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Group-level variation in co-feeding tolerance between two sanctuary-housed communities of chimpanzees (*Pan troglodytes*)

Edwin J.C. van Leeuwen[1,2,3] (iD) | Sanne Van Donink[1] | Marcel Eens[1] | Jeroen M.G. Stevens[1,2]

[1]Department of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp, Wilrijk, Belgium

[2]Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium

[3]Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence
Edwin J. C. van Leeuwen, Behavioural Ecology and Ecophysiology Group, Department of Biology, University of Antwerp, Wilrijk, Belgium.
Email: ejcvanleeuwen@gmail.com

Abstract

Social tolerance in group-living animals can be viewed as a counterweight against competitive interests necessary to obtain coexistence equilibrium and maintain group cohesion. As such, it forms an interesting phenomenon to study at the group level, but how can this be done most informatively? Here, we use three group-level co-feeding assays and social network analysis to study social tolerance in two groups of chimpanzees living under similar circumstances within a sanctuary to i) reassess whether social tolerance may be a group-specific parameter in chimpanzees and derive inferences about its long-term stability, and ii) compare the characteristics and resultant patterns between two established and one new assay. We show that the three assays expose the same (predicted) group-level differences in social tolerance as in the previous study eight years ago, thereby providing preliminary evidence for stability in group-specific levels of social tolerance in chimpanzees, despite changing group compositions. Furthermore, from an experimental point of view, we identify the new assay as more valid than the two established ones based on the consideration that resources may deplete at different rates across groups, which would consequently alter the need for tolerance differentially. We discuss implications for the study of social tolerance and highlight the importance of taking into account intraspecific variation in social animals.

KEYWORDS
co-feeding tolerance, culture, *Pan troglodytes*, social climate, social tolerance, temporal stability

1 | INTRODUCTION

Social tolerance lies at the basis of many individual and social behaviours that bear substantial weight for survival and reproductive success, and can be seen as one way of coping with conflicts of interest that arise when animals live together in social groups (De Waal, 2010). Defined as "the propensity to be in proximity to conspecifics around valuable resources with little or no aggression" (Cronin & Sánchez, 2012), social tolerance facilitates amongst others information transmission (van Schaik et al., 2003), cooperative engagement (Cronin et al., 2014; Hare et al., 2007; Melis et al., 2006) and reciprocal resource exchange (Cronin et al., 2010). Tolerating conspecifics could therefore be seen as a mechanism by which group members can adaptively overcome the competitive inter-individual forces

(e.g., regarding food resources and mating opportunities) that in themselves promote social distancing (De Waal, 1986). In this light, social tolerance has been invoked to predict and explain a plethora of behavioural phenomena. Cognisant of the many existing definitions and operationalisations (DeTroy under review), the broad proclivity to endure conspecifics' presence (around valuable resources) and specific signatures of aggression dynamics (low rates and/or the prevalence of counter-aggression (Thierry, 2007) have, for instance, been used to categorise macaque species into 4 grades of social tolerance ranging from despotic to egalitarian (Balasubramaniam et al., 2018; Sueur et al., 2011; Thierry, 2007). In turn, these categorisations have been used to explain variation in observed patterns of resource partitioning (Rebout et al., 2017) and reproductive skew (Schülke & Ostner, 2008). More broadly, social tolerance is often seen as a facilitator for more specific behaviours with the potential to influence individuals' fitness, like social learning (van Schaik, 2003), and collaboration or prosociality (Cronin, 2017; Horn et al., 2016; Yamamoto et al., 2009).

Recently, an explicit appreciation for intraspecific (group-level) variation in social behaviour has emerged (e.g., Stevens et al., 2008; Schradin, 2013; van de Waal, 2018; Kaufhold & van Leeuwen, 2019). Whereas social tolerance has typically been viewed as a species-level characteristic reflecting species' social structure – the pattern and nature of social relationship amongst individuals within a group (Fichtel et al., 2018; Kappeler & van Schaik, 2002) – this re-appreciation of intraspecific variation (cf. (Kaufhold & van Leeuwen, 2019; Lott, 1984)) warrants a more detailed *within-species* investigation. For instance, groups of wild-ranging vervet monkeys have been reported to differ in their inclination to preferably associate with same- or opposing-sex partners and in the extent to which the stability of social bonds is affected by sex combinations, dominance and kinship (Borgeaud et al., 2016). Similarly, chimpanzee communities at the Chimfunshi Wildlife Orphanage Trust have been shown to substantially differ in their expressions of social tolerance, both as measured by natural roaming tendencies (i.e., proximity and grooming) and by experimental assays tapping into equal resource distribution and co-feeding tolerance (Cronin et al., 2014; van Leeuwen et al., 2018). Such differences in group-level social climate are important to identify for they provide the basis for statistical extrapolations of single-group findings to the species level and for calibrating phylogenetic analyses concerned with tracing the evolutionary roots of the studied phenotype (Garamszegi, 2014; Kaufhold & van Leeuwen, 2019). At the same time, the observation that similar groups vary in their expression of social tolerance begs the question of whether these differences are stable over time (also see (van Leeuwen et al., 2018)).

