SOCIAL SCIENCES

Chimpanzees behave prosocially in a group-specific manner

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Chimpanzees act cooperatively in the wild, but whether they afford benefits to others, and whether their tendency to act prosocially varies across communities, is unclear. Here, we show that chimpanzees from neighboring communities provide valuable resources to group members at personal cost, and that the magnitude of their prosocial behavior is group specific. Provided with a resource-donation experiment allowing free (partner) choice, we observed an increase in prosocial acts across the study period in most of the chimpanzees. When group members could profit (test condition), chimpanzees provided resources more frequently and for longer durations than when their acts produced inaccessible resources (control condition). Strikingly, chimpanzees' prosocial behavior was group specific, with more socially tolerant groups acting more prosocially. We conclude that chimpanzees may purposely behave prosocially toward group members, and that the notion of group-specific sociality in non-human animals should crucially inform discussions on the evolution of prosocial behavior.

INTRODUCTION

Humans regularly confer benefits on others, even at a cost to themselves (1, 2). The extent to which humans act prosocially has been suggested to be at the root of humans' unique social abilities, arguably unparalleled in the animal kingdom (2–5). In an attempt to explore the evolutionary trajectory of this prosocial behavior, chimpanzees, as one of humans' closest living relatives, have been studied extensively in prosocial paradigms, both in the wild and under controlled settings in captivity. To date, however, the evidence concerning chimpanzee prosociality remains equivocal.

Prosocial behavior has been defined as "any behavior voluntarily performed by one individual to benefit another" (6–8). On the one hand, evidence exists that wild chimpanzees spontaneously engage in prosocial behavior, for instance, in the form of food sharing, third-party consolation after fights, and infant adoption (9, 10). These observations have been corroborated by experimental paradigms in which chimpanzees readily helped experimenters obtain an out-of-reach object (11) and transferred useful objects to conspecifics without receiving anything in return (12, 13), although the extent to which instrumental helping in apes can be deemed "prosocial" is currently a hot topic of debate [see (14–16)]. On the other hand, evidence from so-called prosocial choice tests [see (8)] has culminated in the conclusion that "chimpanzees are indifferent to the welfare of others" (17). In these studies, in the experimental condition, one individual of a preselected dyad is presented with a choice between delivering a preferred food item only to themselves and to themselves and their partner, in contrast to a control condition, in which the surplus food item would be delivered to an empty cage

(instead of their partner). If the chimpanzee chooses the "both-food" option more than the "alone-food" option in the experimental, but not the control, condition, the choice is deemed prosocial. In general, these tests have yielded negative outcomes: Chimpanzees do not seem to confer benefits on conspecifics at no cost to themselves [(17–20); cf. (21, 22)].

Typically, the experimental paradigms used to investigate prosociality in chimpanzees have prioritized experimental rigor at the expense of ecological validity. To capture natural social dynamics between chimpanzees, in this case, prosocial behavior, we propose to move the experimental paradigm from indoor testing with human-imposed selection of chimpanzee dyads to outdoor testing with free partner choice [also see (8, 23, 24)]. Moreover, on the basis of recent findings evidencing substantial variation in social dynamics across multiple groups of chimpanzees (25, 26), we conjecture that the endeavor to investigate chimpanzee prosociality has been blind-sighted by single-group testing (27), with incongruent findings potentially attributable to intergroup differences between chimpanzee communities.

Here, we introduce a new methodological approach, which reveals large-group differences in prosocial behavior among chimpanzees (*Pan troglodytes*). Instead of giving chimpanzees isolated and time-restricted choices, we presented prosocial opportunities for extended periods of time to three groups of chimpanzees living under naturalistic conditions at a Zambian sanctuary (N = 94; table S1 and fig. S1). During this time, the chimpanzees had access to a button that, when pushed, released juice from a distant fountain, benefiting any conspecifics present at the fountain, but not the pusher themselves. We investigated whether chimpanzees would increasingly push for each other over time, whether they would push more often when the result of their acts would benefit group members compared to nobody (i.e., a control condition), and, given the recent evidence for substantial intraspecific variation in chimpanzee sociality (25, 26), whether group identity would moderate the extent and selectivity of chimpanzees' prosocial behavior.

To familiarize the chimpanzees with the experimental paradigm, we implemented the test setup in their enclosures and let them freely explore all possible contingencies. Each group was presented with

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the test setup for ±10 two-hour familiarization sessions before the actual experiment started. During these sessions, whenever a chimpanzee touched the button, the fountain was covertly activated from outside the enclosure. These interventions progressed from releasing juice from the fountain whenever a chimpanzee placed a foot or hand on the button to releasing juice only upon observing behaviors that resembled accurate pushing. The purpose of these familiarization sessions was to maximize the number of chimpanzees becoming knowledgeable of the workings of the setup. To further increase the likelihood of tapping into intentional prosocial behavior, subsequently, in the analyses of the test sessions (±30 two-hour sessions per group during which no interventions from the experimenters took place), we included only those chimpanzees that pushed the button three times or more ($N = 29$; for more details, see the Supplementary Materials) (Fig. 1).

