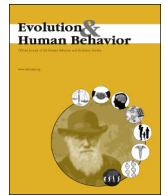




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Original Article

Population-level variability in the social climates of four chimpanzee societies

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ABSTRACT

Recent debates have questioned the extent to which culturally-transmitted norms drive behavioral variation in resource sharing across human populations. We shed new light on this discussion by examining the group-level variation in the social dynamics and resource sharing of chimpanzees, a species that is highly social and forms long-term community associations but differs from humans in the extent to which cultural norms are adopted and enforced. We rely on theory developed in primate socioecology to guide our investigation in four neighboring chimpanzee groups at a sanctuary in Zambia. We used a combination of experimental and observational approaches to assess the distribution of resource holding potential in each group. In the first assessment, we measured the proportion of the population that gathered in a resource-rich zone, in the second we assessed naturally occurring social spacing via social network analysis, and in the third we assessed the degree to which benefits were equally distributed within the group. We report significant, stable group-level variation across these multiple measures, indicating that group-level variation in resource sharing and social tolerance is not necessarily reliant upon human-like cultural norms.

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1. Introduction

Human societies vary in their patterns of social interactions. This variation has been documented both through longitudinal ethnographic studies of naturally occurring interactions and, more recently, through cross-sectional, multicultural investigations of fairness, cooperation and punishment in economic games. However, it is heavily debated whether behavioral differences across human populations emerge from shared cultural norms and internalized motivations (Gaechter, Herrmann, & Thoni, 2010; Henrich et al., 2001, 2010, 2012a, 2012b) or local variation in response to current environmental conditions (Gurven, Zanolini, & Schniter, 2008; Lamba & Mace, 2011, 2012; Nettle, Colléony, & Cockerill, 2011). We aim to bring a new perspective to this discussion by considering how differences in individual adaptive strategies can drive variation in social interactions within a group, relying on the predictive models developed in primate socioecology (e.g., Sterck, Watts, & Van Schaik, 1997; van Schaik, 1989; Wrangham, 1980). Specifically, we will examine group-level variation in the social tolerance of chimpanzees, a highly social, patrilocal species that diverged from the lineage leading to modern humans approximately 4–8 million years ago (Goodall, 1986; Langergraber et al., 2012; Nishida & Kawanaka, 1972; Patterson, Richter, Gnerre, Lander, & Reich, 2006), and a species that

differs from humans in the extent to which cultural norms are adopted and enforced.

Although chimpanzees do not demonstrate human-like cultural norms, chimpanzees do have typical ways of interacting that are reinforced through social interactions. For example, subordinates tend to display certain gestures when meeting a dominant individual and violations of this behavioral pattern can result in aggression (Goodall, 1986). However, chimpanzee “rules,” unlike human norms, are not agent-neutral. Subordinate chimpanzees failing to submit to the dominant might suffer from aggression from the dominant (the affected party), but not from other (unaffected) group members. Chimpanzees do not appear to punish the violations of third parties (Riedl, Jensen, Call, & Tomasello, 2012). Although some data suggest that chimpanzees may “police” others to minimize social conflict (Flack, Girvan, De Waal, & Krakauer, 2006; von Rohr et al., 2012), there is as of yet no evidence that rules by which chimpanzees police groupmates differ across groups reflecting group-specific norms.

The governance of chimpanzee behavior seems to differ from human norms in many respects. Human norms are rich in their social interpretation: Norms describe the ‘right’ way to do things, the way things ‘ought’ to be done, the way ‘we’ do things (Bruner, 1993). Already early in life, human children appear to spontaneously detect such norms in many behaviors (Rakoczy & Schmidt, 2012). Crucially, children will not only follow norms, but actively enforce them when observing someone performing an action “incorrectly,” often protesting using normative language about what people ought to be doing (Rakoczy, Warneken, & Tomasello, 2008). Although some studies

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report behavioral changes in chimpanzees' problem solving strategies that lead to a match with the predominant behavior in a group (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Whiten, Horner, & de Waal, 2005), chimpanzees do not show robust evidence of conformity as is evident early in human development and ubiquitous across human societies (Haun & Tomasello, 2011; van Leeuwen, Cronin, Schuette, Call, & Haun, 2013; van Leeuwen & Haun, 2013; von Rohr, Burkart, & van Schaik, 2011). Thus, by examining the magnitude of variation in patterns of social interactions across chimpanzee groups, we stand to gain some insight into the extent of population-level variation that may emerge from sources other than an extensive system of shared and enforced cultural norms.