Here, we study the two chimpanzee communities of the Chimfunshi Wildlife Orphanage Trust that match most closely in group size and composition (Group 3 and Group 4, also see (Cronin, van Leeuwen, et al., 2014)) by administering three group-level co-feeding assays. All three assays comprise linear adjustments for group size such that larger groups receive more resources across a larger resource zone (see (Cronin et al., 2015; Cronin, van Leeuwen, et al., 2014)). Two assays have been successfully used before, one ("the peanut swing") in chimpanzees (Cronin, van Leeuwen, et al., 2014)

and one ("the peanut plot") in bonobos (Cronin et al., 2015). The third assay ("the juice pipe") was devised to improve certain features of the other two assays, with the current study functioning as a validation of its measurement construct. The main goals of the study were to i) assess whether the originally reported group differences in social tolerance were still existent after 8 years, despite changes in group composition, and ii) implement and evaluate the quality of a new assay to assess social tolerance in group-living animals.

2 | METHODS

2.1 | Subjects and data collection

Subjects were 24 chimpanzees of Group 3 and 4 at the Project Area in the Chimfunshi Wildlife Orphanage Trust, Zambia (Table 1). The chimpanzees at the CWOT live in Miombo woodland enclosures (sizes 47 and 62 acres, respectively) and remain outside overnight and during the day except for 2 hr mid-day when the majority of chimpanzees voluntarily enter a building attached to each enclosure for supplemental feeding. Data were collected between June and August 2019. These same two groups were sampled in the original study in June 2011 (Cronin, van Leeuwen, et al., 2014; original group sizes (male/female): Group 3 $N = 13$ (6/7), Group 4 $N = 13$ (8/5)) – finding that Group 4 was significantly more tolerant than Group 3 – enabling us to make inferences about a potential level of stability in group-level social tolerance in chimpanzees across an eight-year time gap.

With respect to the STRANGE-ness of the study subjects (Webster & Rutz, 2020), we note that 15 out of the 24 chimpanzees were born in the wild, which means that they have minimally lost their mothers at a young age, before being brought over to the sanctuary. The ratio of wild versus captive born subjects was similar for both groups (Table 1). Unpublished data on behavioural differences between the wild versus captive born subjects at Chimfunshi indicate no detectable deviations in proximity and grooming networks. Both groups have had experience with a limited number

TABLE 1 Composition of the two chimpanzee groups at the start of the study in 2019

	Group 3	Group 4
Adults (>12 years)	7 (3/4)	9 (7/2)
Juveniles (3–11 years)	3 (1/2)	4 (2/2)[a]
Infants (< 3 years)	1 (1/0)	0
Total group size	11 (5/6)	13 (9/4)
Wild-born individuals[b]	6 (2/4)	9 (5/4)

Note: Age class based on combination of birth records and estimates upon arrival at the sanctuary. "Adult" corresponds to >12 years, "juvenile" to 3–11 years, and "infant" to <3 years. The number of males and females is shown in parentheses (male/female).

[a]Including two recently integrated females.

[b]All wild-born individuals were genetically identified as *Pan troglodytes schweinfurthii*, except for the two newly arrived females who have not been tested yet.

FIGURE 1 Depicted are still frames of (a) the peanut swing, (b) the peanut plot and (c) the juice pipe assay [Colour figure can be viewed at wileyonlinelibrary.com]

of experimental tests, most prominently the co-feeding measures (peanut swing and juice pipe experiment) in recent years. More details on the group compositions including genetic background at the level of sub-species can be found in Table 1.

2.2 | Ethics statement

The study was approved by the Chimfunshi Research Advisory Board (project: C044) and conformed to the nationwide legal requirements as stipulated by the Zambia Wildlife Authority (Table 1).

2.3 | Co-feeding assays

We administered three group-level co-feeding assays: the peanut swing (Cronin, van Leeuwen, et al., 2014), the peanut plot (Cronin et al., 2015) and the newly devised "juice pipe" (DeTroy et al., under review).

The peanut swing (Figure 1a) consisted of a sliced-through (in length) bamboo tree in which a pre-determined number of peanuts (12/chimpanzee aged>3yrs) were distributed across a pre-determined length (20cm/chimpanzee aged>3yrs). The peanuts were deployed in the enclosure by forcefully protruding the swing towards the fence, causing the peanuts to spread in the enclosure over a ±1 m width. Before the peanuts were thrown in the enclosure, the chimpanzees were attracted to the fence by shaking a bucket with peanuts whilst indicating vocally that the peanut swing session was about to start. Sessions would only start when all subjects were within sight of the experiment location. Given that the peanut swing experiment has been administered multiple times in the respective groups spanning multiple years, we did not incorporate familiarisation sessions before commencing with the test sessions. We administered 8 test sessions in Group 3 and 12 test sessions in Group 4.[1]

[1]Owing to logistical challenges (some individuals of Group 3 had to be held inside for a number of days, during which we did not perform tests), we were unable to administer the desired 12 sessions for Group 3 for the assays.