RESULTS

Despite the cost of pushing the button (i.e., the pushing chimpanzee could not drink at the fountain simultaneously), across all groups, the pushing frequency and duration with at least one group member benefiting increased over the course of the experiment (Pearson's product-moment correlation between prosocial behavior and time as expressed in session number: frequency, $t = 3.26$, df $= 483$, $P < 0.002$, $r = 0.147$; duration, $t = 9.21$, df $= 483$, $P < 0.001$, $r = 0.387$, $N = 29$; see Fig. 2), indicating that the chimpanzees acted prosocially and were not averse to group members benefiting from their actions. In roughly one-third of the pushing acts (1174 of 3636), however, the pusher joined or moved toward the chimpanzees at
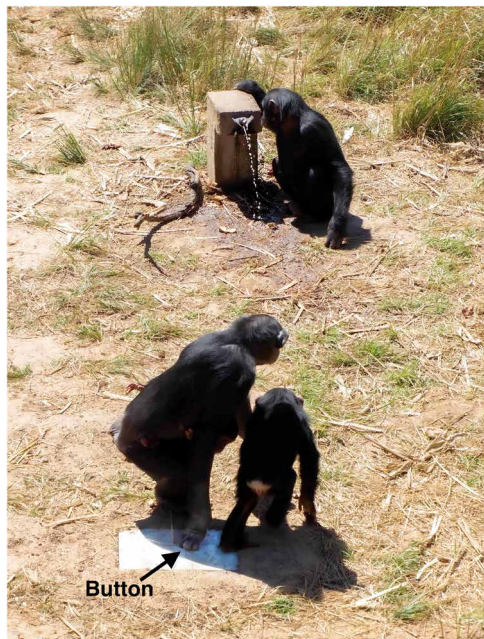
Fig. 1. Experimental setup illustrating prosocial fruit-juice donating. Fruit juice could be provided to group members by pushing a button. The pushing actor could not benefit from the juice concurrently. The photograph shows an adult female (with infant) providing juice for a sub-adult group member. For a schematic illustration of the setup, see fig. S2. Photo credit: Clara Dubois (Leipzig University).

the fountain, indicating that they wanted to benefit from their actions themselves. This behavior points to an egoistic motive yet does not rule out the very act being prosocial (i.e., benefiting others) (6, 8, 28). Even with these possibly egoistically motivated pushing acts (henceforth "egoistic acts") removed from the analysis, the chimpanzees increased their pushing frequency and duration over the course of the experiment (frequency: $t = 2.52$, df $= 483$, $P = 0.012$, $r = 0.114$; duration: $t = 9.72$, df $= 483$, $P < 0.001$, $r = 0.405$, $N = 29$).

When the chimpanzees' pushing efforts produced juice from a fountain outside their enclosure (i.e., the control condition), they pushed the button significantly less often and for shorter durations than when group members could profit from their acts (Wilcoxon signed-rank test, both frequency and duration: $P < 0.0001$; $N = 29$; Fig. 3). This finding indicates that the chimpanzees were not just pushing the button out of curiosity or interest but, instead, purposely pushed it and produced resources for group members. Given the opacity of the workings of the experimental setup (i.e., the hose connections ran underground), and chimpanzees' documented proclivity to continue attempting options that have ceased to render the previously experienced result (29, 30), it is not unexpected that the chimpanzees remained somewhat active even in the control condition (see Fig. 3).

Remarkably, the three chimpanzee groups differed substantially in their prosocial dynamics. First, controlled for exposure time, the groups expressed different magnitudes of prosociality (Kruskal-Wallis rank sum test: $\chi^2 = 8.43$, df $= 2$, $P = 0.015$; Fig. 4A), with the pushers in "Group_4" being significantly more prosocial (operationalized in terms of frequency/time with at least one group member benefiting at the fountain) than in both "Group_1" (Wilcoxon rank sum test: $W = 16$, $P = 0.044$) and "Group_2" ($W = 11$, $P = 0.005$). The same group-specific tendencies were observed when counting only the non-egoistic pushing acts ($\chi^2 = 7.44$, df $= 2$, $P = 0.024$; Fig. 4B; Group_1 versus Group_4: $W = 13$, $P = 0.020$; Group_2 versus Group_4: $W = 16$, $P = 0.015$; Group_1 versus Group_2: $P = $ NS).

Second, when the chimpanzees could behave prosocially (i.e., in the test condition), the groups differed significantly in their ratios of providing benefits to others (i.e., being prosocial) versus pushing the button in the absence of group members, which could also indicate an egoistic motive (Kruskal-Wallis rank sum test: $\chi^2 = 8.28$, df $= 2$, $P = 0.016$, $N = 29$; Fig. 5A; Group_1 versus Group_4: $W = 13.5$, $P = 0.026$; Group_2 versus Group_4: $P = $ NS; Group_1 versus Group_2: $W = 24.5$, $P = 0.011$; for details on the individual level, see fig. S4). Third, whenever the pushing act benefited others, the groups differed in the same direction with respect to the number of group members that benefited from the prosocial pushing acts ($\chi^2 = 10.28$, df $= 2$, $P = 0.012$, $N = 29$; Fig. 5B; Group_1 versus Group_4: $W = 13$, $P = 0.020$; Group_2 versus Group_4: $P = $ NS; Group_1 versus Group_2: $W = 21$, $P = 0.008$; for details on the individual level, see fig. S5). The fact that chimpanzees in the smallest ($N = 11$) and largest ($N = 44$) group were benefiting more group members per prosocial act than in the medium-sized group ($N = 25$) shows that this result is not simply a consequence of having more potential recipients in the group, i.e., group size. Intriguingly, both these group-dependent prosocial patterns mapped onto the chimpanzees' respective group-level social tolerance, a factor known to facilitate the emergence of prosocial and cooperative behaviors ($\chi^2 = 16.83$, df $= 2$, $P < 0.001$; Fig. 5C) (28, 31).

