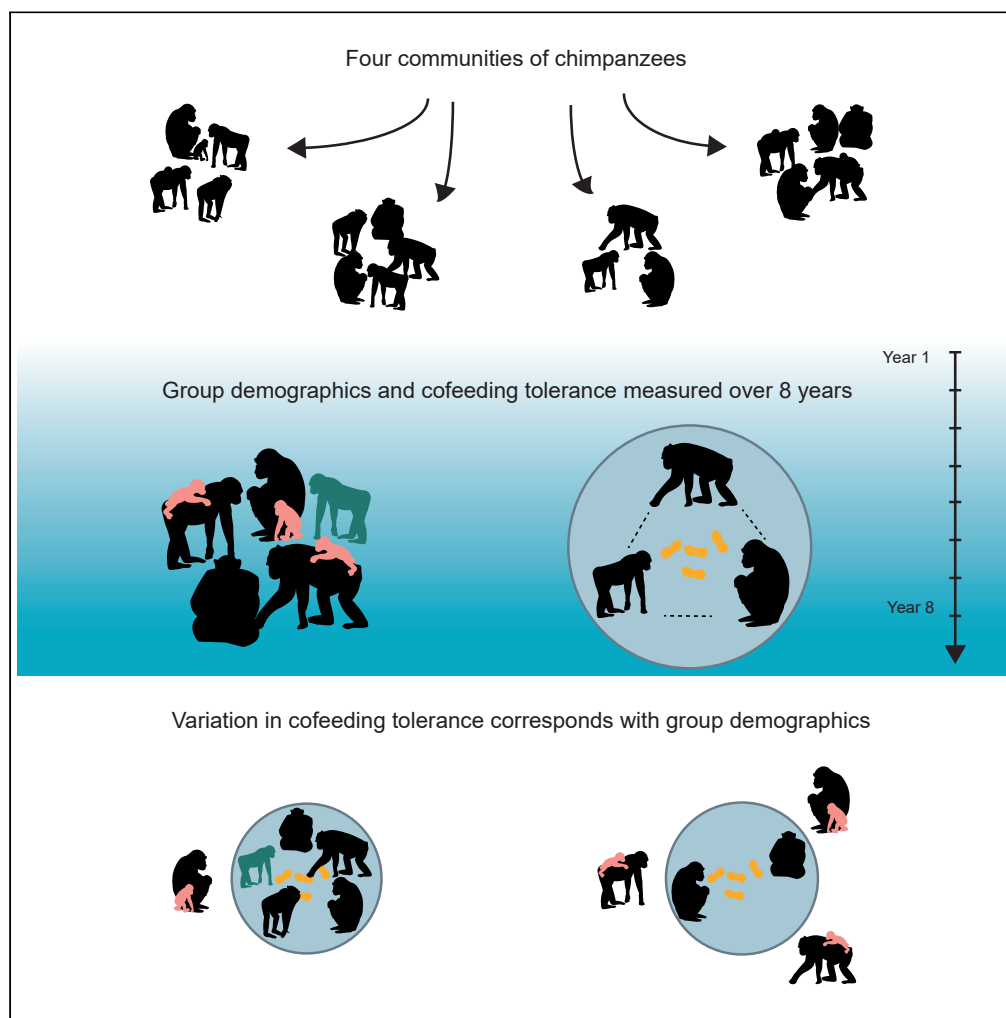


Article

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HIGHLIGHTS

Four groups of chimpanzees showed large variation in their cofeeding tolerance

Cross-sectional and longitudinal variation could largely be explained by demographics

Mothers with infants were associated with lower cofeeding tolerance

Young females were associated with higher cofeeding tolerance

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Article

Cofeeding tolerance in chimpanzees depends on group composition: A longitudinal study across four communities

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SUMMARY

Social tolerance is generally treated as a stable, species-specific characteristic. Recent research, however, has questioned this position and emphasized the importance of intraspecific variation. We investigate the temporal stability of social tolerance in four groups of sanctuary-housed chimpanzees over eight years using a commonly employed measure: experimental cofeeding tolerance. We then draw on longitudinal data on the demographic composition of each group to identify the factors associated with cofeeding tolerance. We find appreciable levels of variation in cofeeding tolerance across both groups and years that correspond closely to changes in group-level demographic composition. For example, cofeeding tolerance is lower when there are many females with young infants. These results suggest that social tolerance may be a “responding trait” of chimpanzee sociality, reflecting individual-level behavioral responses to social changes. Additional, experimental research is needed to better model the causal drivers of social tolerance within and among species.