The peanut plot (Figure 1b) was identical to the peanut swing, except for the means by which the peanuts were deployed in the enclosure and the onset for the chimpanzees. The peanuts were distributed in the enclosure in a rectangle on the ground (cleared of grass) with a pre-determined length (20cm/chimpanzee aged>3 years) and 1m width, whilst the chimpanzees were in the indoor holding facility for their mid-day feeding. Before the peanuts were placed in the chimpanzees' enclosure, they were shown to the chimpanzees in their indoor facility. The chimpanzees were also able to see the placing of the peanuts, which served a similar function as the bucket shaking and vocal announcement in the peanut swing experiment (i.e., creating group-wide attention to the experiment). Upon their release from the building, the chimpanzees would directly find the peanuts in their enclosure (aided by vocal attraction by the experimenter), after which the session began (T_0 = arrival of the first chimpanzee in the resource zone). The chimpanzees were made acquainted with the location of the peanuts and the fact that a peanut plot session would take place on a given day by three familiarisation sessions which took place before the test sessions started. During these familiarisation sessions (one per day), the experimenter would show the bucket with peanuts to all chimpanzees inside the holding facility and deploy the peanuts in the peanut plot in full sight of the chimpanzees (similar to the later test sessions). Only the test sessions were included in the analyses. We administered 8 test sessions in Group 3 and 12 test sessions in Group 4.

The juice pipe (Figure 1c) comprises a new assay devised to present a more continuous co-feeding challenge than the peanut swing and peanut plot, which both revolve around depleting resources. The juice pipe consisted of a metal pipe with upward-facing holes (to enable a sprinkler effect) cemented in the chimpanzees' enclosures. Holes were drilled at a distance of 12.5 cm, resulting in eight holes per metre. This assay presented the chimpanzees with a continuous source of fruit juice for the entire test session. In line with the peanut assays, the length of the pipe was scaled to group size (25cm/chimpanzee; i.e., one metre per four individuals and two holes per individual). The reason that we applied an additional 5cm/chimpanzee compared to the swing and plot assay is because the

width from which resources can be consumed in the juice pipe assay is smaller than in the peanut assays. Note that this difference in scaling was systematically applied to both groups and as such should not influence the group comparison results. Key improvements of the juice pipe assay over the peanut assays are (i) the resource cannot be taken away, (ii) the resource is equally available throughout the entire study session and (iii) the critical zone in which chimpanzees are counted as "present" in the resource zone remains exactly proportional to group size throughout the study session (whereas this may change rapidly, owing to heterogeneous resource depletion, during the peanut assays). Similar to the peanut swing experiment, right before the start of session, the experimenter indicated vocally that the juice pipe session was about to start. Sessions would only start when all subjects were within sight of the experiment location. The juice pipe assay was piloted during three familiarisation days before the actual testing commenced. During these familiarisation sessions as well as later in the test sessions, the chimpanzees were alerted to the location of the juice pipe by vocal signals (i.e., imitating the food provisioning call) and by showing a bottle of juice close to the respective location. Given that the location of the juice pipe was close to the location where also the peanut measures were administered, the chimpanzees in both groups readily attended and started drinking the juice upon opening the juice flow. Only the test sessions were included in the analyses. We administered seven test sessions in Group 3 and twelve test sessions in Group 4.

For the scaling of the resource zones relative to group size, we summed the number of individuals within the groups that were plausibly able and motivated to eat twelve pieces. A similar reasoning was applied to the protocol for the juice pipe experiment, which provided only small amounts of juice from the holes. Thus, we scaled the length of the resource zone by the number of chimpanzees in the group that were 3 years or older.

2.4 | Experimental procedure and coding

Between June and August 2019, we administered one experiment in each group almost every day. The choice for the type of experiment on a given day and for each group was randomised so that no recurring pattern could be detected by the chimpanzees. The peanut swing and juice pipe experiments were balanced more or less equally between before noon and afternoon experiments. For the peanut plot experiment this was not possible, as it could only take place in the afternoon (i.e., immediately upon releasing the chimpanzees from their indoor holding facility). We always conducted the experiments consecutively and never simultaneously in both groups. All assays followed the same general procedure. The chimpanzees were alerted to the experiment vocally and visually, after which the session commenced upon having identified all group members within eye sight (±100 metres for both groups). The session start was represented by swinging the peanuts into the enclosure (swing), opening the doors of the holding facility (plot) or turning on the fruit juice sprinkler system (juice pipe). T_0 was

determined by the arrival of the first chimpanzee in the resource zone, which was defined as the zone in which a chimpanzee could access the resource, set to 1m around the border of the peanut rectangles and 50 cm around the juice pipe. A session consisted of eight scan points with fifteen sec intervals (i.e. two minutes in total[2]), starting at T_{15} (in s). Only one session was administered per group per day.