Socioecological theory provides a framework for predicting how environmental factors generate variation in the quality of social relationships in a given primate society, with specific predictions about how cooperative and tolerant individuals will be toward one another (reviewed in Sterck et al., 1997). Although the model has evolved since its original proposal (reviewed in Thierry, 2008), one tenet that has remained unchanged and has influenced thinking in the field of animal behavior is that individuals will monopolize access to resources that improve their reproductive potential if possible. According to primate socioecological theory, the most valuable resource for females is food, whereas for males the most valuable resource is females (van Hooff & van Schaik, 1994; van Schaik, 1989; Wrangham, 1980). Generally speaking, the spatial distribution of food predicts the distribution and social relationships of females, and this in turn predicts the distribution and social relationships of males. When resources are dispersed, one or a few individuals cannot monopolize them, and the resource holding potential of most group members is nearly equal. In this situation, societies with weak or egalitarian dominance hierarchies are expected. However, when resources are clumped, competition for access leads to the formation of dominance hierarchies which predict individual tendencies to claim (or relinquish) resources (de Waal & Luttrell, 1989). The model predicts that the physical or strategic ability of high ranking individuals to monopolize access to resources will predict the amount of tolerance expressed toward groupmates, with individuals tolerating others or forming selective alliances if they cannot monopolize the resources on their own (Wrangham, 1980). This framework could prove useful to the current debate over the role of cultural norms in cross-cultural variation in human resource sharing as it delineates how individual strategies to maximize resource holding under various social and ecological conditions generate variation at the group level in resource sharing and tolerance for others.

We focus our investigation on patterns of social interactions across four groups of chimpanzees under similar environmental conditions at a sanctuary. Unlike most previous studies of group differences in chimpanzee behavior, we question whether chimpanzee groups differ in their style of interacting with groupmates instead of focusing on the presence or absence of a specific behavior (see also Sapolsky & Share, 2004). Specifically, we investigate whether the groups differ in multiple measures of social tolerance. Social tolerance has been defined as the propensity to be in proximity to conspecifics around valuable resources with little or no aggression (Cronin & Sánchez, 2012). In relation to socioecological theory, this concept is useful because it captures the variation in resource holding potential among individuals within groups. Furthermore, we focus on tolerance because it has become central to hypotheses on the evolution of cooperation, prosociality and fairness in non-human primates (Amici, Call, & Aureli, 2012; Brosnan, 2006; Burkart & van Schaik, 2013; Cronin, 2012; Cronin & Sánchez, 2012; Hare, Melis, Woods, Hastings, & Wrangham, 2007), and much of the recent debate on the source of human variation in behavior has centered around explaining variation in human decision making in these same domains (e.g., Henrich et al., 2004; Lamba & Mace, 2011; Nettle et al., 2011).

We measure social tolerance in situations in which valuable resources are present that have the possibility to elicit competition

and aggression. In the first assessment, we provide a desirable food resource to each social group and quantify the extent to which the resource holding potential is distributed among group members by quantifying the proportion the social group simultaneously present in the resource zone. In the second assessment, we observe how individuals spatially organize themselves in their large enclosures where food and potential mates are naturally distributed without experimental manipulation, providing another measure of the degree to which individuals in each group tolerate the close physical presence of conspecifics. Both nearing a limited resource in the presence of others and spatial cohesion have been previously employed as measures of social tolerance for inter- and intraspecific comparisons (de Waal & Luttrell, 1989). In the final assessment, we repeatedly provide a single, monopolizable food item to the group and measure the degree to which the distribution of resources differs from an equal distribution (see also Burkart & van Schaik, 2013).

Admittedly, the behaviors we investigate across chimpanzee groups here differ in many ways from the behaviors measured in cross-cultural studies of human behavior. Studies of human variation in resource sharing commonly rely on economic games such as the dictator game, ultimatum game, or public goods game conducted in dyads or small, arranged groups (e.g. Henrich et al., 2001, 2010), whereas here we rely more heavily on the simultaneous behavior of entire groups and incorporate observational approaches rather than relying on controlled experiments only. Reliance on naturalistic observation in addition to economic games should increase the validity of the findings (e.g., Gurven & Winking, 2008; Wiessner, 2009), and the naturalistic approach is not entirely incompatible with recent studies of human variation in resource sharing. For example, Lamba and Mace (2011) quantified how community members allocated salt in a natural setting to measure sources of variation in cooperation, and Nettle (2012) recently demonstrated group-level variation in cooperation through purely observational studies of social interactions occurring in different neighborhoods. Therefore, it is our hope that these findings have comparative value when considered alongside data emerging from the human literature.

Taken together, these measures provide a holistic view of social tolerance at a unique location where multiple stable social groups of semi-wild chimpanzees live in one continuous stretch of woodland forest. We assess tolerance at the level of the social group in order to contribute to an understanding of how different societies of the same species may vary in the absence of human-like cultural norms. We combine controlled, experimental testing with naturalistic observations of chimpanzees in order to gauge social tolerance in more than one context. These data provide the first characterization of the variation in social tolerance expressed across multiple chimpanzee groups and succinctly demonstrate the existence of meaningful, group-level variation in chimpanzee social climates in the absence of human-like cultural norms.