The emergent link between prosociality and social tolerance—here defined as the probability of being in close proximity without
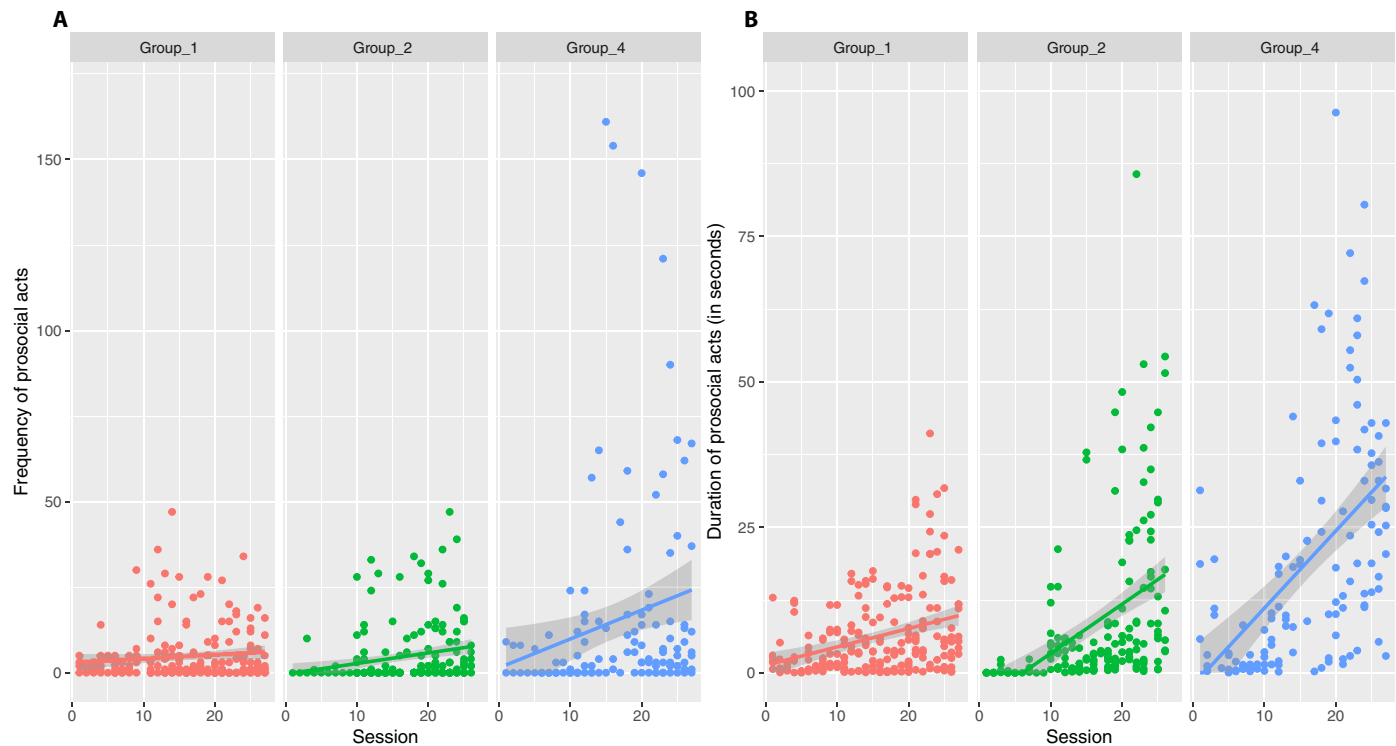
Fig. 2. Chimpanzees' prosocial acts over the course of the experiment. Across the three groups, both the (**A**) frequency and (**B**) duration of the chimpanzees' prosocial acts increased over time. The increase in prosocial behavior was observed in most of the chimpanzees (fig. S3). Dots represent individual data points, lines represent predicted values, and the gray zone around the lines represents 95% confidence intervals.
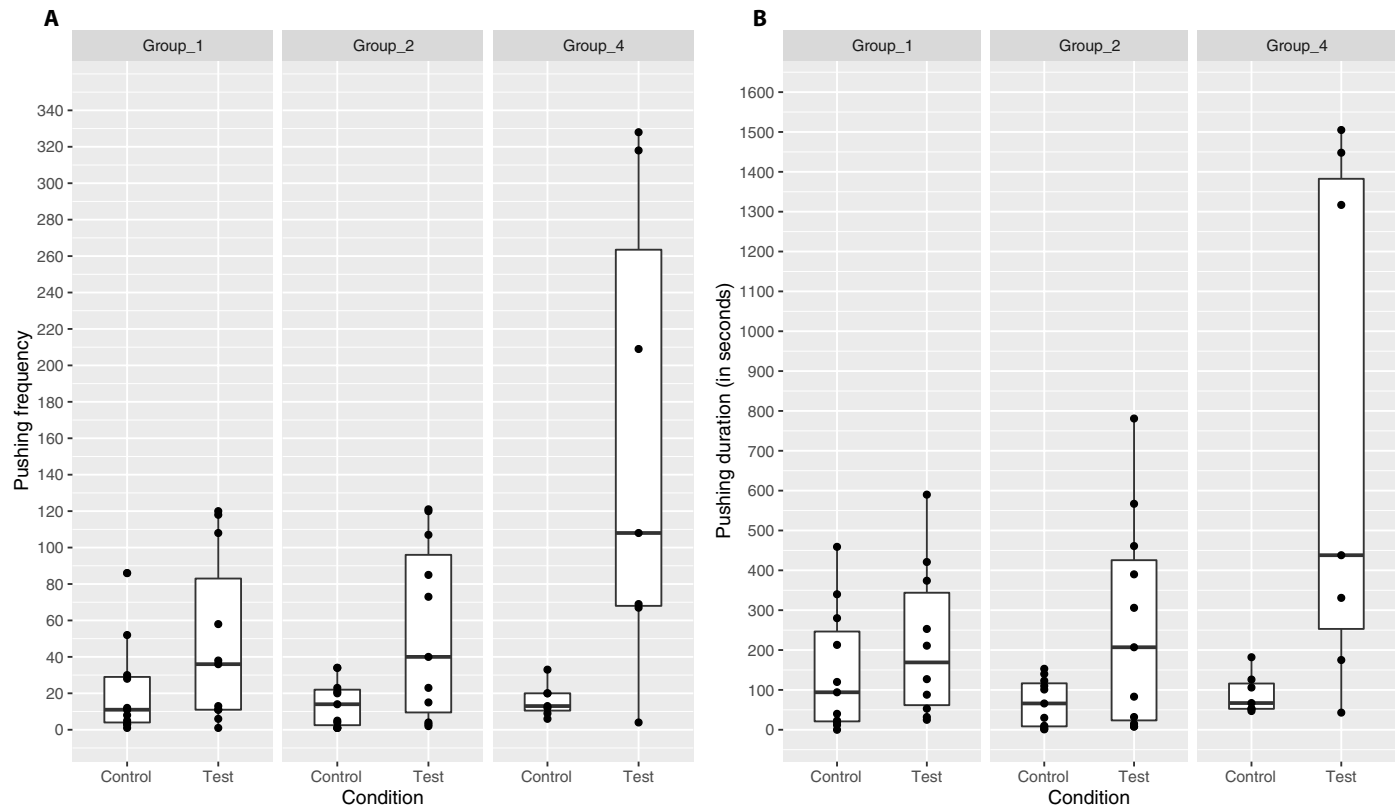
Fig. 3. Chimpanzees' prosocial behavior in the test versus control condition. Chimpanzees provided more fruit juice when group members could benefit from their actions (test) compared to when the juice was released out of all chimpanzees' reach (control), both as measured in the (**A**) frequency and (**B**) duration of pushing acts.

