

## Bonobos Show Limited Social Tolerance in a Group Setting: A Comparison with Chimpanzees and a Test of the Relational Model

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### Key Words

*Pan paniscus* · *Pan troglodytes* · Cofeeding · Social relationship · Group dynamics · Tolerance

### Abstract

Social tolerance is a core aspect of primate social relationships with implications for the evolution of cooperation, prosociality and social learning. We measured the social tolerance of bonobos in an experiment recently validated with chimpanzees to allow for a comparative assessment of group-level tolerance, and found that the bonobo group studied here exhibited lower social tolerance on average than chimpanzees in this paradigm. Furthermore, following the Relational Model of de Waal, we investigated whether bonobos responded to an increased potential for social conflict with tolerance, conflict avoidance or conflict escalation, and found that only behaviours indicative of conflict escalation differed across conditions. Taken together, these findings contribute to the current debate over the level of social tolerance of bonobos and lend support to the position that the social tolerance of bonobos may not be notably high compared with other primates.

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### Introduction

Together with the type of dominance hierarchy (despotic or egalitarian) and the degree of nepotism (kin bias), social tolerance is used to characterize relationships in primate species [Sterck et al., 1997]. Social tolerance is defined as the propensity to be in proximity to conspecifics around valuable resources with little or no aggression, and is described along a continuum [Cronin et al., 2014]. According to the Relational Model proposed by de Waal [1996, 2000], tolerance is one of three outcomes that

can result when individuals are in social conflict, together with conflict avoidance and conflict escalation through aggression. Which outcome occurs will depend upon the value of the resource causing potential conflict, the risk of bodily harm if aggression occurs, and the value of the relationship. Therefore, measures of social tolerance can provide additional insight into the nature of primate relationships. Furthermore, social tolerance has recently acquired a central role in hypotheses about the evolution of social learning, cooperation, prosociality and fairness in non-human primates and humans [van Schaik, 2003; Brosnan, 2006; Hare et al., 2007; Snowdon and Cronin, 2007; Cronin and Snowdon, 2008; Burkart et al., 2009; Cronin et al., 2010; Amici et al., 2012; Cronin, 2012; Burkart and van Schaik, 2013], so an understanding of variation in social tolerance within and between species promises to advance our understanding of these social phenomena as well.

However, interpreting comparative data on social tolerance is difficult given the plethora of approaches to measuring it (e.g. dyadic cofeeding or codrinking tests [Melis et al., 2006; Hare et al., 2007; Amici et al., 2012]; measures of food equity in a larger group setting [de Waal, 1986; Burkart and van Schaik, 2013; Cronin et al., 2014]; observation of social behaviour [Thierry et al., 2000; Thierry, 2007]). We are in need of a uniform research framework in which comparative data can be collected in order to advance our understanding of how relationships differ in social tolerance and whether these differences have been shaped by the evolutionary history of a species.

Two species that are of particular interest with respect to social tolerance are the members of the genus *Pan*. Both chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) share the position of our closest living relative, having diverged from each other approximately 2 million years ago [Bradley and Vigilant, 2002]; both species diverged from the lineage leading to humans between 4 and 8 million years ago [Hobolth et al., 2007; Langergraber et al., 2012]. However, the two species are described as very different in social behaviour and social cognition, despite their recent evolutionary split [Boesch et al., 2002; Herrmann et al., 2010; Hare et al., 2012; Rilling et al., 2012]. Specifically, the degree of social tolerance they express has recently been highlighted as a major difference between the two *Pan* species.

One body of data suggests that bonobos exhibit a degree of social tolerance that is high among primates in general, and specifically a degree of social tolerance greater than that expressed by chimpanzees. For example, Hare and Kwetuenda [2010] tested whether bonobos, alone in a room with food, would open a door to allow another bonobo to enter the room in which they were feeding. In effect, the authors measured the propensity of dyads to prefer close proximity to others in the presence of a valuable resource, food. The authors found that the majority of the 7 bonobos tested opened a door allowing a conspecific access to their room (and their food) more often than they opened a door to an empty room. Furthermore, the bonobos opened the door allowing conspecific access more quickly than they opened a door allowing themselves access to additional food. Given that they showed these behaviours consistently across trials and aggression was virtually absent, the authors concluded that the bonobos preferred to share their food and feed in the close proximity of others rather than feed alone [see also Tan and Hare, 2013]. Additional studies report that, in comparison to chimpanzees, bonobos more often enter into close proximity to group mates and cofeed when presented with a desirable, monopolizable food source [Hare et al., 2007; Wobber et al., 2010b]. Taken together, these findings suggest that adolescent and young adult bonobos exhibit greater social tolerance than

closely related chimpanzees, at least as defined around food and when measured in dyadic settings.

