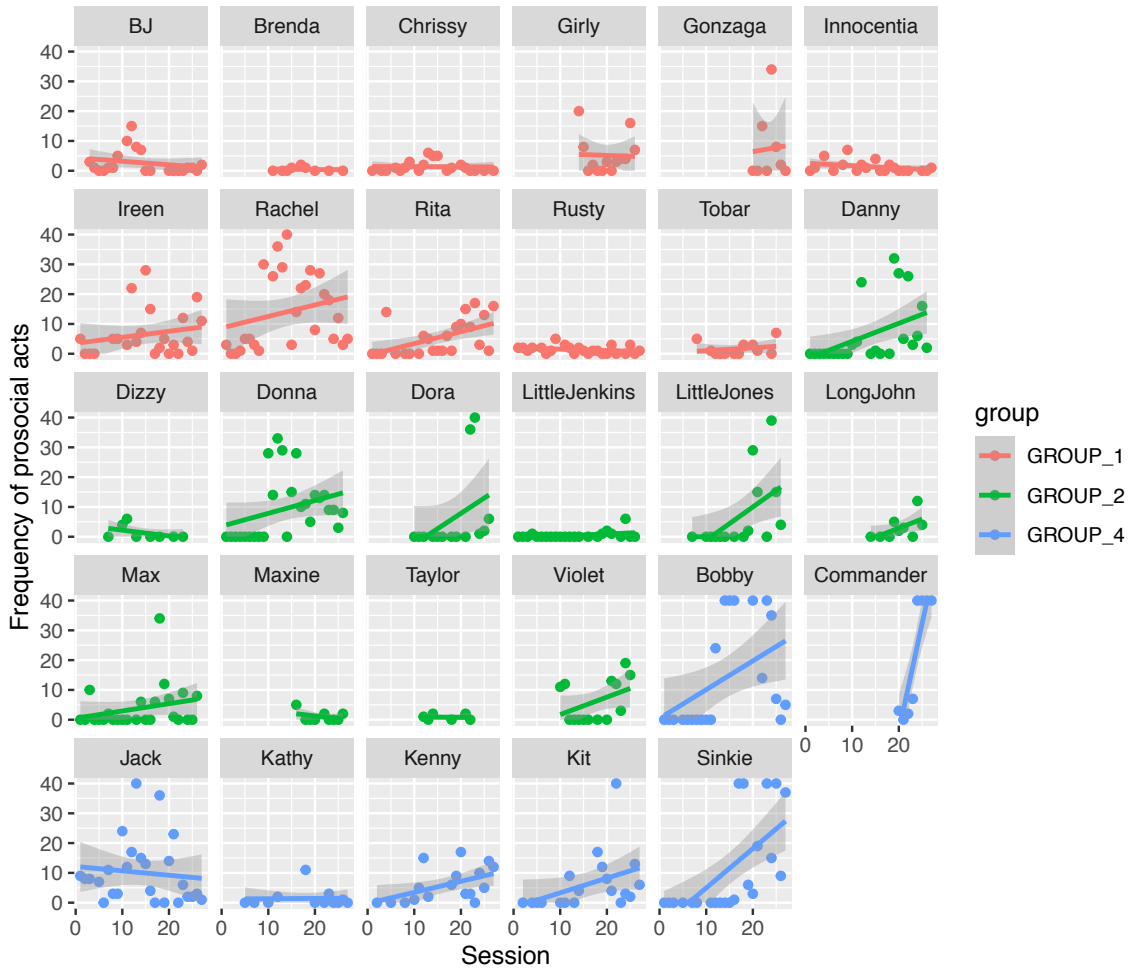

Fig. S3 Chimpanzees' prosocial behavior across time. Prosocial acts increase over the course of the experiment for the majority of chimpanzees across the three study groups. For 19 chimpanzees, the slope across sessions was positive, for 10 chimpanzees the slope was negative (Wilcoxon one-sample test for slope being positive/larger than zero: V=362, p = 0.0006, N = 29).