INTRODUCTION

Successful group living requires individuals to routinely interact in a relaxed and non-antagonistic manner. Interaction styles in which antagonism is rare are often referred to as “socially tolerant”. Humans are assumed to be characterized by unusually high levels of such social tolerance (Cieri et al., 2014; Burkart et al., 2009; Fuentes, 2004; Pisor and Surbeck, 2019), as we are capable of living in large numbers and in close proximity with one another, as well as cooperating on a daily basis with complete strangers (Chudek and Henrich, 2011; Richerson et al., 2016). This social tolerance is hypothesized to have played a key role in the subsequent evolution of our supposedly unique expressions of prosociality, altruism, cooperation, and social learning (Hare, 2017; Cieri et al., 2014; Fuentes, 2004; Fehr and Fischbacher, 2003).

Social tolerance levels have been described in many different socially living species: e.g., voles (McShea, 1990; Lee et al., 2019), domestic chickens (D’Eath and Keeling, 2003), mole rats (Ganem and Bennett, 2004), swallows (Dardenne et al., 2013), crows (Miller et al., 2014), dogs (Bonanni et al., 2017; Hare, 2017), foxes (Hare, 2017), and dolphins (Wild et al., 2020). Researchers have investigated the relationship between social tolerance and group size (larger groups are associated with higher social tolerance (D’Eath and Keeling, 2003; Dardenne et al., 2013)), social learning (social tolerance enables social learning (Wild et al., 2020; Miller et al., 2014; Forss et al., 2016)), and domestication (domesticated species display higher levels of social tolerance than their wild counterparts (Bradshaw, 2016; Bonanni et al., 2017; Hare, 2017; Hare et al., 2012)). Social tolerance has frequently been utilized to characterize and compare entire species and subspecies: for example, the supposedly tolerant social mole rats and intolerant solitary mole rats (Ganem and Bennett, 2004), seasonally tolerant meadow voles and consistently intolerant prairie voles (Lee et al., 2019), tolerant domesticated foxes and intolerant wild foxes (Hare, 2017), or tolerant dogs and intolerant wolves (Hare et al., 2012).

This comparative approach is especially common in studies of primates, where the construct of social tolerance has played a central role in describing and differentiating the social behavior of related species. Macaque species are organized in social grades according to their described level of social tolerance (Thierry, 2007; Balasubramaniam et al., 2018), Sumatran orangutans are reported to be more tolerant than Bornean

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orangutans (Forss et al., 2016), redfronted lemurs more tolerant than ringtailed lemurs (Fichtel et al., 2018), and bonobos more tolerant than chimpanzees (Clay and de Waal, 2013; Hare et al., 2012; Tan and Hare, 2013), but see (Jaeggi et al., 2010; Cronin et al., 2015) for conflicting findings. These species-level assumptions have also been advanced to explain and predict interspecific variation in behaviors such as cooperation (Petit et al., 1992; Hare et al., 2007; Cronin, 2017), prosociality (Burkart and van Schaik, 2013; Burkart et al., 2014; Fruth and Hohmann, 2018; Cronin, 2012), and social learning (van Schaik, 2003; Schuppli et al., 2017; van Schaik et al., 1999).

Definitions and operationalizations of social tolerance among primates (and beyond) vary widely, encompassing measures as diverse as post-conflict reconciliation (Duboscq et al., 2013), grooming behavior (Balasubramaniam et al., 2018), and counter-aggression (Balasubramaniam et al., 2012). While there is, to date, no unifying methodological framework for the study of social tolerance, it is often operationalized either as an assessment of the social structure of a group or the expression of specific inter-individual behaviors (see DeTroy et al., Manuscript submitted for publication).

One of the most commonly used measures of socially tolerant behavior is “cofeeding tolerance”, both dyadically (e.g., Amici et al., 2012; Melis et al., 2006) and at a group level (e.g., de Waal, 1986; Calcutt et al., 2014; Cronin et al., 2015; Fichtel et al., 2018). In these contexts, social tolerance has been defined as “the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin and Sánchez, 2012, pp. 4).