However, other studies that similarly measured behaviour around desirable food suggest that bonobos do not exhibit more social tolerance than chimpanzees and may in fact exhibit *less*. Bullinger et al. [2013] failed to replicate the finding reported by Hare and Kwetuenda [2010]. In contrast, these authors found that bonobos and chimpanzees alike preferred to open a door to allow another to join them more often when there was no food present than when there was food present, suggesting that the presence of desirable food actually decreased their motivation to be near conspecifics. In a different approach to studying tolerance, some studies have introduced monopolizable food into groups of bonobos and chimpanzees to study patterns of food transfers and the social behaviour exhibited in the presence of the desired food. De Waal [1992] introduced bundles of browse to groups of chimpanzees and bonobos and found that bonobos showed a higher proportion of non-tolerant transfers (i.e. stealing and obtaining food by force) compared to the chimpanzees. In a similar approach, Jaeggi et al. [2010] presented zoo-housed groups of chimpanzees and bonobos with a paper bag stuffed with preferred food and measured the amount of proximity and food sharing that followed. The authors found that in both species individuals in possession of the bag predominantly responded negatively when others approached, yet chimpanzees were more likely than bonobos to allow others to eat some of the food and to actively offer food to others. The authors also concluded that tolerance was precluded by despotism among bonobos, but not among chimpanzees. The finding that dominance impeded tolerance in bonobos was again found in a later study with a different group of bonobos [Stevens et al., 2015]. In a later comparative study using a similar approach but adding data from an additional group of bonobos, Jaeggi et al. [2013] reported that bonobos experienced higher levels of aggressive reactions to food requests and a lower success rate in obtaining food from the food possessors than did the chimpanzees. Furthermore, the authors suggested that bonobos experienced more stress in this situation, interpreting the increased grooming and other appeasement gestures shown by bonobos as a tension reduction mechanism. This 'stress' interpretation corresponds with hormonal data indicating that bonobos experience a stress response (change in salivary cortisol) when anticipating competition over food [Hohmann et al., 2009; Wobber et al., 2010a], an effect not found in chimpanzees [Wobber et al., 2010a].

Taken together, there are conflicting lines of evidence, and it is not clear whether bonobos show more social tolerance than chimpanzees. Therefore, we set out to measure the social tolerance of a group of bonobos and compare their behaviour to multiple groups of chimpanzees recently tested in the same paradigm [Cronin et al., 2014]. In this design, we deliver a desirable food resource (peanuts) into the social group such that the number of peanuts and the surface area that they cover is scaled by group size, and measure the proportion of the group that simultaneously occupies the resource zone as an indicator of social tolerance. As in the studies by de Waal [1992] and Jaeggi et al. [2010, 2013], this approach assesses tolerance in a group setting rather than in extracted dyads, therefore measuring tolerance in a typical social composition and providing the most accurate account of the social tolerance expressed within bonobo and chimpanzee societies [see also de Waal, 1986]. In contrast to the previous studies, however, this design also has the benefit of allowing for comparison of social tolerance across social groups of different sizes. Furthermore, measures of social tolerance ob-

**Table 1.** The study group, ranked according to age

ID	Sex	Origin	Birth	Parents	Age, years
Lina	F	San Diego Zoo	28/07/1985	Vernon × Loretta	27
Vifijo	M	Planckendael	23/07/1994	Kidogo II × Hortense	18
Djanao	F	Berlin Zoo	27/03/1995	Santi × Yala	17
Louisoko	M	Stuttgart Zoo	19/04/1998	Masikini × <i>Lina</i>	14
Lucuma	M	Stuttgart Zoo	29/10/2002	Kirembo × <i>Lina</i>	10
Busira	F	Wuppertal Zoo	16/02/2004	Birogu × Eja	8
Habari	M	Planckendael	29/01/2006	<i>Vifijo</i> × <i>Djanao</i>	6
Lingoye	F	Stuttgart Zoo	29/11/2007	Kirembo × <i>Lina</i>	5
Nayoki	F	Planckendael	24/03/2012	Unknown × <i>Djanao</i>	0

Individuals shown in italics indicate relatives that were present in the group.

tained in this design have been found to positively correlate measures obtained from two other approaches to studying tolerance in chimpanzees (one observational, one experimental), lending more validity to this approach [Cronin et al., 2014].