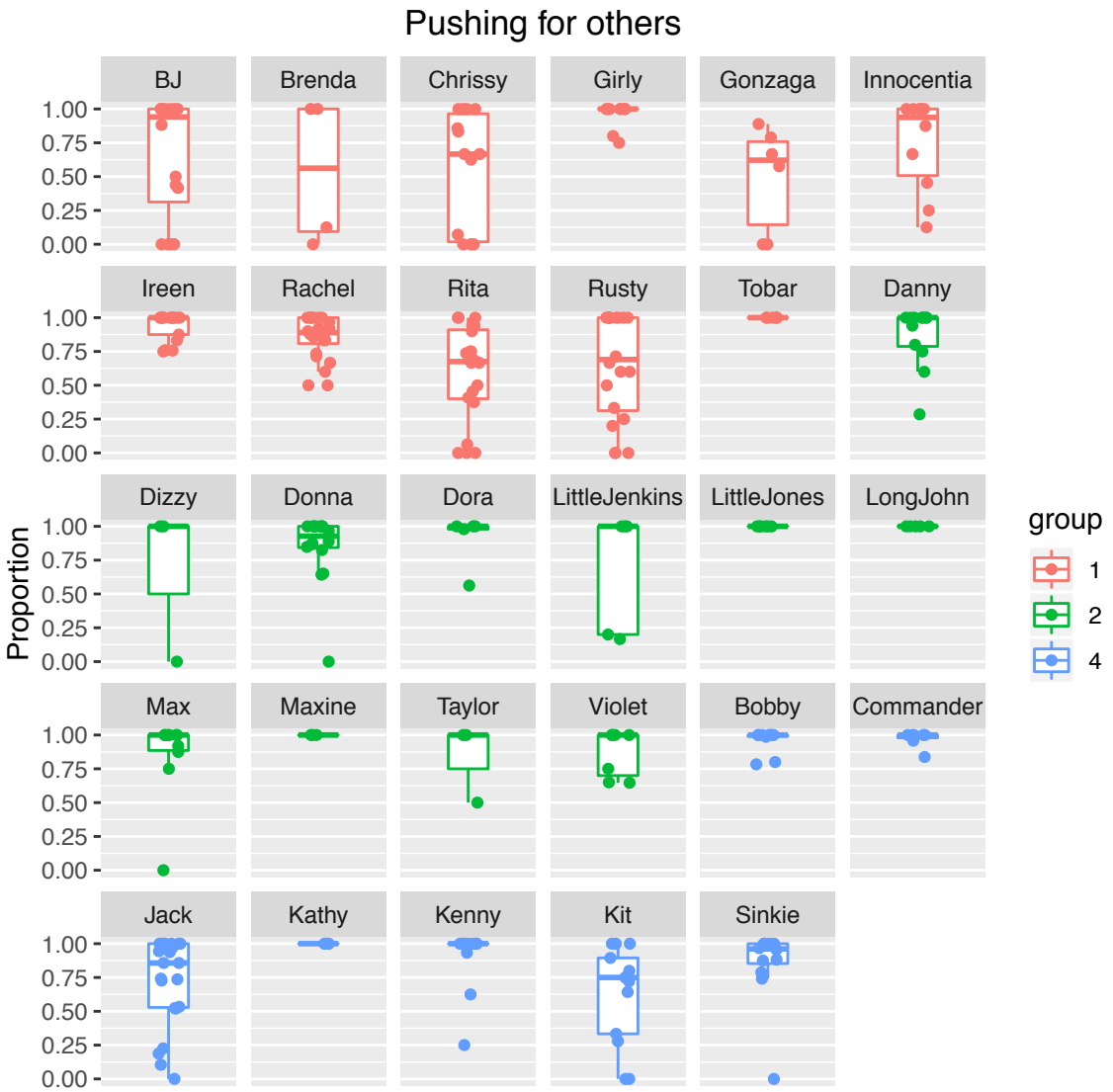

Fig. S4 Chimpanzees' prosocial versus egoistical pushing depends on their group identity. Individual plots (colored by group) for the proportion of pushing acts that were performed when group members were present at the fountain to benefit from the juice (indicating a prosocial motive) versus nobody present (indicating an egoistic motive). Dots represent averages per session expressed in medians (bold horizontal lines) and interquartile ranges (boxes with vertical lines).