Recent research has highlighted the importance of measuring and theorizing about the drivers of “intraspecific” variation in social tolerance. Cronin et al. (Cronin et al., 2014), for example, investigated the co-feeding tolerance levels of four groups of separately living sanctuary chimpanzees. The study utilized a group co-feeding paradigm in which a food resource (peanuts) was distributed within a predetermined feeding area. Cofeeding tolerance was then operationalized as the proportion of the group present in the feeding zone over the course of 2 min. The study found large inter-group differences in the proportion of the group able and motivated to forage in close proximity to each other, a pattern that was reflected in additional measures of sociality (Cronin et al., 2014). This finding is consistent with previous research on differences in sociality in wild populations. For example, two studies have assessed social tolerance in wild chimpanzees with a wide array of different measures (e.g. time spent in parties, meat sharing, female grooming, and medicinal plant use) and found a consistent pattern of cross-site differences that corresponded to differences in socially learned skills (van Schaik et al., 1999; van Schaik, 2003).

Researchers have also found differences in social behavior between groups of chimpanzees within the same field site. For example, two communities at Kibale have shown differences in female gregariousness (Watts, 2012) and clique formation (Wakefield, 2013), which has been proposed to be (partially) the result of reduced feeding competition and increased group size (Wakefield, 2013). More general inter-community differences in sociality among males have also been found between the south and east groups of Tai, with differences in aggressive and cooperative behaviors and some measures of general gregariousness being reported, possibly resulting from differing levels of within- and between-group competition, as well as demographic differences (Preis et al., 2019b). These two groups have also been shown to display cultural differences in a wide array of behaviors ranging from tool use to hunting behavior (Luncz and Boesch, 2015). The two communities of chimpanzees at Budongo—Sonso and Waibira—have also shown differences in their meat sharing behavior (Hobaiter et al., 2017), the reasons for which remain to be determined. These findings, combined with those on captive populations, demonstrate that groups of chimpanzees can be characterized by different social styles and that these differences can be observed even when the groups are living under comparable ecological conditions (Cronin et al., 2014).

An important outstanding question, however, pertains to the temporal stability of such intraspecific, cross-group differences in social styles. Longitudinal study of group-specific social tolerance would provide important information about the possible mechanisms by which intraspecific variation in sociality emerges: possibly by group-specific (cultural) interaction styles (e.g., van Leeuwen et al., 2018), or by more transient individual- or demography-dependent phenomena, or by some combination of both.

Certain aspects of chimpanzee sociality are known to be temporally stable; for example, dyadic relationships can be maintained over many years (Gilby and Wrangham, 2008; Kossi et al., 2012; Langergraber

et al., 2009; Rosati et al., 2020), as can some alpha male tenures (Goodall, 1986). It is unclear, however, to which extent this stability extends to group-level social styles. In one of the few studies on temporal change in primate social styles, Sapolsky and Share (Sapolsky and Share, 2004) observed the *de novo* emergence and continuation of a socially tolerant and relaxed social climate (e.g., higher rates of grooming and affiliation) in a troop of wild baboons over a 20-year period. This change was instigated by the abrupt deaths of many of the troop's more aggressive males, resulting in a troop with an unusually high number of relatively peaceful males. The resultant peaceful climate persisted over generations (Sapolsky and Share, 2004). Another study reported short-term changes in sociability in the Kasekala chimpanzees between 1977 and 1979 (Goodall, 1986). These differences were attributed to the differing number of estrous females present in the group over time, as estrous females were shown to be more gregarious and to attract more males than anestrus females. These reports provide provisional support for a certain level of temporal flexibility in primate social climates and suggest that they may be influenced by group demographics.

The current state of knowledge concerning the effect of demographic variables on chimpanzee sociality and, more specifically, social tolerance, however, is ambiguous. Male and female chimpanzees differ in their sociability with males being more gregarious and having more and stronger bonds to other males than females (Lonsdorf et al., 2014; Pepper et al., 1999; Wilson, 2012). These sex-based differences could lead to groups with a higher ratio of males to females being more socially cohesive and possibly more socially tolerant of one another. A low female-to-male ratio could also increase males' willingness to tolerate females as a mating strategy (Pruetz and Lindshield, 2012). On the other hand, more males and therefore fewer females in a group could increase scramble competition for access to females and therefore decrease males' tolerance of one another (Fawcett and Muhumuza, 2000).

The possible effect of females on group-level sociality is further complicated by their state of estrus. Being in estrus has been found to increase female chimpanzees' gregariousness (Pepper et al., 1999), with some researchers finding estrous females to be as gregarious as males (Matsumoto-Oda, 1999), which might lead them to also be more socially tolerant of other females and males. Estrous females also attract males (Hashimoto et al., 2001; Matsumoto-Oda, 1999), which can lead to an overall increase in sociability within a group (Goodall, 1986).