In the current study we further manipulated the social conflict in the experiment by first testing the bonobos on grass where the peanuts were more easily accessible, and then adding a second condition in which the peanuts were covered with leaf litter which required sustained time in the resource area in order to obtain the food. Following the Relational Model [de Waal, 1996, 2000], we sought to determine whether the bonobos responded to the increased potential for social conflict (from the grass to the leaf litter condition) with behavioural changes indicating tolerance, conflict avoidance or conflict escalation through aggression. Finally, we returned to the original condition (without leaf litter) to rule out that the observed differences between the first and second condition were due to learning, habituation or some other effect driven by the order of presentation.

## Methods

### *Study Site and Subjects*

The study took place at the Wild Animal Park Planckendael in Belgium in September and October of 2012. The subjects of this study were 8 bonobos (4 males, 4 females) from one social group (table 1). The one infant present in the group was excluded from analyses (aged 6 months, daughter of Djanao). The bonobos were housed as a single group day and night, except during 2 h in the morning, when they were separated during the cleaning of the enclosure. The experiment took place on their outdoor island (3,000 m<sup>2</sup>). In addition to the peanuts provided in this study, the bonobos were provided with 5 feedings per day that consisted mainly of fruit, vegetables and browse. Water was available *ad libitum* at all times, and on the island the bonobos had free access to edible plants and shrubs.

### *Procedure*

Sessions occurred between 9.00 and 11.00 h, and only 1 session was conducted per day. Before the bonobos were released outside from their indoor sleeping rooms, an experimenter familiar to the bonobos walked past the rooms and onto the outdoor island carrying and audibly shak-

ing a bucket of peanuts. Peanuts were selected because they are a highly preferred food of all bonobos in the group. Once on the outdoor island, the experimenter distributed 96 peanuts over a  $1.6 \times 1$  m area (hereafter 'the resource zone'). The quantity of peanuts was determined by multiplying the group size by 12 (excluding infants), and the surface area created a density of 60 nuts/m. These calculations were chosen to match a recent study of 4 chimpanzee groups [Cronin et al., 2014] in order to generate one measure of social tolerance that would be directly comparable between this group of bonobos and 4 groups of chimpanzees. Once the peanuts were distributed and the experimenter had left the island, the bonobos were released to the outdoor island and their behaviour was filmed for 10 min from an upper viewing deck. It was not feasible to track the behaviour of all bonobos on the island, so the video was centred on the resource zone.

The bonobos were tested in two conditions that differed in the amount of social conflict they produced. Specifically, we manipulated whether the peanuts could be easily removed from the plot and eaten elsewhere on the island where interindividual distances were greater. In the 'grass' condition, the peanuts were scattered on the short grass typically present on the island. In the 'leaf litter' condition, leaf litter was placed in the resource zone, and then the peanuts were scattered in the leaf litter. The conditions were presented in an ABA design (grass-1, leaf litter, grass-2) to account for order effects, and each condition presentation consisted of 5 sessions for a total of 15 sessions. All sessions were completed within 1 month.

#### *Data Collection*

From the video data we continuously coded for each individual whether they were within reach (1 m) of the resource zone, using the software Interact (Mangold International GmbH). This coding continued for 10 min, beginning when the bonobos were released from the indoor enclosure. The borders of the resource zone remained constant for coding regardless of the depletion of the peanuts over time.

During sessions, an experimenter naïve to the behavioural categories who had been trained on the institutional bonobo ethogram (based on original ethograms by de Waal [1988, 1992]) narrated all occurrences of behaviours. Later, using the video footage and narration, the experimenter coded behaviour using the Noldus Observer software (version 10.5). All behaviours occurring at least once in this study are listed in table 2. Behaviours occurring within 2 m of the edges of the resource zone were captured on video and thus coded; those that occurred elsewhere on the island were not captured for analysis.

#### *Data Analysis*

To quantify the amount of social tolerance bonobos demonstrated in this assay, we quantified the mean proportion of the group present in the 10 sessions of the grass condition (grass-1 and grass-2). Specifically, for comparison with the chimpanzee data, we calculated the proportion of the social group simultaneously present in the resource zone in 15-second scans for the first 2 min of each session, and averaged these values to obtain a single session value. The first 2 min were chosen because this was the time at which all peanuts were typically consumed when placed on the short grass; the grass condition was chosen to allow comparison with the chimpanzee assay which also took place on short grass [Cronin et al., 2014]. We also calculated the total duration in the plot for each subject in all conditions for the full 10 min from the continuous video recording.