We video-recorded all sessions from two vantage points. Subsequently, for each scan, we scored the number of chimpanzees co-feeding in the resource zone from video. Additionally, we scored all agonistic interactions that occurred in the resource zone during the experiments. Agonistic interactions included both non-contact and contact aggression in which the aggressor showed display behaviour (with pilo-erection) and/or targeted hitting, kicking or biting. Furthermore, in the peanut assays, whenever an individual left the resource zone, we scored whether this departure was (a) characterised by relaxed locomotion (which we then attributed to individual satiation or resource depletion), or (b) preceded directly (<5 s) by one or more other chimpanzees entering the resource zone and/or coincided with a dispute over resources (which we then labelled as "competition"). Finally, for each individual in the resource zone, we coded the identities of all their neighbours (i.e., within arm-length distance). From these data, we calculated simple ratio association indices following:

$$\frac{x}{x + Y_{AB} + Y_A + Y_B}$$

with x, number of sampling periods with A and B observed associated; Y_A, number of sampling periods with just A identified; Y_b, number of sampling periods with just B identified; Y_{ab}, number of sampling periods with A and B identified but not associated (Whitehead, 2008). To aggregate the data across the three co-feeding measures (to increase the resolution of associations), the sampling period was set to "scan." Specifically, we were interested in the coefficient of variation across associations (i.e., SD/mean association) – also known as "social differentiation." This measure represents the uniformity of associations across dyads, with relatively low values indicating a relatively uniform strength of associations across dyads (Whitehead, 2008), and has been proven useful for comparing networks with different sizes (Wakefield, 2013), whereas its antecedent, the mean association indices, are prone to be affected by group size (Whitehead, 2008). To test for group differences in social differentiation, we applied a modified signed-likelihood ratio test (Krishnamoorthy & Lee, 2014) with the "cvequality" package in R (Marwick & Krishnamoorthy, 2019). From the proximity networks, we also extracted modularity scores. The modularity score indicates sub-grouping within a social network and thus provides an indication of how fragmented the social group is. Modularity scores close to 0 indicate a purely random distribution of relationships whilst scores

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[2]This was roughly the time the chimpanzees needed to consume all peanuts in Cronin et al. (Cronin et al., 2014b).

close to 1 indicate strong hierarchical clustering (Pasquaretta et al., 2014). Pasquaretta and colleagues (2014) studied 24 species of primates and concluded that modularity had opposing effects on network efficiency, showing that tolerant species have more efficient networks. Hence, we used modularity as another proxy for social tolerance.

The proximity networks were calculated in SOCPROG (Whitehead, 2009). Graphics were aligned by the "fastgreedy community detection" algorithm as implemented in the R package "igraph" (Csárdi & Nepusz, 2006).

2.5 | Statistical analysis

We modelled co-feeding tolerance at the scan level using Generalized Linear Mixed Models with beta error distribution and logit link function (Baayen, 2008). As response variable, we used the proportion of the group that was co-feeding in the resource zone. To remain consistent with previous applications of the respective co-feeding tests (Cronin et al., 2015; Cronin, van Leeuwen, et al., 2014), here, we only included chimpanzees of minimum 3 years old because at a younger age chimpanzee infants are typically attached to their mothers, especially in competitive situations. The full model consisted of the fixed effects "group," "assay," "session" and "scan." To test whether co-feeding measures (i.e., "assay") had differential effects on co-feeding tolerance (including its progression over time within sessions) in the two groups, we included the three-way interaction between "group," "assay" and "scan" as fixed effect in the model. The random effects structure consisted of the intercept for "session" and the slopes of "assay" (dummy coded into two variables) and "scan number" (z-transformed) including its interaction nested in "session." This random effects structure relaxed the assumption that the slopes of co-feeding tolerance over time (i.e., "scan") are the same for all three assays.

Before assessing the impact of single parameters, we conducted a full-null model comparison using a likelihood ratio test (Dobson, 2002; Forstmeier & Schielzeth, 2011). The null model comprised the fixed effects "session" and "scan" (i.e., we controlled for their respective effects on the response but did not have any a priori predictions about their influence) and the same random effects structure as the full model. Inspection of the model parameters was done using likelihood ratio tests with the "drop1" function (test set to "chi-square") and, for the estimates and standard errors, the "summary" function. Post hoc assessments of contrasts (i.e., between the two groups for the three different assays) were done using the "emmeans" R package (Lenth, 2020), which computes marginal means per specified factor level and provides estimated differences for the specified contrasts (on the log odds ratio scale). Our primary interest was assessing group differences in co-feeding tolerance. Therefore, when we found a significant increase in model fit of the full compared to the null model, we first assessed the effect of "group" as a main effect (i.e., the full model without interaction). We did the same for the main effect of "assay." Subsequently, we assessed the

model including the interaction (i.e., the full model). Model stability was evaluated by excluding sessions one at a time from the data and comparing the model estimates derived for these data with those derived for the full dataset (indicating no influential subjects to exist; see Figure S1). The full model was fitted with a dispersion parameter closely mimicking the underlying data structure (dispersion ratio observed/simulated data = 0.923, p = .216; (Hartig, 2020)), enabling meaningful model inspection. Collinearity amongst the predictors was assessed by checking variance inflation factors (VIF; (Field et al., 2012)) with the function "vif" of the package "car" (Fox & Weisberg, 2019) based on a standard linear model lacking the interaction and random effects. This revealed collinearity to be no issue (maximum VIF: 1.06).

All models were fitted in R (v 4.0.2: (R Core Team, 2020)) using the function "glmmTMB" of the R package "glmmTMB" (Brooks et al., 2017). P-values <0.05 were considered significant; p-values for the post hoc contrasts were adjusted for multiple testing using the Tukey correction. All data are available in a Dryad Repository (van Leeuwen et al., 2021).