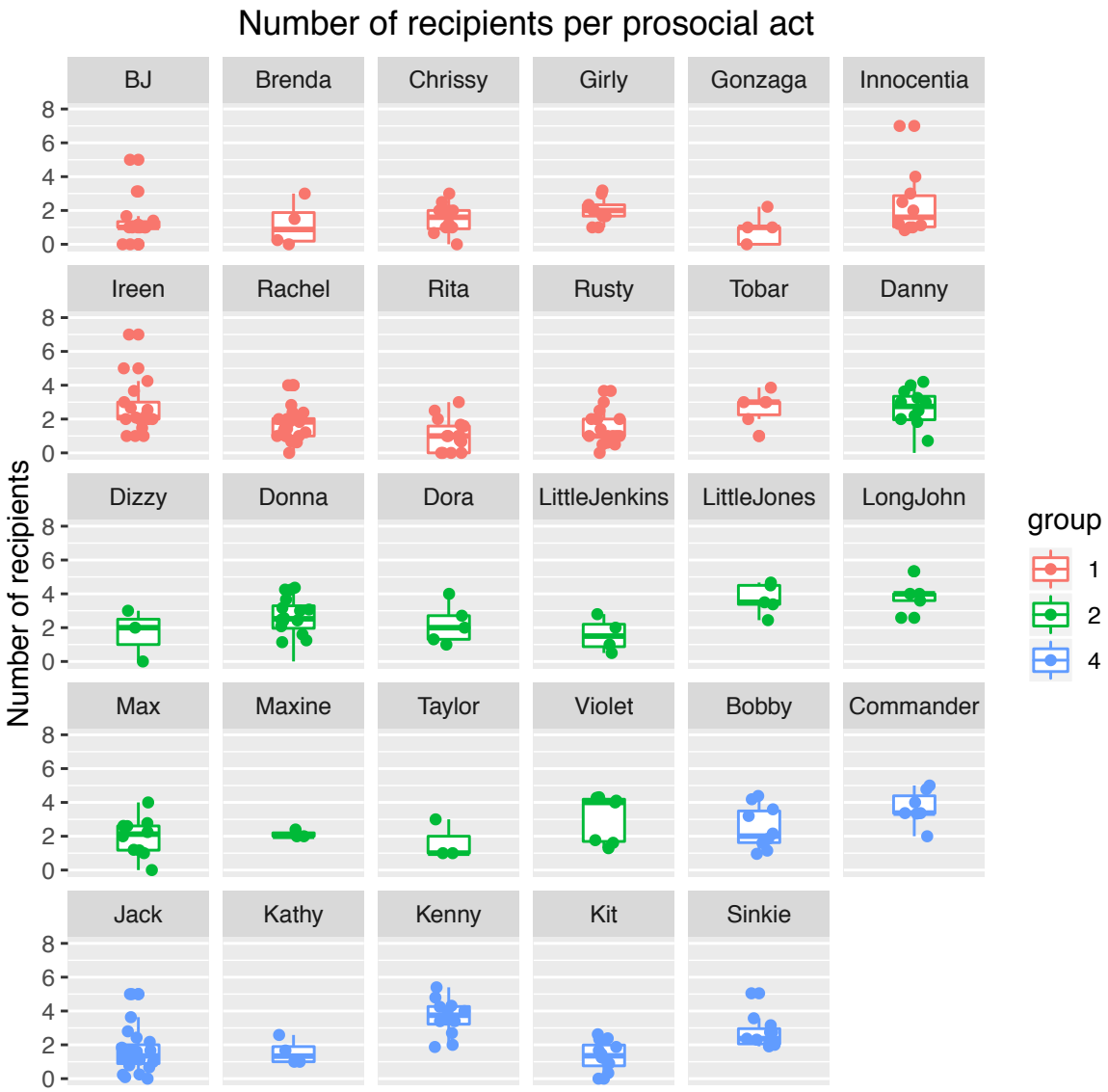

Fig. S5 Chimpanzees benefit different numbers of group members depending on their group. Individual plots (colored by group) for the number of benefitting group members per pushing act. Dots represent averages per session expressed in medians (bold horizontal lines) and interquartile ranges (boxes with vertical lines).