2. Methods

2.1. Study site and subjects

The study took place at Chimfunshi Wildlife Orphanage Trust in Zambia. Chimpanzee social groups were originally comprised of juveniles orphaned by hunting or the pet trade, and increased in size due to breeding in the groups. Each social group now comprises a mix of wild-born and sanctuary-born individuals, and the only additions to the groups for more than 5 years have been due to births. The chimpanzees remain outside overnight and during the day except for 2 hours mid-day when the majority of chimpanzees voluntarily enter a building attached to each enclosure for feeding. At the start of the study, the population sizes of Groups 1, 2, 3 and 4 were 23, 42, 13, and 13 individuals, respectively. The composition of the groups (age, sex, origin) and enclosure sizes are presented in Table 1.

This research was approved by the local ethics committee of the host sanctuary (the Chimfunshi Research Advisory Board) and the Max Planck Society. This research strictly adhered to the legal requirements of the country in which it was conducted (Zambia) and the American Society of Primatologists and the International Primatological Society's Principles for the Ethical Treatment of Nonhuman Primates.

2.2. The peanut swing experiment

In order to assess social tolerance, we provided the entire social group with a desirable food (peanuts) and measured the propensity of each group to be near conspecifics in the presence of this resource, or the extent to which the resource holding potential is distributed among group members. To ensure that the measures were comparable across groups of different sizes, we created a situation such that the quantity of peanuts and surface area that the peanuts covered scaled relative to the size of the group. Specifically, the number of peanuts delivered to each group was determined by multiplying the group size by 12 (excluding chimpanzees younger than 3 years, and one adult male in group 4 who was housed inside as an injury healed) and the surface area covered by the nuts was closely approximated to 60 nuts per square meter. The key measurement was the proportion of the social group that simultaneously entered within reach of the nuts.

Before the peanuts were delivered into the group, the chimpanzee caretakers and researchers called the entire group of chimpanzees to the area using words and intonation familiar to the chimpanzees to indicate feeding. The researchers did not deliver the peanuts until all members of the group were visible. The peanuts were packed into large pieces of bamboo cut in half lengthwise and attached with short ropes to bamboo poles. After the peanuts were packed into the bamboo at 60 nuts per meter, researchers lifted the “peanut swing” up and over the fence using the bamboo poles (Fig. 1a), and allowed the packed bamboo to swing downward off pole extensions to drop the peanuts into the enclosure. The peanuts scattered approximately 1 meter wide along the predetermined length upon falling into the enclosure.

The procedure was repeated between 8 and 11 times per group in June 2011 between 0800 and 1115 or 1400 and 1800 hours, with a near equal number of sessions occurring in the morning and afternoon in each group. Depending on the size of the group, two or three video cameras were used per session, providing one video recording from a heightened vantage point (viewing deck or ladder) and one to two videos recording from the ground. From video, we coded the number of individuals simultaneously present within 1 meter of the peanuts at 15-second intervals for the first 2 minutes after the peanuts dropped (Fig. 1b). Nearly all peanuts were eaten within the first 2 minutes. We chose 1 meter as a reasonable distance from which the chimpanzees could sit/stand and potentially still reach peanuts, referred to below as the “peanut zone.” We excluded chimpanzees younger than 3 years of age from this assessment (as they were often on their mothers, and were not included in the calculation of the number of nuts to deliver to the group).

All scans for one session were averaged to obtain a single measure per session of the number of individuals present. To facilitate



Fig. 1. The peanut swing experiment. (a) Still image from video showing researchers preparing to deliver peanuts to the social group via peanut-filled bamboo troughs. The length of the bamboo trough and number of nuts it contains scaled linearly with group size. (b) Still image from video immediately after the peanuts were delivered to the group. The proportion of the group that enters within reach of the peanuts is scored from video taken from in front of the group (as shown here) and from above (as shown in panel (a)). These images show Group 2.

comparisons across groups of different sizes, we divided the number present in the zone by the total group size to determine the proportion of the group that was present in the peanut zone. A second observer independently coded 25% of the sessions, and interobserver reliability for mean proportion present during the session was high ($N = 10$, Spearman $r^2 = 0.950$, $P < 0.001$).

2.3. Social spacing

We then proceeded to investigate whether the differences observed in the peanut swing experiment reflected differences in the social spacing expressed by the chimpanzees when they were freely interacting in their outdoor enclosures where resources are naturally distributed. Therefore, we created social networks based on observed proximity for two chimpanzee groups. Social network analyses are not yet well-developed for comparing across groups of different sizes (Pinter-Wollman et al., 2013) but are a powerful way to compare social dynamics of groups of similar sizes (Whitehead, 2008). We chose to focus this investigation on Group 3 and Group 4 because they are closely matched for population size, age structure, sex ratio, origin (proportion wild-born), intragroup relatedness, and enclosure size (Table 1).