3 | RESULTS

3.1 | Co-feeding tolerance

The full model provided a better fit to the data than the null model (likelihood ratio test: $\chi^2 = 87.08$, $df = 10$, $p < .001$), which justified further inspection of the parameter estimates.

Overall, the proportion of group members co-feeding in the resource zone was significantly higher for the chimpanzees in Group 4 (mean ± SE: 0.55 ± 0.22) compared to Group 3 (mean ± SE: 0.48 ± 0.18; LRT: $\chi^2 = 6.99$, $df = 1$, $p = .008$; Table 2 for details). Post hoc contrast testing showed that this group effect was mainly driven by the juice pipe assay, in which the odds for chimpanzees in Group 4 to co-feed in the resource zone were 2.05 times (95% CI: 1.35–3.10) larger than in Group 3 ($p < .001$; for the other two assays: $p_{swing} = 0.236$, $p_{plot} = 0.780$; Figure 2a).

The experimental assays also affected co-feeding tolerance differently (LRT: $\chi^2 = 37.30$, $df = 2$, $p < .001$), with the juice pipe assay inducing

TABLE 2 Results from the GLMM examining the effects of group and assay (and scan and session as control variables) on co-feeding tolerance

Term	Estimate	SE	Lower CI	Upper CI	p
Intercept	0.679	0.146	a	a	a
Group4	0.332	0.114	0.100	0.564	<.004
Assay_plot	−1.068	0.180	−1.440	−0.696	<.001
Assay_swing	−1.066	0.193	−1.460	−0.670	<.001
Scan	−0.387	0.033	−0.454	−0.319	<.001
Session	−0.009	0.017	−0.044	0.027	.613

aNot indicated because of having a very limited interpretation.
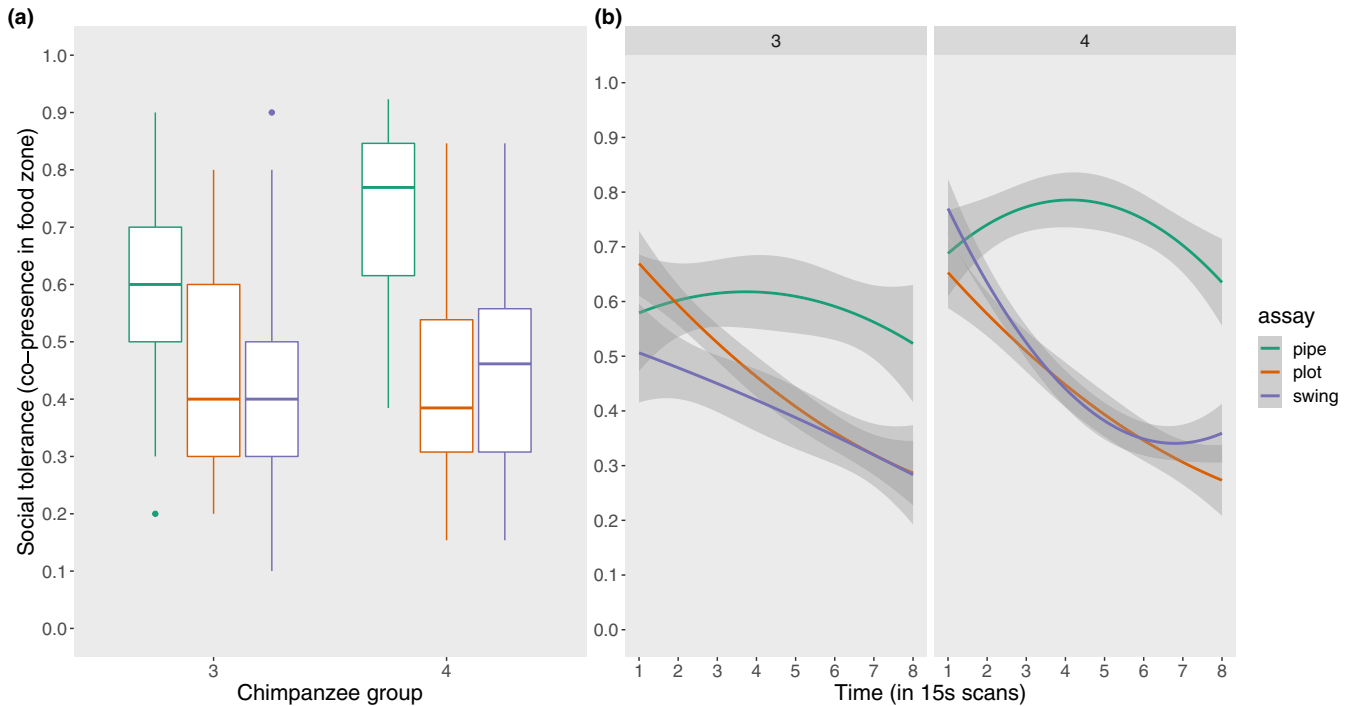
(a)

(b)

FIGURE 2 Co-feeding scores (proportion of group present in resource zone: *y*-axis) of the two chimpanzee communities per experimental assay with (a) mean depictions with interquartile ranges (boxes) and medians (bold horizontal lines), and (b) mean scores per scan point with model predictions (coloured lines) and 95% confidence intervals (shaded area around the lines) [Colour figure can be viewed at wileyonlinelibrary.com]

higher tolerance levels (mean ± *SE*: 0.68 ± 0.19) than the peanut swing (mean ± *SE*: 0.45 ± 0.18) and the peanut plot assay (mean ± *SE*: 0.44 ± 0.18; pipe versus swing: estimate ± *SE*: 1.066 ± 0.193, *p* < .001; pipe versus plot: estimate ± *SD*: 1.068 ± 0.180, *p* < .001; swing versus plot: 0.001 ± 0.256, *p* = .996; also Table 2).