A

B
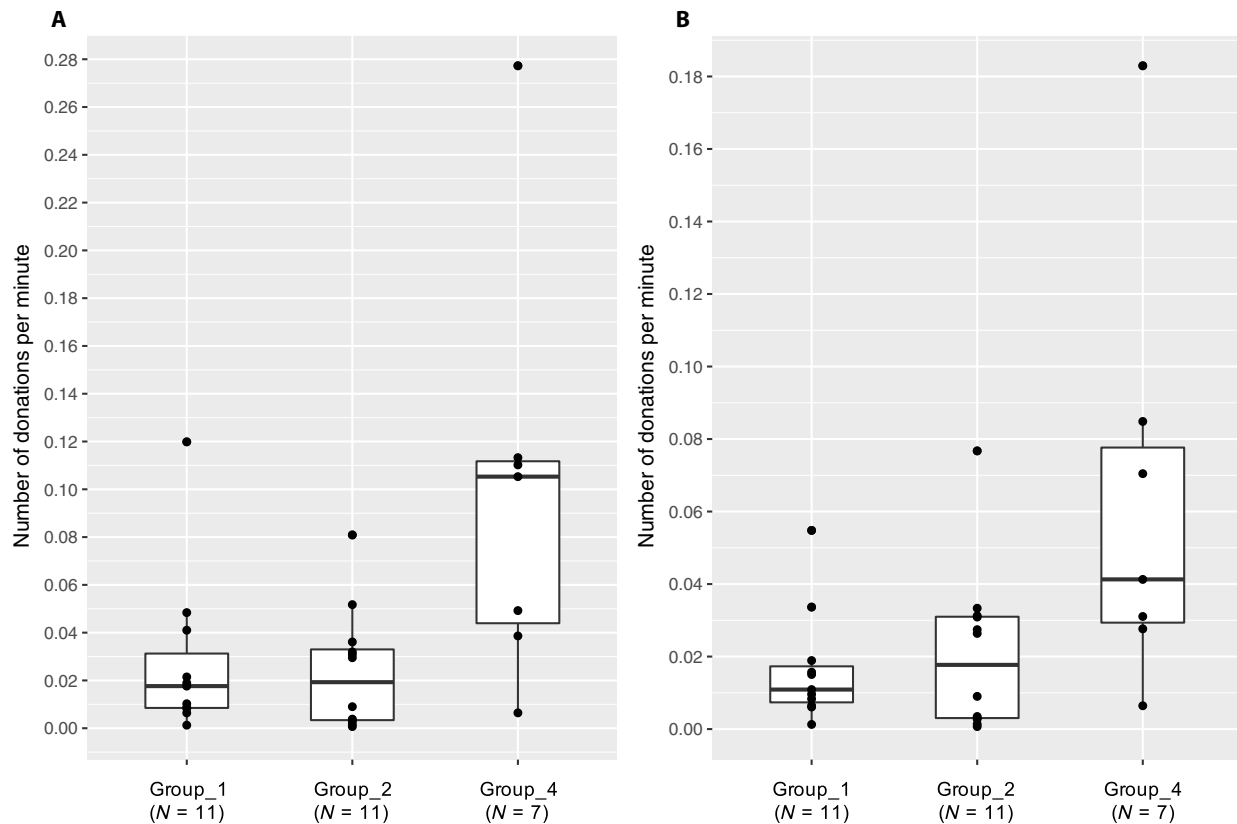
Fig. 4. Frequency of chimpanzees' prosocial fruit-juice donations across the three study groups. Prosociality as measured by the number of fruit-juice donations per minute differed between the groups, both when (**A**) all pushing acts were included and (**B**) with only the non-egoistic acts analyzed. 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).