At Chimfunshi, every day a trained staff member conducted a series of 10-minute focal follows for 1 hour on each group. Observations took place outside of the mid-day feeding time, between either 8.30 and 11.00 or 14.30 and 17.00, with a near equal number of morning and afternoon follows. Focal subjects were selected through systematic, randomized sampling of the chimpanzees' enclosure as seen from the fence (van Leeuwen, Cronin, Haun, Mundry, & Bodamer, 2012). Videos were coded in Nijmegen, the Netherlands using the software INTERACT (Mangold International GmbH). Prior to coding

Table 1

Composition of the four groups at the start of the study (April 2011).

	Group 1	Group 2	Group 3	Group 4
Adults	14 (6/8)	20 (3/17)	9 (4/5)	10 (5/5)
Juveniles	9 (6/3)	20 (9/11)	2 (1/1)	2 (2/0)
Infants	0	2 (0/2)	2 (1/1)	1 (1/0)
Total group size	23 (12/11)	42 (12/30)	13 (6/7)	13 (8/5)
Wild-born individuals	8 (4/4)	15 (3/12)	9 (4/5)	9 (5/4)

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).

these videos, all members of the coding team demonstrated “high” interobserver reliability with a lead coder (Cohen’s kappa ≥ 0.85).

To address whether the groups differed in their propensity to be in proximity to conspecifics, we created weighted social networks based on two types of information: (a) frequency of 1-meter proximity to conspecifics (non-directional) and (b) frequency of approaching to within 1 meter of conspecifics (directional). We chose 1 meter as a meaningful distance as this is about the length of a chimpanzee arm, and being within 1 meter indicates that an individual could be physically contacted by another. The proximity and approach metrics are not independent and thus are assessed separately, but when considered together provide a more comprehensive overview of the propensity to be near others, and who within the social groups is responsible for creating the proximity.

We created social networks utilizing 6 months of focal follow data, creating a time window around the peanut swing data collection (peanut swing June 2011; observational data April through September 2011). The average number of focal follows per chimpanzee was 15.85 (range 1 to 40). Associations were scored dyadically, thus information accumulated on chimpanzees who were not currently the focal subject as well if they associated with the focal. The data set consisted of 271 focal follows on Group 3 and 317 focal follows on Group 4, for a total of 98 hours of observation. We used 1/0 sampling per dyad per day to achieve maximum independence of the data (Whitehead, 2008); thus if two individuals were observed associating once or more on the same day they received a “1,” otherwise that dyad was scored as “0.” The total number of associations scored per individual ranged from 13 to 94.

To create the proximity and approach networks, we extracted twice-weight association indices (Whitehead, 2008). The twice-weight index was chosen as it is the least biased when there is an increased possibility of observing individuals who were associated over those alone (Cairns & Schwager, 1987; Wakefield, 2013).

The twice-weight association index (AI) is calculated as:

$$x / (x + 2y_{AB} + y_A + y_B)$$

where x = the number of sampling periods (days) in which individual A and individual B were associated, y_A = the number of sampling periods in which only A was identified, and y_B = the number of sampling periods in which only B was identified, and y_{AB} = the number of sampling periods in which both A and B were identified but not associated with each other. “Identified” in the above definitions refers to an individual being captured on video that day, either as a focal subject or as present in the subgroup of another focal subject.

The resulting social networks are presented as sociograms with individuals represented as nodes and the weight of the lines (edges) between nodes determined by the value of the dyadic AI. The nodes are positioned such that nodes with stronger association indices are closer on the graph but the graph conforms to a frame with uniform edge lengths (based on the Fruchterman Reingold algorithm; Cohen, 1988). In addition to presenting the graphs visually, we chose to calculate network measures that best reflect spatial cohesion. We used a two-sample permutation test to compare the median AI of the two groups (Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007). We also report the mean AI, social differentiation, mean clustering coefficient, and modularity for each group. Calculations were performed in SOCPROG (Whitehead, 2009), aside from the permutation test which was conducted in R using the package “coin” (R Core Team, 2013). Networks were visualized using Gephi (Bastian, Heymann, & Jacomy, 2009).

Conceptually, the mean AI and social differentiation provide an indication of the strength of associations in the group and how uniform the strength of associations is across dyads, respectively. Social differentiation has been proven useful for comparing networks within and between species (Wakefield, 2013; Whitehead, 2008), and is an estimate of the coefficient of variation of the true association indices (Whitehead, 2008). Groups could have equivalent mean