The number of infants and juveniles could also affect group-level sociability. On the one hand, the presence of an infant is likely to decrease its mothers' willingness to be in close proximity to other individuals—especially adult males—so as to avoid male aggression (Lowe et al., 2019; Otali and Gilchrist, 2006). On the other hand, infants and juveniles typically experience high levels of tolerance from adult chimpanzees (von Rohr et al., 2011). Infants and juveniles may also lead to increased social tolerance by providing play partners, as play behavior has been proposed to decrease stress and increase tolerance in feeding contexts among captive primates (Norscia and Palagi, 2011; Palagi et al., 2004). Hence, it is conceivable that the various demographic factors outlined above affect group-level social tolerance in opposing ways. For example, a large number of infants and juveniles in a group could decrease “cofeeding tolerance” because the mothers, especially those with smaller infants, stay away from the feeding context, while, at the same time, increase “overall social tolerance” by providing opportunities for group members to relieve stress through play behavior.

Another aspect of chimpanzee sociality that was originally assumed to have a large influence on both male and female relationships is kinship (Goodall, 1986). Subsequent research, however, has found little robust support for the effect of kinship on association patterns (Goldberg and Wrangham, 1997; Langergraber et al., 2009; Lehmann and Boesch, 2009; Mitani et al., 2000; cf. Surbeck et al., 2017), cooperation (Eppley et al., 2013; Langergraber et al., 2007; Mitani et al., 2000), or grooming behavior (Gomes et al., 2009; Rodrigues and Boevig, 2019; cf. Foerster et al., 2015; Lehmann et al., 2006). Taken together, these results suggest that kinship plays at most a limited role in group-level chimpanzee sociality.

Finally, larger group size appears to lead to the formation of cliques and less overall group cohesiveness (Lehmann and Boesch, 2004; Wakefield, 2013) but appears to have little effect on other aspects of group sociality among chimpanzees (Lehmann and Boesch, 2004). Research on social tolerance among Japanese macaques also found no effect of group size on social tolerance (Kaigaishi et al., 2019). On the other hand—as mentioned above—research on social tolerance among non-primates has found a positive relationship between group size and social tolerance (D'Eath and Keeling, 2003; Dardenne et al., 2013).

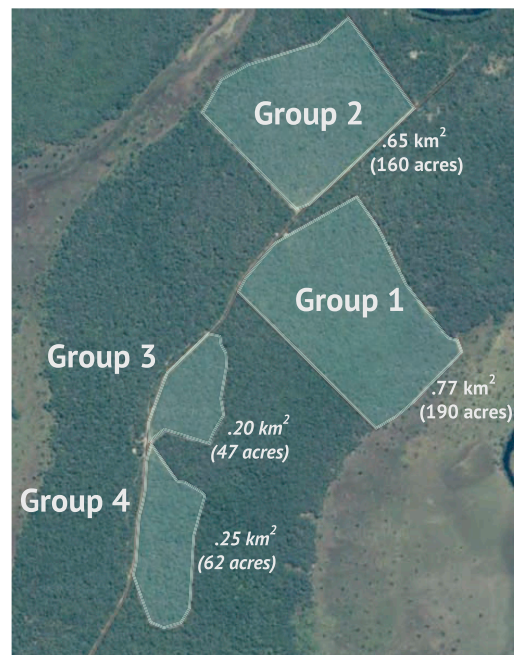


Figure 1. Aerial view of the enclosures

Aerial view of the four enclosures at Chimfunshi (modified from Google Maps).

In the current study, we investigate whether there is temporal variability in group-specific social tolerance using the same cofeeding tolerance assay (referred to as the “peanut swing”, see [Figure S1](#) and [Video S1](#) for more details on the experimental setup) in the same chimpanzee groups as those described in Cronin et al. (Cronin et al., 2014) but now longitudinally over the course of 8 years. Given the lack of precedents, we approach this study in an exploratory manner. Our primary aims are to (1) identify the extent of variability of cofeeding tolerance (a) between the groups and (b) within the groups over time. Furthermore, based on previous research demonstrating the importance of demographic variables, we investigate (2) whether group demographics are associated with group-level cofeeding tolerance as measured by our experimental assay. Specifically, we explore the associations of cofeeding tolerance with (a) the number of females vs. males, (b) the number of kin vs. non-kin, as well as (c) the fraction of individuals belonging to different age-groups (e.g., infants, juveniles, adolescents, and adults). Due to the exploratory nature of this study and the lack of consistent findings in the extant literature, we do not formulate directed hypotheses concerning these variables.