To address whether bonobos demonstrated a level of social tolerance that differed from chimpanzees, species comparisons were made by a 1-way analysis of variance on social groups and a planned comparison contrasting the bonobo group to the 4 chimpanzee groups (Scheffé test, self-written R script). To address whether the time bonobos spent in the resource zone differed across conditions, we conducted a repeated measures ANOVA followed by paired sample t tests on the log-transformed durations that individuals spent in the plot across conditions, utilizing the full 10 min of continuous observational data.

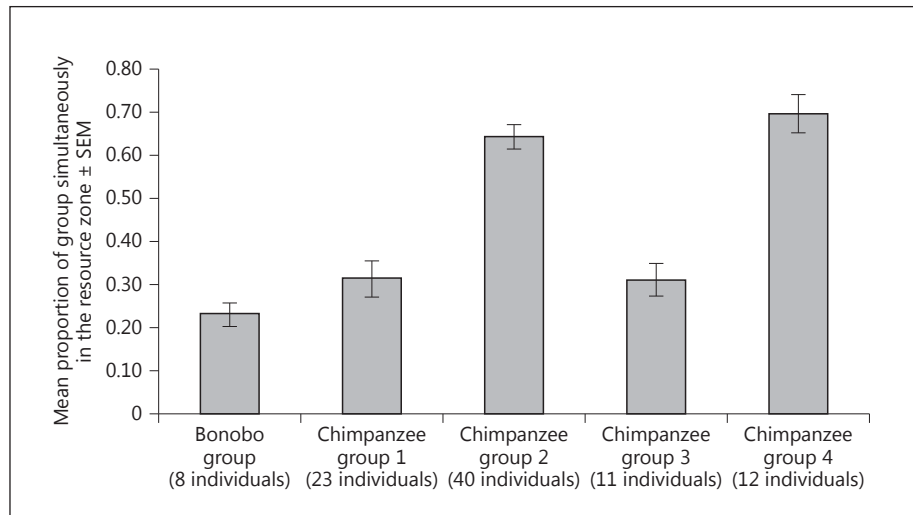
To determine whether the bonobos responded to the increase in social conflict with conflict avoidance, tolerance or conflict escalation, we attempted to classify the behaviours in the bonobo ethogram based on the categories described in the Relational Model. The classification is provided in table 2. Previous work has suggested that peering behaviour is indicative of tolerance if it is not

**Table 2.** Ethogram, showing only behaviours occurring in this study

<i>Tolerance</i>	
Peering	Subject stares into the face of receiver from a distance of less than 30 cm for at least 5 s
Affiliative touch	Subject touches the body of the receiver with hand or fingers in a relaxed and non-aggressive manner
Buddy walk	Subject walks next to receiver, has put an arm on the shoulder of receiver
Lateral embrace	Subject gently places one arm around receiver's shoulder, back or waist, or putting both arms around the other while pulling the other closer
<i>Conflict avoidance</i>	
Displacement	Subject approaches receiver and forces receiver to leave
Shielding	Subject positions himself between receiver and a food item, object or infant apparently desired by receiver
<i>Conflict escalation</i>	
Flee	Subject moves away from receiver after receiver has behaved aggressively towards subject
Aggressive intention	Sudden tense hand or body movements in the direction of another individual in a non-playful context, or hitting or kicking another individual without locomotion
Direct display	Tense running in the direction of, or parallel to, or closely passing by another individual usually while pushing an object, resulting in collision or other contact aggression
Charge	Subject shows tense running toward the receiver
Forced claim	Subject takes away food from receiver in a forced and aggressive manner with resistance or protest from the receiver
<i>Other</i>	
Gesture	Subject makes gestural movements with hand(s) towards a receiver without further specification, can include holding out hand, beckoning and similar
Grin	A silent retraction of the lips resulting in partial or complete exposure of the gums and teeth with the face directed to the partner, most often in a submissive context and/or accompanied with vocalization
Individual play	Subject performs play-like behaviour including locomotor play, or plays with objects or other items on his own, without interaction with others
Temper tantrum	Subject throws himself hysterically on the floor or platform, spinning around and screaming

followed by aggression [Vervaecke et al., 2000; Stevens et al., 2005]. We examined our data for whether peering events were followed by an aggressive reaction (within 1 min) and none was, so all were included in the tolerant behaviour category. Sociosexual behaviour, kissing or grooming [de Waal, 1992] were not observed in the resource zone in any of the trials. Each category of behaviour was analysed by a non-parametric Friedman's test given the non-normal distribution of the data and small sample size. One bonobo (Vifijo) never entered the area surrounding the resource zone captured on video and was therefore excluded from the behavioural analysis.