association indices but different social differentiation scores; the group with the greater social differentiation value would have more varied (strong and weak) connections whereas the group with the lower social differentiation score would have association indices generally similar to the mean value. In relation to social tolerance, the group with the higher AI and lower social differentiation would likely represent a case where social space near conspecifics was more uniformly accessed, rather than a case where social access was specific to certain dyadic combinations. Presumably, the former case would also indicate that individuals could maintain proximity to nearly any other individual in the group with a low risk of aggression (otherwise proximity would be avoided). The mean clustering coefficient is a measure of how well the associates of one individual are themselves associated (Flack et al., 2006; Sueur, Jacobs, Amblard, Petit, & King, 2011; Whitehead, 2008), while modularity provides an indication of group fragmentation that is useful for comparing across social groups (Voelkl & Kasper, 2009). High modularity would suggest that the group could be divided into subgroups without breaking as many strong associations as groups with lower modularity scores. In other words, lower modularity suggests more group cohesion. Therefore, in relation to social tolerance, the final two measures provide a slightly different view into whether specific subgroups are tolerating the close proximity of others or whether tolerance for close proximity is more equally distributed throughout the group and relatively independent of potential subgroups. Additional information on network calculations is provided in the Electronic Supplementary Material (available on the journal’s Web site at www.ehbonline.org).

In order to create the social networks based on approaches, we again used 1/0 sampling per dyad per day (taking into account the direction of approach) to achieve maximum independence of the data. For this directional, weighted network we assessed the mean weighted in-degree per group. The in-degree is calculated as the number of times that an individual was approached, standardized by the number of follows on that social group. This provides an indication of the tendency of individuals to move into the social space of specific other group members (Whitehead, 2008). Because of the dominant role of alpha males in chimpanzee societies, we additionally report the weighted in-degree per alpha male.

2.4. The equity test

Finally, we administered an additional test of social tolerance that has been previously applied across species that measures the equity of the distribution of benefits within a group, or the degree to which resource holding potential is distributed among group members (Burkart & van Schaik, 2013). In this experiment, once the entire social group was visible, an experimenter repeatedly tossed one peanut into the enclosure in a pre-determined, unvarying location and recorded who in the social group obtained the food. The test was conducted over 4 days in 1 week in June 2012 in each group. The data collected on the first day were not analyzed as the initial session was intended to familiarize the chimpanzees with the procedure. Given the variation in group size, we attempted to standardize the test across groups by analyzing the distribution of food in the group on each day up to the point that the number of peanuts tossed into the group equalled the group size. The evenness of the resulting food distribution is calculated using Pielou’s measure of J' (Pielou, 1977) which is H'/H'_{\max} where H' is the Shannon diversity index and H'_{\max} is the maximum value possible for H' (Shannon, 1948). The resulting J' value can vary between 0 (completely uneven distribution) and 1 (completely even distribution). We choose to include this test of tolerance to provide a basis for comparison with previous reports using this index across species (Burkart & van Schaik, 2013). We interpret results across groups of different sizes with caution as different group sizes can lead to different levels of satiation by monopolizing individuals and focus primarily on the two social groups matched for group size (Groups 3 and 4), but

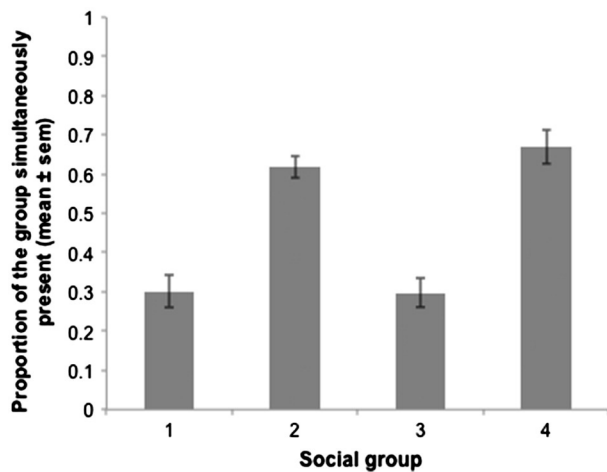


Fig. 2. Proportion of the social group simultaneously gathering in the peanut zone. Groups 1 and 3 differ significantly from Groups 2 and 4.

present all findings. Data from all experiments are available from the corresponding author upon request.

3. Results

3.1. The peanut swing experiment

The four social groups differed significantly in the proportion of the group present in the peanut zone (ANOVA $F_{3,33} = 27.3, P < 0.01$, Fig. 2). Post hoc comparisons using the Tukey HSD test indicated that the proportion of the social group gathered in the peanut zone in Groups 2 and 4 was significantly greater than in Groups 1 and 3 (both $P < 0.001$), however Group 2 did not differ from Group 4 ($P = 0.765$) and Group 1 did not differ from Group 3 ($P = 1.00$; mean \pm s.e.m. Group 1: 0.300 ± 0.040 ; Group 2: 0.618 ± 0.028 ; Group 3: 0.297 ± 0.036 ; Group 4: $0.669 \pm 0.043, P < 0.01$).

3.2. Social spacing

The proximity-based networks for Group 3 and Group 4 are shown in Fig. 3. The network measures calculated for these networks are provided in Table 2. The result of the permutation test comparing the association indices for Group 3 and Group 4 indicated that the group medians were significantly different from each other (difference in medians = 0.015, 95% CI for difference: $[-0.03, -0.01], P = 0.037$).