Notably, the assays induced tolerance levels in Group 3 and 4 to a different extent (LRT interaction effect: $\chi^2 = 6.01$, *df* =2, *p* =.049[3]; Figure 2a). Whilst in absolute proportions the plot experiment (Group 3 versus Group 4:0.45 versus 0.44) yielded similar patterns in both groups, the swing (Group 3 versus Group 4:0.40 versus 0.48) and pipe experiments (Group 3 versus Group 4:0.59 versus 0.73) increasingly depicted Group 4 as more tolerant than Group 3 (Figure 2a). Furthermore, we observed different tolerance patterns as a function of time (15-s intervals) for all three assays (LRT interaction assay and scan: $\chi^2 = 29.80$, *df* = 2, *p* < .001) with relative steady decreases for both the peanut assays, and more equal levels of co-feeding tolerance – with a minor peak half-way the experiment – in the juice pipe assay (Figure 2b). In both groups, co-feeding tolerance decreased slightly across sessions, but the effect was not significant (LRT: $\chi^2 = 0.33$, *df* = 1, *p* = .57; Figure S2).

As a post hoc inspection, in the assays with depleting food resources (the peanut swing and plot), we checked for differences in the number of chimpanzees in the resource zone at the first scan point, following the rationale that the number of peanuts eaten

around the first time point will have a relatively large impact on the motivation to remain in the resource zone during subsequent time points. In other words, if many peanuts are consumed at T_1, there will be relatively few peanuts left to be consumed in T_{2-8}. Note that this number is of particular interest to our study objective: a high level of co-feeding tolerance would allow for a relatively high number of chimpanzees in the resource zone.

For the peanut plot, no group differences were observed in the number of chimpanzees co-feeding in the resource zone at the first scan point (LRT: $\chi^2 = 1.99$, *df* = 2, *p* = .158; Group 3: mean ± *SD* = 0.65 ± 0.05, *N* = 8; Group 4 mean ± *SD* = 0.57 ± 0.16, *N* = 12). For the peanut swing, Group 4 started off with significantly higher levels of co-feeding tolerance than Group 3 ($\chi^2 = 6.33$, *df* = 2, *p* = .012; Group 3: mean ± *SD* = 0.50 ± 0.30, *N* = 8; Group 4 mean ± *SD* = 0.78 ± 0.11, *N* = 12). The steeper decrease of the proportion of co-feeding group members in Group 4 compared to Group 3 in the peanut swing experiment was mostly driven by the rapid depletion of resources causing individuals to leave the resource zone rather than increased competition (Figure S4).

3.2 | Aggression and competition in the resource zone

The mean frequencies of aggressive instances per individual across all test sessions did not differ between groups (Wilcoxon rank-sum test: W = 53, *p* =.469; mean ± *SD*; Group 3:0.203 ± 0.321 Group

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[3]The three-way interaction between group, assay and scan was not significant (LRT: $\chi^2 = 2.91$, *df* =2, *p* =.233).

4:0.199 ± 0.172; Figure S3). Departures from the resource zone could most frequently (~12%, n = 334) be attributed to intrinsic motivations rather than competition (Figure S4). In relation to the scan intervals across sessions, the highest proportion of departures owing to competition (~40%) was found between T_1 and T_2 (see Figure S4).

3.3 | Social network metrics

For each possible dyad, a simple ratio association index was calculated. The mean ± SD association index for Group 3 was 0.097 ± 0.119. For Group 4, the mean ± SD association index was 0.117 ± 0.087. Given that association indices are likely affected by group size (and the groups under study differed in that respect), no statistical test was performed on the association indices (Whitehead, 2008). The modified signed-likelihood ratio test showed that the coefficient of variation was significantly higher in Group 3 (1.225) than in Group 4 (0.743) (MSLRT = 6.67, p = .0098). This implies that individuals in Group 3 were more particular in who they decided to co-feed next to than individuals in Group 4. The community detection algorithm ("fastgreedy") identified two relatively independent clusters in Group 3 and Group 4 (see Figure 3), yet with Group 3 having a higher modularity score (0.11) than Group 4 (0.06). Here, we note that the one peripheral chimpanzee in Group 4 was a recently (±6 months) introduced young adult female who had never before engaged with conspecifics. Group 3 has been stable (i.e. without newly introduced chimpanzees) since 1999.