From the scan data we created a sociogram based on shared presence in the resource zone to enable visualization of the identity of individuals regularly occupying the resource zone together. The sociogram was created by calculating the simple ratio association index [Ginsberg and Young, 1992; Whitehead, 2008], and associations were counted only once per test session to



**Fig. 1.** Mean proportion of social group  $\pm$  SEM that was simultaneously present in the resource zone. The number of individuals (excluding infants) in each social group is shown in the parentheses on the x-axis. Each group was tested in between 8 and 11 sessions. Data shown here are for bonobos in grass-1 and grass-2 conditions, the conditions comparable to the chimpanzee experiment. Chimpanzee data from Cronin et al. [2014].

ensure independence of data (e.g. the sampling period was set to 1 day). The association indices were calculated using the program SOCPROG [Whitehead, 2009], and the networks were visualized using the program Gephi [Bastian et al., 2009].

Aside from the social network analyses, all analyses were conducted in R version 2.15.1 [R Core Team, 2013]; all tests were 2-tailed, and findings were considered significant at  $p < 0.05$ .

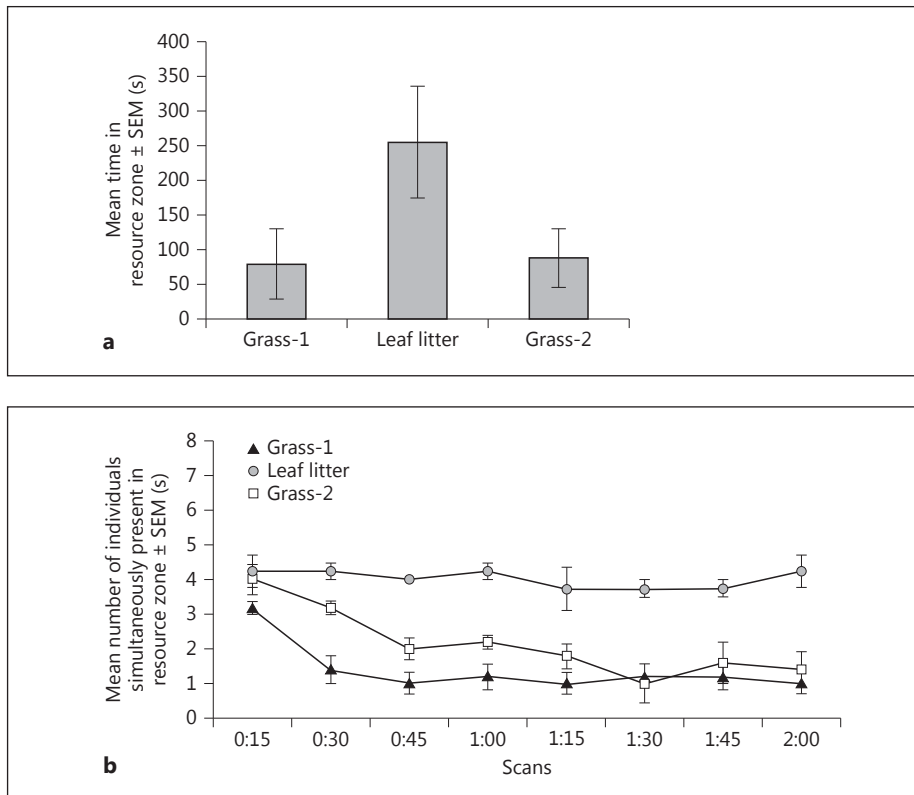
#### *Ethics Statement*

The research complied with the protocols approved by the Wild Animal Park Planckendael and adhered to the legal requirements of the country in which the research was conducted (Belgium). The study complies with all aspects of *Folia Primatologica's* Ethical Guidelines.

## **Results**

The bonobos were tested in all 15 sessions, but the fifth day of the leaf litter condition was omitted from the analyses because the bonobos retreated inside mid-session due to rain.