The approach-based directional networks for Group 3 and Group 4 are shown in Fig. 4. The mean weighted in-degree \pm s.e.m. was 0.050 ± 0.009 for Group 3 and 0.116 ± 0.006 for Group 4. The alpha male of Group 3 (sam) and Group 4 (com) had weighted in-degree values of 0.037 and 0.129, respectively. Thus, the alpha male in Group 4 was approached more than average in his group, whereas the alpha male in Group 3 experienced fewer approaches than his group average (Fig. 4a and b).

3.3. The equity test

The highest J' score was obtained by Group 4 and the lowest J' score was obtained by Group 3, the two groups that were matched for population size. The resulting J' measures for Group 1 through 4 were 0.36, 0.21, 0.04 and 0.45, respectively. For comparison with between-species assessments, note that in a group of 10 Japanese macaques $J' = 0.17$, in a group of 7 capuchin monkeys $J' = 0.66$, and in a group of 7 common marmosets $J' = 0.74$ (Burkart & van Schaik, 2013; Fig. 5).

4. Discussion

Interpretation of the patterns of data emerging from human cross-cultural studies can be aided by the integration of data drawn from other species (Nettle, 2009). Here we measure variation in social tolerance across chimpanzee groups and find significant differences in the patterns of social tolerance. We propose that population-level variation among the chimpanzees may be best understood by individual variation in adaptive strategies to maximize benefits in a given social or ecological setting. This individual variation generates variation in the tolerance of dyadic relationships and ultimately impacts the social dynamics at the level of the group (see also Hinde, 1976; Wrangham, 1980). Furthermore, we demonstrate with these data that stable, population-level variation in tolerance and equity can emerge independent of an extensive human-like system of shared and enforced cultural norms.

We first consider the response of the four groups to the two experimental assessments of tolerance. In response to the peanut swing experiment, two groups (Group 2 and Group 4) regularly joined others in close space more so than two other groups (Group 1 and Group 3). Assuming motivation to access the food was equivalent across individuals, it appeared that Group 1 and Group 3 contained individuals (or alliances of individuals) who were capable of excluding others from the resource whereas this was less true of Group 2 and Group 4. Groups tended to respond in nearly the same way each time they were tested, with approximately the same

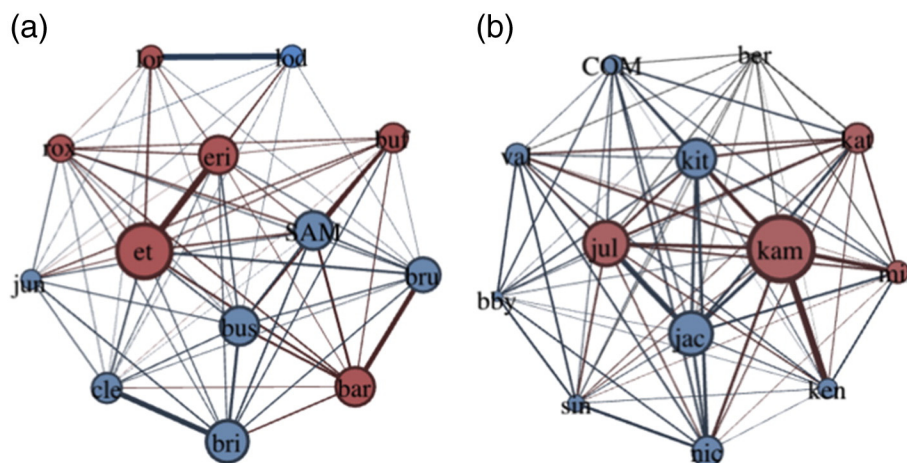


Fig. 3. Undirected social network of proximity for Group 3 (a) and Group 4 (b). A node represents each individual, and the lines (edges) between nodes are weighted by the strength of their association index as calculated based on proximity. Edge weights are comparable across groups; edge weights < 1.5 not shown for either group to improve clarity. Nodes are sized based on their weighted degree (see ESM). Alpha males are in capital letters. In the online color version, nodes representing males are blue and nodes representing females are red.

Table 2
Proximity-based social network measures.