A Pushing for others

B Number of recipients per prosocial act

C Social tolerance
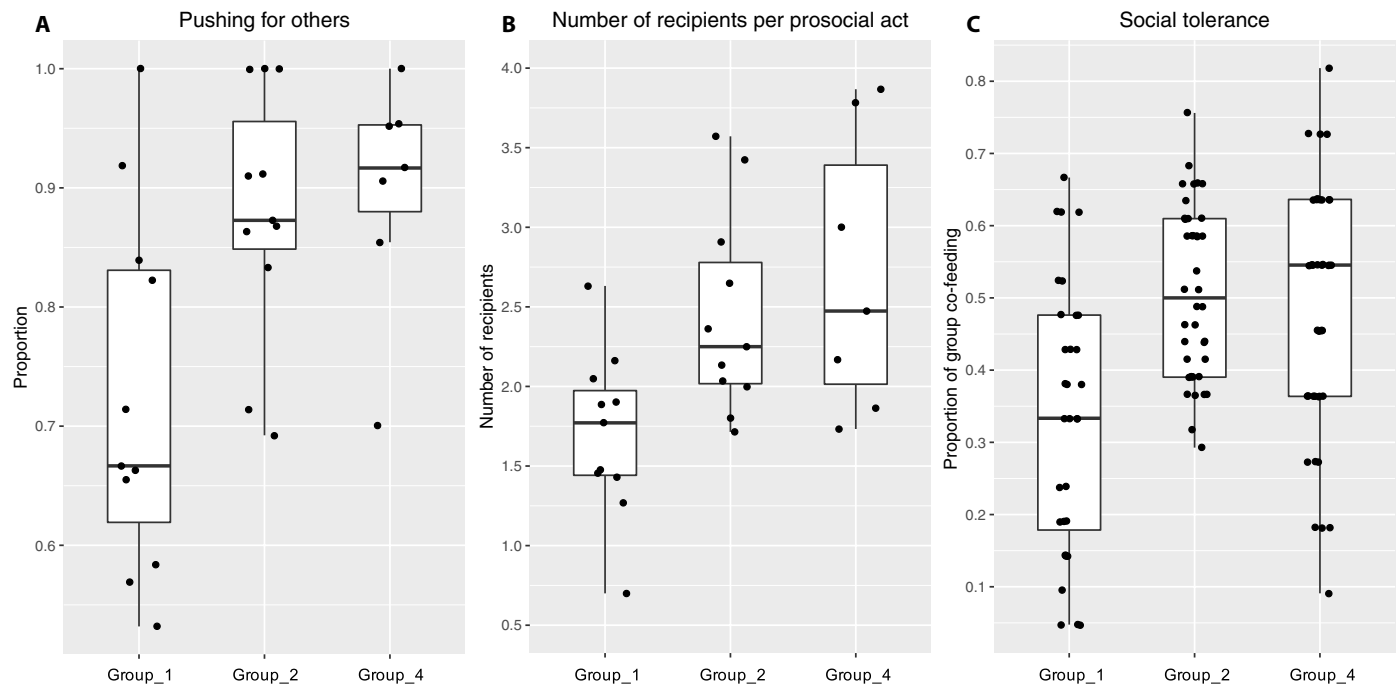
Fig. 5. Chimpanzees' prosocial dynamics map onto their group-specific social climates. Chimpanzees that (**A**) push more for others compared to solitarily and (**B**) provide benefits to more group members per prosocial act belong to (**C**) the most socially tolerant groups (i.e., Group_2 and Group_4: Kruskal-Wallis rank sum test, $\chi^2 = 16.8$, df = 2, $P < 0.001$). (A) and (B) represent averages per individual expressed in medians (bold horizontal lines) and interquartile ranges (boxes with vertical lines). (C) represents scan samples from a validated group assay on social tolerance (for more details, see the Supplementary Materials).