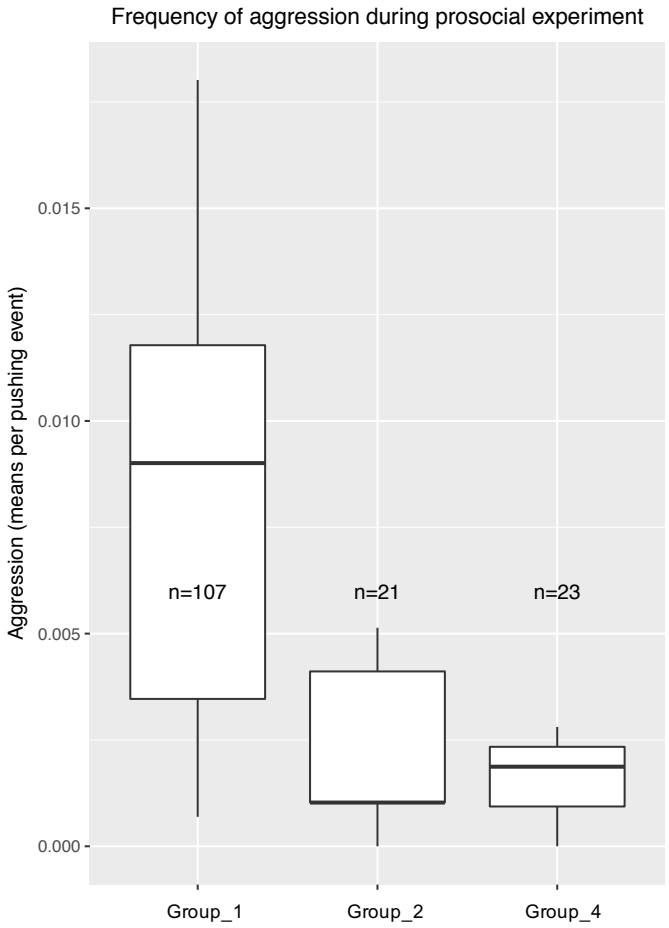

Fig. S6 Group-specific frequency of aggression during the prosociality experiment. Aggression was scored when at least two individuals engaged in physical aggression within the experimental zone (defined as the space between button and fountain). Each aggression was attributed to one aggressor, the plots are based on individual level frequencies (with the N referring to the total number of aggressive encounters).

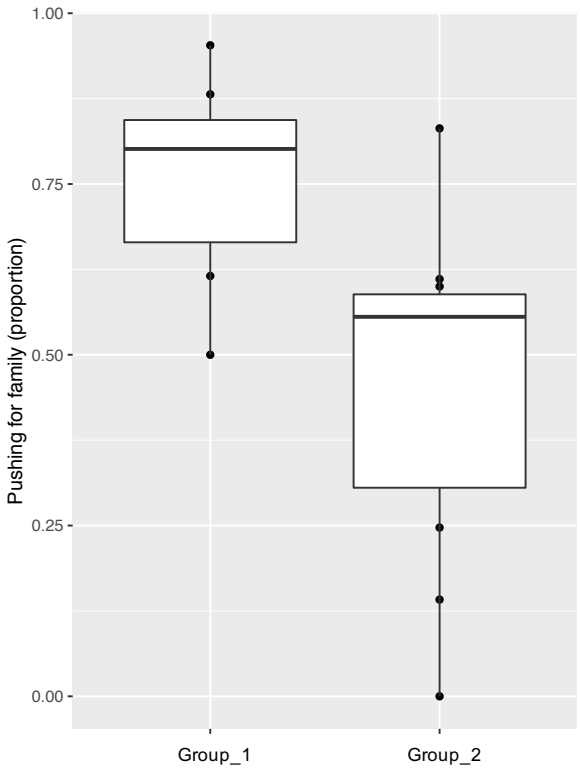

Fig. S7 Chimpanzees' prosocial behavior toward family. Kin-biased prosociality is more pronounced in Group_1 (N=7) versus Group_2 (N=11), controlled for the number of within-group family members relative to group size. Medians are represented by the bold, horizontal lines within the boxes. The boxes represent the interquartile range (IQR), the vertical lines attached to the boxes represent Q1-1.5 IQR (lower) and Q3+1.5 IQR (upper).