Social network measure	Group 3	Group 4
Mean association index	0.056	0.070
Social differentiation (\pm s.e.m.)	0.76 (\pm 0.11)	0.57 (\pm 0.06)
Mean clustering coefficient (\pm s.e.m.)	0.21 (\pm 0.02)	0.28 (\pm 0.04)
Modularity	0.23	0.13

number of individuals entering the resource zone each test day. Although the test was designed to allow for comparison across groups of different sizes, it should be noted that in the larger groups there is more absolute space within the peanut zone and therefore it is possible for one chimpanzee to be in the resource zone but remain at a further distance from a specific other individual (e.g. the alpha male). However, the pattern of response, with one large group and one small group exhibiting high and low tolerance, respectively, suggests that even the greater space provided to the larger groups was still limiting enough that individuals tended to avoid the resource zone in low tolerance groups. Additionally, the distribution of equity test that has been used previously as a proxy for social tolerance across species (Burkart & van Schaik, 2013) indicated that the two groups that were matched for group size and demonstrated low and high tolerance in the peanut swing assessment also showed a corresponding difference in the equity test. Group 4 exhibited the highest equity and Group 3 the lowest, again demonstrating that the monopolization of resources by a few individuals occurred more in Group 3 than Group 4. To put this variation in context, Group 3 scored lower than the measure available for one group of Japanese macaques, classically considered to be low in social tolerance (Thierry, 2007, 2013) while Group 4 scored closer to the measure available for one group of capuchin monkeys than to the chimpanzees of Group 3 (Burkart & van Schaik, 2013). Although statistical consideration of whether these measures are similar to or different from each other is not possible, these data suggest considerable variation in “equity” across groups of the same species that seems to emerge from differential degrees of resource monopolization by the highest ranked individuals.

The propensity to tolerate conspecifics was also assessed via observation of social spacing as it naturally occurred in the large forested enclosures of the chimpanzees. In this assessment, resources such as food and potential mates were distributed naturally rather than experimentally, and the tendency of groups to form cohesive units was assessed. We conducted social network analyses on two

groups with comparable population size, demographics, origin and enclosure size. The sociograms and network measures for Groups 3 and 4 indicated that Group 4 was more socially cohesive, and that most individuals in that group frequently associated with most other individuals. In contrast, Group 3 was more dispersed, and spatial relationships were more heterogeneous with certain dyads exhibiting strong associations and others weak associations, indicating greater social cohesion and therefore greater social tolerance in Group 4 than Group 3 (de Waal & Luttrell, 1989). The difference in social cohesion can be interpreted from the significant difference in association index combined with the large difference in the groups' social differentiation measures, and this was observed regardless of the groups' close match in terms of age structure and kinship ties. The clustering coefficient was greater for Group 4 and the modularity was greater for Group 3, which is consistent with the overall impression of Group 3 being less integrated and unified than Group 4. These findings again support the interpretation that individuals in Group 3 tend to be less tolerant and more avoidant of conspecifics than those in Group 4.

The directional networks derived from the approach data complement this group difference, and demonstrate that in Group 4, nearly every individual approaches nearly every other individual with some regularity while the ability or willingness to approach any other individual appears to be more restricted in Group 3. The Group 4 sociogram in Fig. 4b shows thicker arrows, indicating that approaches happen more frequently in Group 4 than in Group 3. This can be assumed from the proximity network (given that to be in proximity one must have approached at some time), but additional social information is gained by noting that Group 4 has more bidirectional arrows. This indicates that proximity is more likely to be initiated by either individual in the dyad in Group 4 in comparison to Group 3 where approaches are more unidirectional. Group 4 relationships therefore appear to be more symmetrical than in Group 3, potentially reflecting a steeper underlying dominance hierarchy in Group 3 (Thierry, 2013).

This finding is consistent with the interpretation that some individuals in Group 3 may have more resource holding potential than individuals in Group 4, and consequently are able to exclude others from proximity to resources in the environment. This pattern is especially apparent when considering the approaches toward the alpha male in each group (or their “in-degree”); the alpha male of Group 4 (com), is approached by many in the group whereas the alpha male of Group 3 (sam) is not. Within a primate group, the individual in the alpha position is expected to have the most

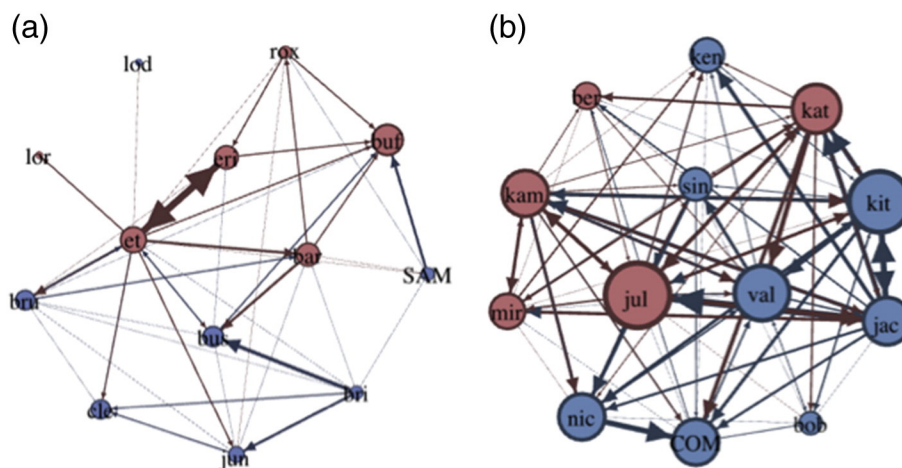


Fig. 4. Directed social network of approaches for Group 3 (a) and Group 4 (b). A node represents each individual, and the lines (edges) between nodes are weighted by the strength of their association index as calculated based on frequency of approaching. Edge weights are comparable across groups, with a minimum edge weight filter of 1.5 applied to both groups to improve clarity. Nodes are sized based on their weighted in-degree (see ESM). Alpha males are in capital letters. In the online color version, nodes representing males are blue and nodes representing females are red.