When considering all bonobo and chimpanzee groups tested in this paradigm, there was a significant difference between social groups in the proportion of the group that was simultaneously present in the resource zone (ANOVA:  $F = 34.12$ , d.f. = 4.42,  $p < 0.001$ ; fig. 1). For the bonobos, this analysis was limited to the 10 sessions of grass-1 and grass-2 to match the condition in which the chimpanzees were tested. Post hoc analyses using the Scheffé post hoc criterion for significance indicated a significant species difference; the average proportion of the group present in the resource zone



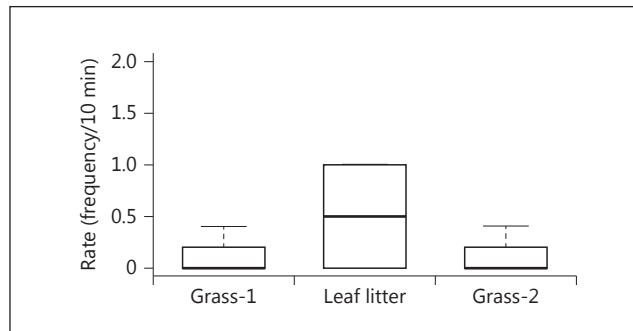
**Fig. 2. a** Mean time ± SEM that individuals spent in the resource zone across conditions. Data taken from continuous coding for 10 min. **b** Mean number of group members ± SEM simultaneously present in the resource zone across conditions as observed in scans taken at 15-second intervals.

was significantly lower for the bonobo group (mean ± SEM  $0.22 \pm 0.03$ ) than for the 4 chimpanzee groups considered together ( $0.47 \pm 0.03$ ,  $F = 41.71$ ,  $d.f. = 4.42$ ,  $p < 0.001$ ). Therefore, bonobos exhibited less social tolerance than chimpanzees by this measure.

The time that the bonobos spent inside the resource zone differed across conditions (ANOVA:  $F = 4.08$ ,  $d.f. = 2.14$ ,  $p = 0.04$ ; fig. 2a), with bonobos spending more time over the 10-min session in the resource zone during the leaf litter condition ( $254.7 \pm 80.2$  s) than grass-1 ( $79.2 \pm 50.8$  s,  $t = 2.67$ ,  $d.f. = 7$ ,  $p = 0.03$ ). Grass-1 and grass-2 did not differ significantly from each other ( $p > 0.05$ ). Figure 2b shows the number of individuals simultaneously present across conditions in the resource zone at each 15-second scan.

Results indicated bonobos spent more time in the plot during the leaf litter condition, as predicted. Thus, following the Relational Model, we sought to determine whether the bonobos responded to the increase in potential conflict between the grass and leaf litter conditions by demonstrating conflict avoidance, tolerance or conflict escalation. Friedman's tests on the behavioural categories of conflict avoidance and





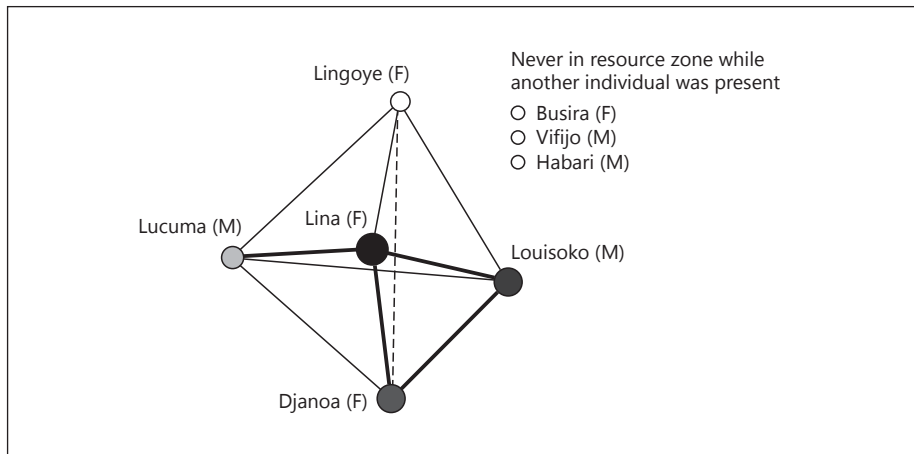
**Fig. 3.** Boxplot showing the median (dark line) and interquartile range (box) of conflict escalation behaviours demonstrated by bonobos in each condition.

tolerance revealed no significant differences across conditions (conflict avoidance:  $\chi^2 = 0.2$ , d.f. = 2,  $p = 0.90$ ; tolerance:  $\chi^2 = 3.0$ , d.f. = 2,  $p = 0.22$ ). However, Friedman's test on the category of conflict escalation did reveal significance ( $\chi^2 = 6.5$ , d.f. = 2,  $p = 0.04$ ; fig. 3). Statistically, follow-up pairwise comparisons were not possible due to the decreased effective sample size resulting from multiple ties of score zero. Descriptively, however, when comparing difference scores between grass-1 and leaf litter, 3 bonobos exhibited zero conflict escalation behaviours in both conditions, and the remaining 4 bonobos showed an increase in conflict escalation behaviours from grass-1 to leaf litter. When comparing difference scores between grass-1 and grass-2, 4 bonobos exhibited zero conflict escalation behaviours in both conditions, 1 showed an increase, and 2 showed a decrease. Given the significant Friedman's result for conflict escalation and consideration of the directional changes in behaviour, a tentative conclusion is that bonobos who entered the resource zone when the social conflict was heightened in the leaf litter condition tended to increase conflict escalation behaviours rather than conflict avoidant or tolerant behaviours.