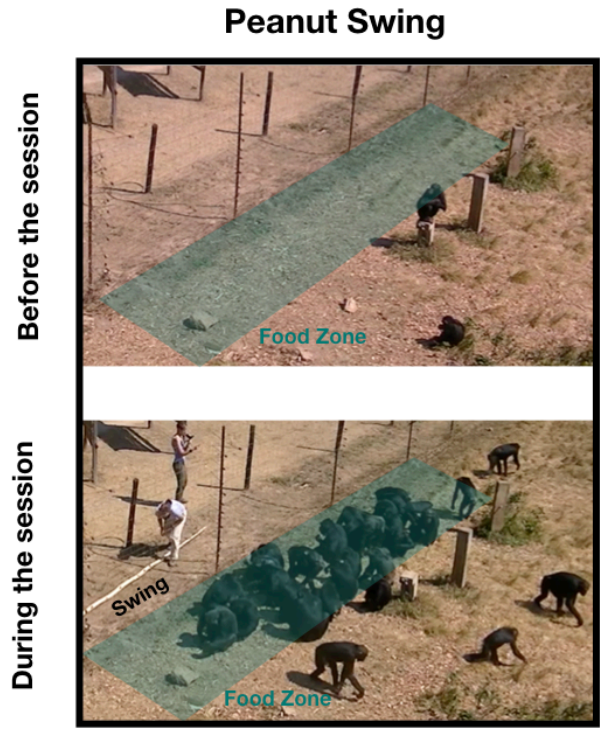

Fig. S8 Experimental setup illustrating the social tolerance test. An assay of group-level co-feeding tolerance as measured by the peanut swing. Peanuts are swung into the enclosure in a pre-designated area (proportional in space and number of peanuts to group size), which during the sessions functions as the zone of interest: the space in which the chimpanzees can co-feed. The number of chimpanzees co-feeding relative to the group size is taken as a measure of social tolerance. Photo Credit: Sarah E. DeTroy (Max Planck Institute for Evolutionary Anthropology).

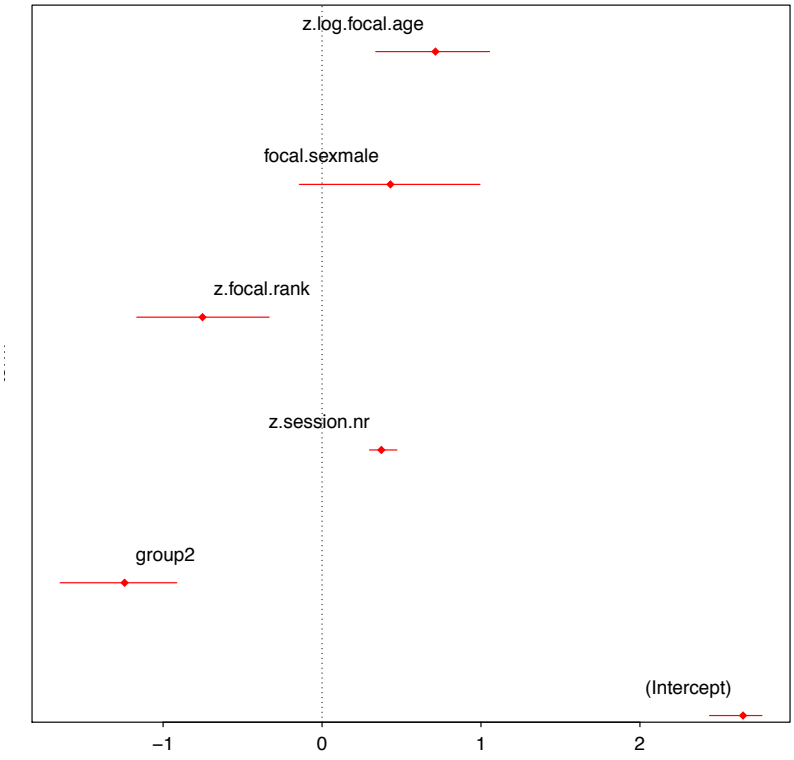

Fig. S9 Model stability check. Lines indicate the range of parameter estimates (on *y*-axis) based on sequential removal (with replacement) of single individuals and re-running the model; diamonds represent the parameter estimates based on the full dataset.

Table S1. Demographic details of the chimpanzees under study.