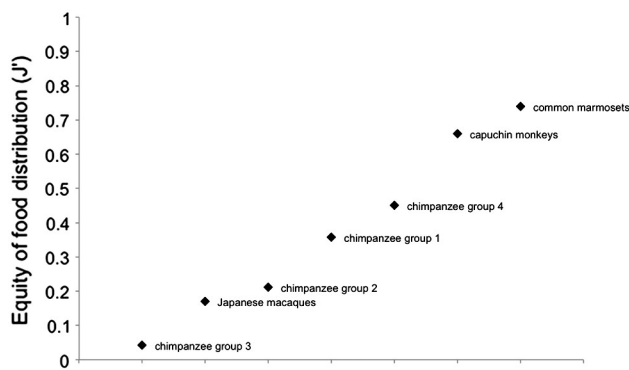


Fig. 5. The equity test. The J' value on the y-axis represents the evenness of the food distribution. Data for Japanese macaques, common marmosets and capuchin monkeys extracted from Burkart and van Schaik (2013).

undisputed access to resources (de Waal & Luttrell, 1989). Here we see that although this hierarchy position has the most access in the group (evidenced in both experimental assessments), the degree to which they exclude others from resources can vary. This variation in resource holding potential may be due to differences in their physical capacity to exclude others, the degree to which they allow resource access to others to foster bonds or reciprocate with potential allies, and/or individual differences in temperament.

There are multiple potential sources of group-level variation in mammalian social behavior that do not rely on shared, enforced norms; among those studying animal behavior the three often-cited sources are population-level genetics, social learning, and environmental determinants (e.g., Langergraber et al., 2011). These four chimpanzee groups do not systematically differ in their genetic backgrounds (van Leeuwen et al., 2012), at least in the sense that the groups were originally formed by orphans as they entered the sanctuary and not grouped by subspecies or geographic origin. Although the social learning of styles of interaction has been documented (de Waal, 1996; de Waal & Johanowicz, 1993; Sapolsky, 2006a, 2006b; Sapolsky & Share, 2004), at this time, we do not have longitudinal data to suggest that the social styles of these chimpanzee groups persist across generations. Finally, at Chimfunshi, the four groups live in one continuous stretch of forest and the probability that food availability, predation risk, or other environmental factors generated these differences is very low.

Therefore, given current data, it seems likely that the group differences emerged, at least in part, from differences in the tendency of key individuals in each group to be willing or able to monopolize resources. These influential individuals were likely maximizing their own fitness potential given a suite of constraints (fighting potential, need for allies, individual temperament), which may have contributed to different social contexts for the rest of the individuals in the group in which a propensity to approach conspecifics was more or less beneficial (see also Bergman, 2006). Among chimpanzee societies, the behavioral style of alpha males can differ dramatically (Foster et al., 2009; Sapolsky, 2000), and here it seems that these styles may have the potential to influence the social climate of the larger group. In the experimental assessment of tolerance, the alpha male of each group regularly centered himself in the peanut zone before the peanuts fell, and his presence probably had downstream effects on the spatial choices of the rest of the group. In the equity test, the alpha male of Group 3 monopolized 98% of the rewards, whereas in Group 4 the alpha male also obtained more rewards than any other individual but more than 50% of the rewards were freely obtained by the next three highest earners in the group. Likewise, the approach networks of Group 3 and 4, we see that group members in Group 3 avoided proximity with the alpha male but that this was not the case in Group 4. Certainly other individuals can also have permeating effects within

the social groups, but focusing on the alpha male serves to highlight how key individuals with different resource holding potential may change the local social environment and influence group-level tolerance in the absence of human-like social norms.

In summary, we demonstrate that intraspecific variation in social interactional styles can emerge at group levels in a primate species that is closely related to our own but lacks conformity to and enforcement of social norms to the extent seen in our own species. With the combination of observational and experimental assessments of social tolerance, and insights drawn from socioecological theory, we have demonstrated that population-level differences in fairness seem to result from the permeating effects of individual adaptive strategies geared toward maximizing one's own resources. We suggest that future investigations of human cross-cultural variation consider taking into account the possibility that group-level differences may emerge from individual differences in the adaptive strategies of influential individuals maximizing their own resource access instead of, or in addition to, social norms.

Supplementary Materials

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2014.05.004>.

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