4 | DISCUSSION

We measured group-level co-feeding tolerance in two communities of chimpanzees to examine whether chimpanzee groups that live in the same ecological niche and consist of similar demographics can differ in their expressions of social tolerance. The rationale for this research question is derived from the general tenet to view social tolerance as a species-specific trait (e.g. (Balasubramaniam et al., 2018; Forss et al., 2016; Hare et al., 2007)). Corroborating recent evidence that has contested this assumption (Cronin, van Leeuwen, et al., 2014; Kaigaishi et al., 2019; van Leeuwen et al., 2018), we show that chimpanzee groups can differ substantially in their expressions of co-feeding tolerance. Specifically, one group was consistently characterised as more tolerant than the other in terms of the proportion of the group that co-fed around valuable resources, the diversity of co-feeding partners and the extent to which the co-feeding parties formed a cohesive (as opposed to fragmented) unit. Given that the sampled groups comprise predominantly one sub-species of chimpanzees (*Pan troglodytes schweinfurthii*) and live under similar ecological conditions where they are managed under the same minimal husbandry protocol, these group differences cannot easily be explained by variation in genetics, ecology or management. Taken together, these findings contribute to the idea that inter-group variation, at least in primates, should be taken into account when generalising to the species level (Borgeaud et al., 2016; van Leeuwen et al., 2018; van de Waal, 2018; Kaufhold & van Leeuwen, 2019).

Building on the initial report evidencing group-level differences in the Chimfunshi chimpanzees (Cronin, van Leeuwen, et al., 2014), we provide evidence that despite changing group compositions owing to deaths, births and new integrations, the group difference in social tolerance remains stable. Compared to the data from the original study (obtained in June 2011; see Cronin, van Leeuwen, et al., 2014), most notably, the two highest ranking males in Group 3 and three mid- and lower-ranking adult females of Group 4 have died. Consequently, there has been an alpha-male change in Group 3, and a skew towards a lower female/male ratio in Group 4. Such perpetuations of group sociality (of which social tolerance could be viewed as a component) are reminiscent of long-lasting pacific cultures in wild baboons (Sapolsky & Share, 2004) and indicate that co-feeding patterns in a group setting do not inevitably and solely result from individuals'
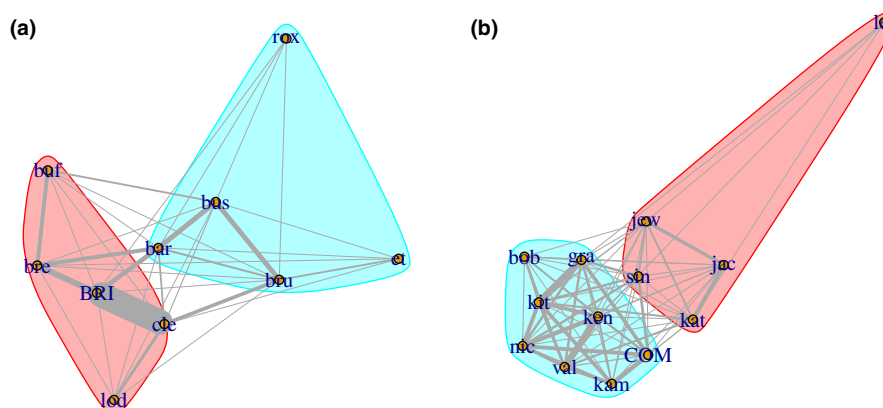

FIGURE 3 The proximity networks for (a) Group 3, and (b) Group 4. The named circles (nodes) represent individual chimpanzees, and the lines connecting them (vertices) represent the strength of association, with thicker lines indicating stronger (i.e. more frequent) associations. Names in capitals represent the alpha males. The diagrams were laid out using the Fruchterman–Reingold weighted algorithm (Fruchterman & Reingold, 1991). This layout increases the uniformity of edge length and minimises edge crossings. Coloured sub-groups (clusters) are derived from the "fastgreedy" community detection algorithm as implemented in "*igraph*." [Colour figure can be viewed at wileyonlinelibrary.com]

competitive or resource-holding abilities (Weisbard & Goy, 1976; De Waal, 1986; cf. Bergman, 2006). In other words, group-level stability in social dynamics is not self-evident in the face of changing group compositions and may indicate the workings of mechanisms that foster within-group homogeneity in addition to the well-established effects of demographic factors on chimpanzee social dynamics (also see DeTroy et al. in review). An alternative explanation for the inferred stability lies in more generic demographic determinants of social behaviour in chimpanzees. Although our measures control for differences in group size, the influence of for instance the female/male ratio could directly affect our response variable. In chimpanzees, competition over food is more severe in adult females than in adult males (Goodall, 1986; Nishida, 2012). Female chimpanzees are outranked by the adult males and exhibit a less clearly defined hierarchy than the males, which results in more uncertainty for instance about access to resources. Given that the female/male ratio was higher in Group 3 (1.20) than in Group 4 (0.44) – just like in the initial study (Group 3:1.17; Group 4:0.63: see Cronin, van Leeuwen, et al., 2014) – this demographic aspect could have contributed to the observed group differences in co-feeding tolerance.