Finally, in order to visualize which bonobos simultaneously occupied the resource zone, we calculated simple-ratio association indices based on the first 2 min of 15-second scan data, collapsing all conditions. The association indices are visualized in the sociogram shown in figure 4. Three of the 8 bonobos never entered the resource zone during this time. Five bonobos did enter the zone, and each was simultaneously present in the zone with every other individual at least once. In the following section we discuss the known rank and kin relationships between these individuals.

## Discussion

Social tolerance is a core aspect of primate social relationships, and the level of social tolerance demonstrated by bonobos has been a topic of recent debate. The resolution of this debate is important for gaining a deeper understanding of the nature of primate social relationships, and for advancing our understanding of the evolution of prosociality, cooperation and fairness. Here, we measured the social tolerance of a group of bonobos using an experimental design recently validated with chimpanzees.



**Fig. 4.** Sociogram of associations in the resource zone, all conditions collapsed. The circles (nodes) represent individuals, and the weight of the lines (edges) connecting the nodes represents the frequency with which the connected individuals were simultaneously in the resource zone. The size and darkness of the nodes represent the frequency with which those individuals spent time in the resource zone simultaneously with others.

We found that the bonobo group studied here exhibited lower social tolerance, measured as the proportion of the group that entered into close proximity to obtain a resource, than chimpanzees tested in the same paradigm.

The species difference that emerged in this study lends support to the claim that the social tolerance of bonobos is not notably high relative to chimpanzees [Jaeggi et al., 2010; Bullinger et al., 2013; Jaeggi et al., 2013]. The bonobos in this study generally avoided conspecifics in the presence of the desirable food when possible. Furthermore, chimpanzees who entered the resource zone tended to remain in the plot to consume the nuts [Cronin et al., 2014], whereas the bonobos quickly collected nuts and then dispersed from conspecifics to consume the nuts they had collected, spending less time in the resource zone even if they did choose to enter.

In the chimpanzee groups previously studied, the alpha male regularly occupied the centre of the resource zone, whereas in the current study the alpha female spent the most time in the zone. Thus, in both species the highest-ranking individuals exercised priority of access. In the chimpanzee study it was not possible to analyse how relationships predicted co-occupation of the resource zone due to limited visibility inhibiting individual identification of the chimpanzees in the zone, but in the present study we see the avoidance of conspecifics in the resource zone was especially apparent for the individuals that were not related to the alpha female (Lina). Her 3 offspring (Louisoko, Lucuma, Lingoye) as well as one other adult female (Djanoa) were also regularly present in the resource zone. The third female, an adolescent that moved into the group recently, and 1 adult and 1 adolescent male were never observed in the resource zone. This corresponds to observations of wild bonobos, where sons of high-ranking females benefit from maternal support in conflicts [Surbeck et al., 2011] and occupy central positions in feeding areas, while lower-ranking males roam in the pe-

riphery [Furuichi and Ihobe, 1994]. High-ranking females have been reported to monopolize desirable food in captivity and preferentially cofeed with other females, but these studies did not include adult male-mother dyads [Parish, 1994].

The behavioural results suggest that social tolerance was not the primary response of bonobos to an increase in social conflict. The time spent in the resource zone increased in the leaf litter condition, so the increase in potential conflict was successfully achieved, making it more difficult for the bonobos to retrieve nuts quickly and move elsewhere. While there was no significant change in tolerant behaviours across conditions, rates of conflict-escalating behaviours significantly differed when the potential social conflict was experimentally increased. Perhaps unsurprisingly, the most frequent conflict escalation behaviour in the high social conflict (leaf litter) condition was forced claim, a behaviour in which one individual takes peanuts from another in an aggressive manner met by resistance from the food possessor [sensu de Waal, 1992]. Furthermore, direct displays and aggressive charges, entirely absent from the grass-1 and grass-2 (low social conflict) conditions, were observed in the leaf litter condition. Although behavioural data are limited to the resource zone, these findings suggest that the bonobo relationships, at least in this group and this paradigm, are best described as conflict escalating rather than tolerant or conflict avoidant [de Waal, 1996].