aggression (*25*)—was also evidenced through the observation of pronounced frequencies of aggression during the prosociality experiment in the low-tolerance group (i.e., Group_1) compared to a near absence of aggression in the relatively high-tolerance groups (i.e., Group_2 and Group_4; fig. S6). Last, scrutinizing one of the most posited mechanisms for the emergence of prosociality, we found that the two groups that could be tested for a kin bias (Group_1 and Group_2; see the Supplementary Materials) differed in the magnitude of nepotism such that the low-tolerance group (i.e., Group_1; see Fig. 5C) was more kin-biased in their prosocial expressions than the high-tolerance group ("pushing for family": estimate ± SD = −2.90 ± 0.81: GLMM (Generalized Linear Mixed Model), $P < 0.001$, $N = 18$; fig. S7; for more details, see the Supplementary Materials). Visualizations of network analyses illustrate that in the low-tolerance group, chimpanzees behaving prosocially toward each other can be clustered predominantly in family groups, whereas in the high-tolerance group, chimpanzees from different family units form prosocial clusters (Fig. 6). In conjunction, these findings suggest that prosociality was expressed in a more egalitarian manner in the more tolerant group.

DISCUSSION

Resolving the controversies that emerged from dyadic, time-constrained experiments in human-controlled contexts (*14–22*), our experimental study in a naturalistic setting shows that chimpanzees behave prosocially in a group context. The voluntary and group-level nature of our experiment allowed temporal autonomy (i.e., ample opportunity to participate) and partner choice, which are typically deprived from chimpanzees in prosociality studies [e.g., (*17*, *18*), see (*8*)], yet highlighted as prerequisites for sustainable forms of cooperation (*24*, *32–34*). The fact that prosocial behavior increased over the course of the experiment for most of the chimpanzees substantiates the conjecture that chimpanzees are invested in each other's welfare (*35–38*), and provides impetus to study animals' prosocial tendencies in more naturalistic experimental settings to derive biologically relevant observations for testing evolutionary scenarios (*31*, *39*).

Group identity proved an influential determinant of prosocial behavior, which identifies a hitherto neglected yet potent force in shaping nonhuman animals' interaction patterns. The presence of within-species intergroup variation may well explain previous inconsistencies in research findings that emerged from studying different populations [e.g., on prosociality, but also inequity aversion and cooperation; see (*27*)] and should pivotally inform future studies trying to generalize to the species level. Social tolerance levels (this study: Fig. 5C), but also previously reported group-specific sociality [frequencies of close proximity and grooming: (*26*)], mapped onto the differential expressions of prosociality across the studied chimpanzee communities. This pattern supports the posited importance of social tolerance in the expression of behaviors that facilitate group living (*31*, *40*, *41*) and warrants the expansion of the cultural differences approach in humans (*42*, *43*) to other animals,
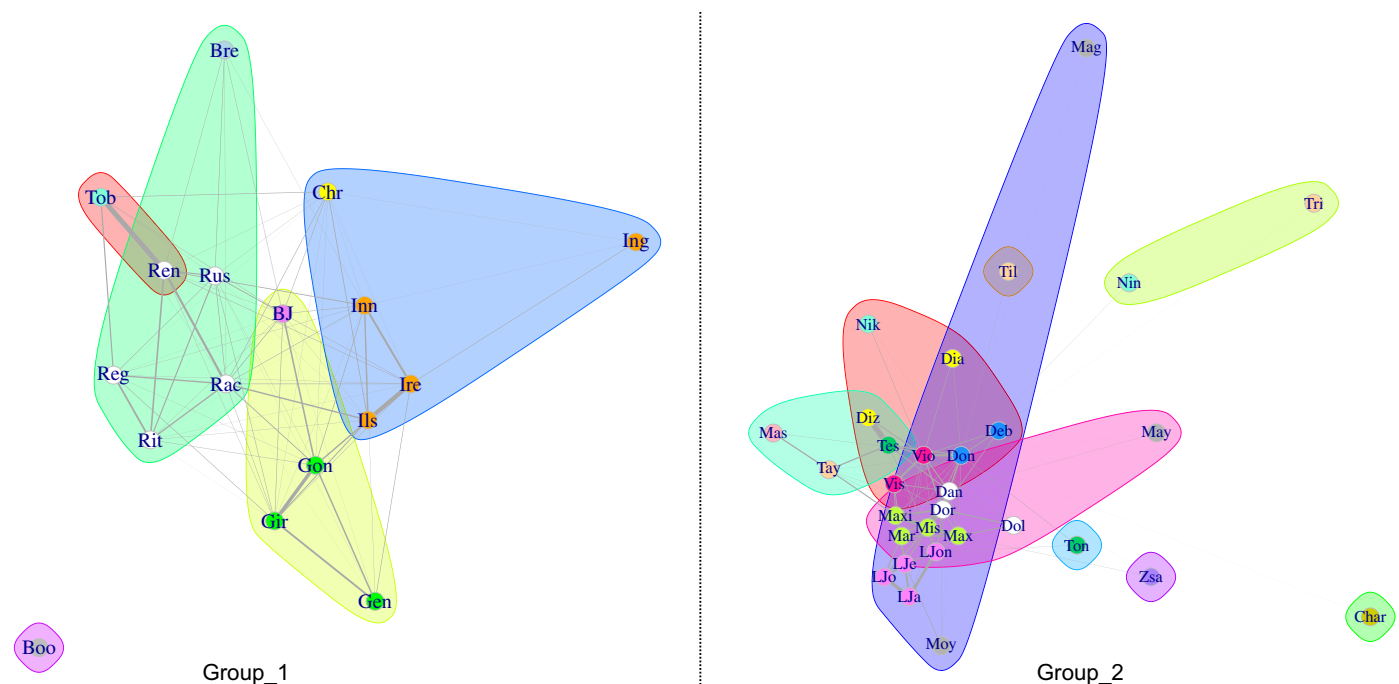
Fig. 6. Network visualizations of the prosocial interactions in the two study groups with more than one family unit: Group_1 (left) and Group_2 (right). The nodes denote the individuals who interacted in the experimental setup by either pushing or drinking and are colored by their maternal family group affiliation (i.e., maternal kin are represented by the same color). The edges represent the dyadic tie strength between individuals who pushed for each other, calculated as a simple ratio index: the number of times individual A pushed for B plus the number of times individual B pushed for A, divided by the total number of times A and B pushed. The network was generated with the R package "asnipe" (*53*). The diagrams were laid out using the Fruchterman-Reingold weighted algorithm (*54*). This layout increases the uniformity of edge length and minimizes edge crossings. The graphs display communities generated by the spinglass algorithm (*55*). This approach is based on the principle that nodes should prefer to be connected with other nodes of the same spin state, i.e. community, and disconnected from nodes of differing spin states. This algorithm has been found to be suitable for detecting communities in small networks (*56*). The graphs were generated using the R package "igraph" (*57*).