Group	Subject	Age*	Sex	Dam	Origin	Subspecies
1	Pal	35,2	male	unknown	wild	schweinfurthii
1	Booboo	34,2	male	unknown	wild	schweinfurthii
1	Girly	34,2	female	unknown	wild	schweinfurthii
1	Tobar	34,2	male	unknown	wild	verus
1	Rita	33,2	female	unknown	wild	schweinfurthii
1	Tara	33,2	male	unknown	wild	schweinfurthii
1	Ingrid	25,2	female	Liza	captive	schweinfurthii
1	Brenda	20,9	female	Bella	captive	schweinfurthii
1	Genny	19,2	female	Girly	captive	schweinfurthii
1	Renate	19,2	female	Rita	captive	schweinfurthii
1	Bob	15,1	male	Big Jane	captive	schweinfurthii
1	Gerard	14,1	male	Girly	captive	not determined
1	Ilse	14	female	Ingrid	captive	not determined
1	Regina	10,5	female	Renate	captive	not determined
1	Rusty	9,6	male	Rita	captive	not determined
1	Chrissie	9,5	female	Cleo	captive	not determined
1	Innocentia	9,4	female	Ingrid	captive	not determined
1	BJ	9	female	Big Jane	captive	not determined
1	Gonzaga	8,4	male	Genny	captive	not determined
1	Irene	4,3	female	Ingrid	captive	not determined
1	Rachel	3,9	female	Renate	captive	not determined
1	Ian	1,5	male	Ilse	captive	not determined
1	Richard	0,9	male	Rita	captive	not determined
1	Gloria	0,3	female	Genny	captive	not determined
1	Ida	0,3	female	Ingrid	captive	not determined
2	Noel	39,2	female	unknown	wild	schweinfurthii
2	Donna	32,2	female	unknown	wild	schweinfurthii
2	Coco	31,2	female	unknown	wild	schweinfurthii
2	Little Jane	31,2	female	unknown	wild	schweinfurthii
2	Maggie	30,2	female	unknown	wild	schweinfurthii
2	Misha	28,2	female	unknown	wild	schweinfurthii
2	Dora	27,2	female	unknown	wild	schweinfurthii
2	Pan	27,2	male	unknown	wild	schweinfurthii
2	Pippa	27,2	female	unknown	wild	schweinfurthii
2	Trixie	26,2	female	unknown	wild	schweinfurthii
2	Zsabu	26,2	male	unknown	wild	schweinfurthii

2	Diana	25,2	female	unknown	wild	schweinfurthii
2	Masya	25,2	female	unknown	wild	schweinfurthii
2	Violet	25,2	female	unknown	wild	schweinfurthii
2	Dolly	19,8	female	Dora	captive	schweinfurthii
2	Carol	19,6	female	Coco	captive	not determined
2	Nikkie	18,9	female	Noel	captive	schweinfurthii
2	Mikey	18,2	male	unknown	wild	schweinfurthii
2	Tess	18,2	female	Tina	captive	not determined
2	Tilly	15,4	female	Trixie	captive	not determined
2	Maxine	15	female	Misha	captive	not determined
2	David	14,7	male	Diana	captive	not determined
2	Debbie	14,5	female	Donna	captive	not determined
2	Claire	14	female	Coco	captive	not determined
2	Doug	13,4	male	Dora	captive	not determined
2	Nina	13,2	female	Noel	captive	not determined
2	Vis	12,1	male	Violet	captive	not determined
2	Daisey	11,6	female	Diana	captive	not determined
2	Mary	10,6	female	Masya	captive	not determined
2	Long John	10,5	male	Little Judy	captive	not determined
2	Max	9,8	male	Misha	captive	not determined
2	Little Jenkins	9,4	female	Little Jane	captive	not determined
2	Moyo	8,8	male	Maggie	captive	not determined
2	Dizzy	8,6	female	Diana	captive	not determined
2	Charity	8,4	female	Carol	captive	not determined
2	Little Jones	5,9	male	Little Jane	captive	not determined
2	Martin	4,1	male	Misha	captive	not determined
2	Danny	4,1	male	Dora	captive	not determined
2	May	3,6	female	Maggie	captive	not determined
2	Chitalu	1,3	female	Claire	captive	not determined
2	Tom	1,3	male	Tilly	captive	not determined
2	Dennis	0,7	male	Daisey	captive	not determined
2	Tina	0,7	female	Tess	captive	not determined
2	Don	0,6	male	Debbie	captive	not determined
3	Buffy	31,2	female	unknown	wild	schweinfurthii
3	Clement	23,2	male	unknown	wild	schweinfurthii
3	Brian	22,2	male	unknown	wild	schweinfurthii
3	Barbie	21,2	female	unknown	wild	schweinfurthii
3	E.T.	21,2	female	unknown	wild	schweinfurthii
3	Roxy	21,2	female	unknown	wild	schweinfurthii