We note that only a longitudinal study including measurements at regular intervals could verify whether co-feeding tolerance can be a stable group-specific trait. More specifically, by measuring co-feeding tolerance over time it becomes possible to see whether demographic changes may influence co-feeding tolerance or whether there might be additional group-level processes at play that induce certain levels of social tolerance contrary or beyond expectations based on demographics factors alone. In fact, a contemporary study investigating longitudinal expressions of co-feeding tolerance in chimpanzees with one of the applied measures – the peanut swing – provisionally reports that whereas a large part of the variation can be explained by demographic variables like the number of mothers with dependent offspring, a significant part of group-level stability remains unexplained (DeTroy et al., 2021). Whether this unexplained portion might be best accounted for by unexplored social factors (like the state of female receptivity or the influence of high-status or dominant individuals) or possibly by reaction norms that are shaped by within-group social learning processes (e.g.,Boesch et al., 2020; Cantor & Whitehead, 2015; van Leeuwen et al., 2018; Sapolsky, 2006)) is an exciting avenue for future research.

A closer look at the three co-feeding assays shows that the main effect of group on differences in co-feeding tolerance was predominantly carried by the juice pipe assay. The peanut swing, which was originally used to assess group-level variation in Chimfunshi (Cronin, van Leeuwen, et al., 2014), revealed no group-level differences in the current study. This finding is noteworthy because it seemingly precludes a direct conclusion with respect to the stability of group differences from the original study to the current one. Yet, a more detailed inspection of the data indicated that within the sessions the chimpanzees in Group 4 started off more tolerantly than Group 3, after which they left the resource zone more quickly plausibly owing to a quicker depletion of the resources (see Figure 2b). Thus, whereas the peanut swing medians do not differ between the groups, the slopes of the scans within sessions suggest similar differences in co-feeding tolerance as revealed by the juice pipe assay.

The juice pipe assay was devised to overcome the issue that resource depletion affects the extent of tolerance required to be in the (pre-determined) resource zone. When a large number of individuals is present from the start of the session, the resource will be depleted very quickly and so determine the likelihood of obtaining resources later in the session. In contrast to the peanut assays in which resources deplete over time (and thus the relevance of being in the resource zone decreases), the juice pipe provides a continued incentive for all group members to be in the resource zone – an incentive that requires tolerance to be satisfied. Hence, the juice pipe assay necessitates a continuous level of social tolerance throughout the session in order to obtain access to the resource (also see (DeTroy et al., 2021)). As such, the juice pipe assay revealed group differences in the sampled groups whilst the established assays (the peanut swing and peanut plot (Cronin De Groot & Stevens, 2015; Cronin, van Leeuwen, et al., 2014)) did not, or did so less delineated (different slopes in the peanut swing, see previous paragraph). We note that the juice pipe assay also differed from the other two assays in the food source (juice instead of peanuts), which could have differently affected individuals' motivation to engage in the experiment, if food preference differs between juice and peanuts. Yet, assuming no systematic group differences in individuals' peanut and juice preferences, this food source dissimilarity is unlikely to explain the observed group differences in co-feeding propensities. The generally higher levels of co-feeding tolerance in the juice pipe assay than in the peanut assays may be related to the fact that the continuous replenishing of the food resource in the former lowers the triggering of competitive motivations and thus allows for a more valid assessment of *tolerating* each other's close presence around valuable food resources (De Waal, 1986).

The comparison between the peanut swing and peanut plot contains particular relevance for the previously reported difference in co-feeding tolerance between bonobos and chimpanzees (Cronin et al., 2015). In this study, bonobos were administered the peanut *plot*, after which their co-feeding tendencies were compared with – and found to be substantially lower than – chimpanzees who were administered the peanut *swing*. Despite the slight difference between the swing and the plot in our study with respect to the progression of co-feeding tolerance over time (i.e. the slope, Figure 2b), the measures predominantly seem to align regarding resultant co-feeding tolerance patterns, both in terms of medians and slopes. As such, our study provides the necessary justification for the conclusion that the bonobo group at Planckendael Zoo (Belgium) in September-October 2012 was substantially less tolerant than two of the chimpanzee groups at Chimfunshi in June 2011 (see (Cronin De Groot & Stevens, 2015; Cronin, van Leeuwen, et al., 2014)). Similarly, the two chimpanzee groups in the current assessment (2019; this study) show roughly twice as much co-feeding tolerance in the peanut plot assay as the bonobo group at Planckendael Zoo in 2012, who were also tested with the peanut plot assay.

In conjunction, our study *i*) corroborates indications of the presence of group-level variation in social tolerance in chimpanzees, *ii*) indicates stability of such variation despite substantial changes in group composition over an 8-year period and *iii*) presents a novel, improved assay to investigate group-level social tolerance in group-living animals. The emergent picture of intraspecific inter-group variation in sociality warrants more detailed investigations into the mechanisms driving such variation and ought to be taken as a precaution against species-level generalisations of one-sample studies (Kaufhold & van Leeuwen, 2019; Stevens et al., 2008) if we were to better understand great ape social dynamics and, relatedly, the evolutionary origins of human "ultra-sociality" (Tomasello, 2014).

CONFLICT OF INTEREST

The authors declare to have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are available in the following Dryad Repository: https://doi.org/10.5061/dryad.kwh70rz2d

ORCID

Edwin J.C. van Leeuwen https://orcid.org/0000-0002-7729-2182

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