especially to species with social learning capacities (*27*). Evidence for the possibility of cultural transmission of prosocial behavior in chimpanzees was recently found in a prosocial choice task in which subjects exposed to generous conspecifics became more prosocial themselves (*22*). Together with the findings that chimpanzees are selective in their prosocial acts [this study; but also see (*22*, *44*, *45*)], these observations call for new investigations into the links between social influences, group-specific climates, and the expression of fitness-affecting behaviors.

Last, the marked group differences in prosociality here reported merit a closer examination of chimpanzees' motives to behave prosocially. At the proximate level, it is possible that the chimpanzees behaved prosocially out of motives other than other-regarding concern (*28*, *46*). The observation that juice providers sometimes approached the fountain post-pushing could indicate that these providers mainly acted out of self-interest (although necessarily with a certain level of inequity tolerance as the vast majority of the provided resource could not be obtained by the provider). While our experimental design does not allow us to tease apart the underlying motivations, it does measure prosocial behavior (*6*, *8*, *28*, *46*). Hence, our findings merit inferences on chimpanzee prosocial behavior and its group-specific expression: Most of the participating chimpanzees displayed sustained and even increasing prosocial behavior over the course of the experiment, although the frequency and scale of their prosociality, including kin bias and aggression, proved consistently group specific. The observation that chimpanzees extend their prosocial behavior to genetically unrelated conspecifics challenges the conclusion that chimpanzee prosociality can be sufficiently explained by the standard evolutionary models centering around (genetic) self-interest [cf. (*47*)]. Moreover, the consistently observed pattern of differential group-specific sociality across the same chimpanzee communities [this study and (*25*, *26*)] shows that chimpanzees' motives for behavioral expression do not necessarily generalize to the species level but may instead be affected, like in humans, by their group-specific social climates (*48*).

MATERIALS AND METHODS
Experimental design
The objectives of the study were to assess experimentally whether chimpanzees behave prosocially in a group setting (allowing 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 nonprofit sanctuary in the Copperbelt region of northern Zambia (12°23′S, 29°32′E) in miombo woodland forest suitable for chimpanzees (*49*). 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 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 m 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 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 m 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.

Experimental procedure
The experiment was conducted in each group with 2-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 pretest 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

Experimental sessions

We conducted 27 test sessions in Group_1 and Group_4 and 26 test sessions in Group_2 (the chimpanzees in Group_3 never participated; for details, see the Supplementary Materials). Test sessions started and ended as described above (see "Experimental procedure") and lasted 2 hours. After 21 test sessions (20 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 eight control sessions per group. During control sessions, all researchers and caretakers stayed at least 5 m 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. Analyses were done on eight test versus eight control sessions that were administered in the respective blocked (AABB) order.

The goal of the control sessions was to test whether pushing behavior was contingent upon juice flow within the chimpanzees' enclosures. Hence, 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, in terms of both frequency and duration, in Fig. 3.

Data coding

All sessions were coded from video. Chimpanzees in close proximity of the experimental setup (comprising both the button and the fountain at all times) were recorded on video and named by the researchers. The main variables coded were as follows: pushing the button (Pushing), including the identity of the pusher, for how long (Pushing Duration), and who was in the fountain zone during the pushing (Fountain Zone). The fountain zone was defined as the area in which chimpanzees could benefit from the juice flow, ~0.5-m distance of the spout (see fig. S2). Individuals present in the fountain zone during a pushing event were thus considered to be the recipients of the prosocial act.