3	Bussie	12,2	male	Barbie	captive	not determined
3	Bruce	6,5	male	Barbie	captive	not determined
3	Lods	6	female	Lori	captive	not determined
3	Brent	2	female	Barbie	captive	not determined
4	Nicky	25,2	male	unknown	wild	schweinfurthii
4	Bobby	23,2	male	unknown	wild	schweinfurthii
4	Sinkie	22,2	male	unknown	wild	schweinfurthii
4	Kambo	20,2	female	unknown	wild	schweinfurthii
4	Kathy	17,2	female	unknown	wild	schweinfurthii
4	Val	16,2	male	unknown	wild	schweinfurthii
4	Commander	15,2	male	unknown	wild	schweinfurthii
4	Kit	11,2	male	Kambo	captive	not determined
4	Jack	8,1	male	Julie	captive	not determined
4	Ken	5	male	Kambo	captive	not determined
4	Jewel	3	male	Julie	captive	not determined

* At the start of the study (April 2016).

Conflicting results, possibly “verus”.

Table S2. Chimpanzees' pushing behavior in the test and control conditions (8 sessions per condition), both in absolute frequency and duration.

Group	Subject	Condition	Pushing frequency	Pushing duration (in sec)
1	BJ*	control	12	120
1	BJ*	test	13	88
1	Brenda	control	3	23
1	Brenda	test	6	32
1	Chrissy	control	28	213
1	Chrissy	test	36	211
1	Girly	control	3	12
1	Girly	test	38	253
1	Gonzaga	control	11	94
1	Gonzaga	test	108	421
1	Innocentia*	control	8	40
1	Innocentia*	test	1	25
1	Ireen	control	30	280
1	Ireen	test	58	374
1	Rachel	control	86	340
1	Rachel	test	118	590
1	Rita	control	52	459
1	Rita	test	120	3161
1	Rusty	control	5	19
1	Rusty	test	11	53
1	Tobar	control	1	0
1	Tobar	test	11	127
2	Danny	control	34	110
2	Danny	test	120	461
2	Donna	control	20	101
2	Donna	test	85	567
2	Dora	control	21	153
2	Dora	test	121	781
2	LittleJenkins*	control	23	123
2	LittleJenkins*	test	15	32
2	LittleJones	control	34	140
2	LittleJones	test	107	306
2	LongJohn	control	1	10

2	LongJohn	test	24	84
2	Max	control	5	30
2	Max	test	40	207
2	Maxine	control	1	1
2	Maxine	test	4	15
2	Moyo	control	1	2
2	Moyo	test	3	8
2	Taylor*	control	14	66
2	Taylor*	test	2	8
2	Violet	control	4	7
2	Violet	test	73	390
4	Bobby	control	13	52
4	Bobby	test	328	1317
4	Commander	control	9	53
4	Commander	test	318	1448
4	Jack	control	20	67
4	Jack	test	67	331
4	Kathy*	control	6	106
4	Kathy*	test	4	43
4	Kenny	control	34	129
4	Kenny	test	69	175
4	Kit	control	12	47
4	Kit	test	108	438
4	Sinkie	control	20	182
4	Sinkie	test	209	1505

*Pushing is more pronounced in the control (n=8) vs. test (n=8) condition, both for frequency and duration.

Table S3. Mean Cohen's κ of the four coders for all relevant variables.

Variable	Mean Cohen's κ
Pushing	.91
Fountain Zone	.97
Post-Pushing Approach	.93
Sucking Fountain	.90
Drinking spoils	.56

Table S4. Generalized Linear Mixed Model output of kinship analysis.

Effect	Estimate ±SD	P
Intercept	3.509 ± 0.557	[a]
Group_2 (ref: Group_1)	-2.900 ± 0.808	<0.001
Session	0.857 ± 0.277	<0.002
Sex of actor (ref: Female)	-0.369 ± 0.770	0.632
Age of actor	1.527 ± 0.781	0.051
Rank of actor[b]	-1.943 ± 0.816	0.017

[a] Not indicated because of having a limited interpretation.

[b] Scaled between 0-1 with 1 being the alpha male. Values based on the average of three independent caretaker (>6 years of experience with current group) reports.

Movie S1

Example video of a chimpanzee providing juice for recipients at the fountain (prosociality assay).

Movie S2

Example video of a “peanut swing” (social tolerance assay).

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