Although care was taken to follow the methods used in the chimpanzee study, some unavoidable differences occurred due to practical constraints. Specifically, at Planckendael the peanuts were placed in the outdoor enclosure while the bonobos were inside, whereas at Chimfunshi the chimpanzees were present in the outdoor enclosure while the peanuts were delivered. De Waal [1992] reported, at least for 1 captive group of chimpanzees, aggression during feeding was lower when chimpanzees were aware that food was coming and had an opportunity to engage in touching, pant hooting and communication of status before the food was available (a 'celebration' period). In the current study, experimenters walked past the bonobos with the peanuts, and informal observation indicated that they were excited by the food and began increasing their social interactions prior to release. However, it is plausible that the lack of opportunity to engage in anticipatory social interactions near the resource zone increased the social tension in bonobos relative to chimpanzees and contributed to the species difference reported here.

Additionally, the bonobos comprise the smallest social group tested in this paradigm to date. It is possible that the challenge does not change linearly above or below some threshold, and the small space provided to the bonobos here required more tolerance than was required of any of the chimpanzee groups.

Therefore, research with additional bonobo groups of varying sizes and behavioural data collection that extends outside the resource zone and includes anticipatory behaviours prior to food distribution is planned to test whether this finding is replicable and generalizable across bonobo groups. Furthermore, we have left unexplored the variation in relationships present *within* groups. Bonobos have been shown to develop differentiated relationships [Stevens et al., 2015; see also Fraser et al., 2008], yet here we provide only a group-level test of the Relational Model. Therefore, it remains to be studied how bonobos of differing relationship qualities respond in situations that have the potential to produce social conflict, as predicted by the Relational Model [de Waal, 1996].

It is conspicuous that we did not observe sexual activity, grooming or kissing during the experiments in our group, in contrast to other groups [de Waal, 1992].

This may have been due to an age effect, as the individuals in the previous studies were younger than the animals in our group (average age in de Waal [1992]: 7 years; Hare et al. [2007]: 9.6 years; Hare and Kwetuenda [2010]: no ages provided; Tan and Hare [2013]: 6.9 years; this study: 13 years), and it has been shown that the rates of sociosexual behaviour decrease with age in captive bonobos [Stevens et al., 2008]. It is likely that tolerance, as measured in this study, is also influenced by age (note that in the study that failed to find high social tolerance in bonobos while replicating a previous design, the average age was 15 years [Bullinger et al., 2013]). Similarly, the bonobos' rearing history may also explain differences in tolerance between studies. Although Wobber and Hare [2011] did not find differences in cognitive performance between orphaned and mother-reared apes, Clay and de Waal [2013] suggested that mother-reared bonobos show better emotional regulation and social competence. It is possible that these behavioural differences extend towards food-related strategies, including mechanisms to avoid food competition. Therefore, it is noteworthy that all subjects in the present study have been mother-reared, while those in the food-sharing studies by Hare and colleagues were orphans [Hare and Kwetuenda, 2010; Tan and Hare, 2013]. Future studies should look into variation in tolerance in relation to the rearing history of the individuals.

Expanding to additional groups will also bring us closer to answering the pertinent question of whether there is a species-typical level of social tolerance at all. Thus far, intraspecific variation in social tolerance has been examined only rarely [Brosnan, 2006; Melis et al., 2006; Cronin et al., 2014]. However, the flexibility of primate social dynamics is becoming increasingly apparent, with social groups of the same species showing variation in mating systems, social spacing and hierarchical structure [Sapolsky, 2006; Henzi et al., 2013; Kappeler et al., 2013; Schradin, 2013]. Previous work on captive bonobo groups also warns against generalizations from data stemming from a single captive group, as groups were found to differ in expression of dominance relationships and social bonding [Stevens et al., 2008].

The bonobos' avoidance reaction seen here may have far-reaching implications; increasing interindividual distances in the presence of desirable food limits opportunities for social learning about food acquisition [van Schaik, 2003], prosocial behaviours that involve resource transfer [Cronin, 2012], and cooperative behaviours that necessitate simultaneous proximity to conspecifics and desirable resources [Cronin and Sánchez, 2012]. Although social learning, prosociality and cooperation may still be expressed in contexts lacking tangible, desirable resources (e.g. learning about predators, prosocially aiding in aggressive interactions, cooperating to defend territory), in contexts that stimulate conspecific avoidance as seen here, it is possible that opportunities for social learning, cooperation and prosociality may be more restricted in bonobos than in more socially tolerant species.

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