A pushing event was defined by an individual pushing down the button and juice coming out of the fountain. The start of a pushing event was marked by the moment an individual pushed down the button. The duration of the pushing event was measured from the starting time until the individual stopped pushing. A new pushing event was coded if the pushing was interrupted for more than 2 s. We interpret pushing events as more meaningful than pushing durations for the reason that, by definition, events consist of separate decisions, whereas durations can comprise more (shorter pushes) or less (longer pushes) dependent decisions to act prosocially. For this reason, where we do not provide separate results on durations, we report results of analyses on the pushing events.

Some infants were not strong enough to push the button on their own. Hence, we excluded all infants under the age of three from the analysis (also to prevent the number of recipients of the prosocial act being affected by dependent offspring carried by mothers). Furthermore, we coded when a pushing individual approached and entered the fountain zone within 30 s after pushing (Post-Pushing Approach). Any attempts of a pushing individual to obtain some juice by sucking the fountain (Sucking Fountain) or scrounging leftovers from the ground (Drinking Spoils) within this time frame were also coded.

The videos were coded by four researchers. Cohen's κ was calculated for each variable for all pairs of coders based on the coding of one 2-hour session (including 73 pushing events). The mean Cohen's κ was calculated per variable as an overall interrater reliability (IRR), as suggested by Light (50) (see table S3). IRR was overall high (all κ > 0.89), except for the variable "Drinking Spoils," which only had a moderate agreement of κ = 0.56 [see Landis and Koch (51) for the evaluation of the magnitudes of Cohen's κ]. The moderate agreement for Drinking Spoils was likely due to the fact that some chimpanzees sometimes attempted to lick the spoils from the ground but only did so tentatively because the juice was mixed with soil. Hence, the coding for whether or not a chimpanzee was actually drinking the spoils was clouded. To be conservative, we interpreted all pushing events with Post-Pushing Approaches (thus including Sucking Fountain and Drinking Spoils) to be Egoistically Motivated. Furthermore, we present results both including and excluding the Egoistically Motivated acts, and where we do not (Figs. 5 and 6), we analyzed chimpanzees' prosocial behavior without egoistic acts. Overall, we analyzed only those subjects who pushed the button at least three times to avoid the inclusion of accidental, nondeliberate events. Corroborating analyses with only those subjects included that (i) pushed at least three times and (ii) pushed significantly more often in the test compared to the control sessions (see the Supplementary Materials) indicated qualitatively equivalent findings for all presented analyses.

The coding was done in Microsoft Excel and in ELAN (52), a program developed and provided by the Language Archive group at the Max Planck Institute for Psycholinguistics in Nijmegen (The Netherlands).

Group-level social tolerance

To assess group-level social tolerance, we used a co-feeding paradigm as per Cronin et al. (25): the peanut swing. The peanut swing consisted of a bamboo trunk cut in half lengthwise filled with peanuts. The number of peanuts delivered to the group was determined by multiplying the number of ≥3-year individuals by 12 (i.e., 12 peanuts per chimpanzee). The length of the bamboo was determined by the size of the group, 1 m for every five chimpanzees, resulting in, for example, 4.2 m for the 21 individuals (age ≥3 years) in Group_1. Once delivered to the group via the bamboo swing (e.g., movie S2), there were ~60 peanuts available to the chimpanzees per square meter.

The measurements were conducted in the morning between 9:00 a.m. and 11:30 a.m. or in the afternoon between 1:45 p.m. and 4:15 p.m. (alternated within groups). The peanut swing was placed in front of the fence, and the chimpanzees were called over, partly with the help of the caretakers. Once the entire group was within eyesight, the peanuts were tossed through the fence into the enclosure (see Movie S2). Video recording from two vantage points began before the start of the test and continued for at least 2 min following the delivery of the peanuts. Sessions that were disrupted by, for example, passing cars or visitors were excluded. Sessions were conducted

at most once per day per group. The peanut swing experiment was conducted during the same time frame as the juice fountain experiment from May to June 2016. The number of peanut swing sessions for groups 1, 2, and 4 was 4, 5, and 5, respectively.

The measure of interest in the peanut swing experiment is the proportion of the group that simultaneously gathers in the zone where the peanuts are delivered (25). All individuals within 1 m of the original place where the peanuts fell (and hence capable of reaching them) were considered as being present in the zone (see fig. S8). Sessions were coded at 15-s intervals for the first 2 min after the peanuts were delivered, which led to eight measurements per session. In all sessions, the peanuts were eaten within 2 min. For comparison between the groups, we coded the number of chimpanzees in the peanut zone at any given time scan, relative to the group size (25). All coding was conducted from video using a VLC player and transcribed into an Excel spreadsheet.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/9/eabc7982/DC1

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Citation: E. J. C. van Leeuwen, S. E. DeTroy, S. P. Kaufhold, C. Dubois, S. Schütte, J. Call, D. B. M. Haun, Chimpanzees behave prosocially in a group-specific manner. *Sci. Adv.* **7**, eabc7982 (2021).

Science Advances

Chimpanzees behave prosocially in a group-specific manner

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