Lastly, in the final year of data collection, we introduced a group-level tolerance measure which employed a codrinking instead of a cofeeding paradigm (referred to as the “juice pipe” see [Figure S1](#) and [Video S2](#) for more details on the experimental setup) to cross-check the validity of our main assay by comparing the outcomes of both approaches.

The study took place at Chimfunshi Wildlife Orphanage Trust (Chimfunshi) in four neighboring groups of chimpanzees comprising approximately 100 individuals. See [Figure 1](#) for geographic details and [Table 1](#) for demographic details. For further information about these populations and relevant animal care protocols, see the [Transparent methods](#) section “Study site and subjects”.

RESULTS

To model the cofeeding tolerance of our chimpanzee groups, we built a statistical model that explicitly follows the structure of the experimental setup. The experiment was repeated several times in each year, in each group. We thus estimate effects unique to the interaction of group and year. Measurements of cofeeding in each experimental session were taken at fixed time points after the introduction of peanuts. We explicitly account for the effects of peanut depletion on inferred cofeeding tolerance with a dynamic

Table 1. Demographic overview

Group	Individuals	Pct. female	Pct. maternal kin
1	23–25	0.56–0.67	0.7–0.79
2	42–52	0.61–0.71	0.9–0.92
3	10–14	0.57–0.67	0.4–0.58
4	11–13	0.18–0.38	0.27–0.45

The range (min-max) of the number of individuals, the percentage of females, and the percentage of individual with maternal kin, in each of the four groups, from 2011 to 2018. See also [Table S1](#).

consumption model within each experimental session (for more details, see the [Transparent methods](#) section “A statistical model for the peanut swing data generating process” and [Figures S2–S7](#)).

Cofeeding tolerance by year and group

[Figure 2](#) plots the time series of maximal cofeeding tolerance by group. Maximal cofeeding tolerance can be understood as the model-estimated initial tolerance level—the proportion of the group present before any of the peanuts are consumed or carried away—which accounts for differential rates of resource depletion across the groups. We observe evidence of reliable differences in cofeeding tolerance both across chimpanzee groups within years and evidence of reliable difference across years within groups. This provides evidence that cofeeding tolerance is not a temporally stable, group- or species-level property. However, the range of variation here does not span the full set of possible values, and so we cannot rule out the possibility of a species-specific range of cofeeding tolerance levels—with, for example, these groups of chimpanzees being more tolerant than a species with a different, consistently lower range of estimated tolerance values.

Variation in cofeeding tolerance across years and groups

We observe evidence of reliable changes in cofeeding tolerance across both years and groups in [Figure 2](#). This variation is quantified in [Transparent methods Figure S8](#). We find that there is reliably greater across-group variation in cofeeding tolerance in some years (i.e., 2011 and 2012) than in other years (i.e., 2015 and 2016). There is also evidence that some groups (i.e., group 1) show greater temporal variability in cofeeding tolerance than other groups (i.e., group 2 or 4). Finally, we find evidence of greater inter-group differences within years than intra-group differences across years in maximal cofeeding tolerance (for more details, see [Transparent methods](#) section “Variation in cofeeding tolerance across years and groups”).

Demographic correlates of cofeeding tolerance

To assess the demographic predictors of the observed variation, both across groups as well as within groups over time, we used two models: a multi-level model with group-specific coefficient vectors (that reflect the within-group effects of covariates) and a standard model with a single coefficient vector shared across all groups (that can reflect the between-group effects of covariates). [Figure 3](#) plots the results of both of these models and illustrates the demographic predictors of maximal cofeeding tolerance. An increasing frequency of juvenile and adolescent female chimpanzees in the population is associated with increased cofeeding tolerance in both within-group and between-group models. An increasing frequency of young infants under three years of age is also associated with decreased cofeeding tolerance in both within-group and between-group models. Additional effects of group size and maternal kin frequency are apparent in between-group analyses.

Counter-factual predictive simulations

To further investigate the extent to which cofeeding tolerance is explained by demographic variables, we ran predictive simulations of the time series of maximal cofeeding tolerance by group, conditional on counterfactually removing variation in demographic variables. Counterfactually removing demographic variation across groups, we find that inter-group differences are attenuated but not completely removed, implying some random effects of group outside of those attributable to differences in demographic composition: group 1 remains the least tolerant and group 2 the most tolerant group (see [Transparent methods Figures S9–S12](#)). These simulation analyses demonstrate that demographic variation explains much of the intra-group variation—and some, but not all, of the inter-group variation—in maximal

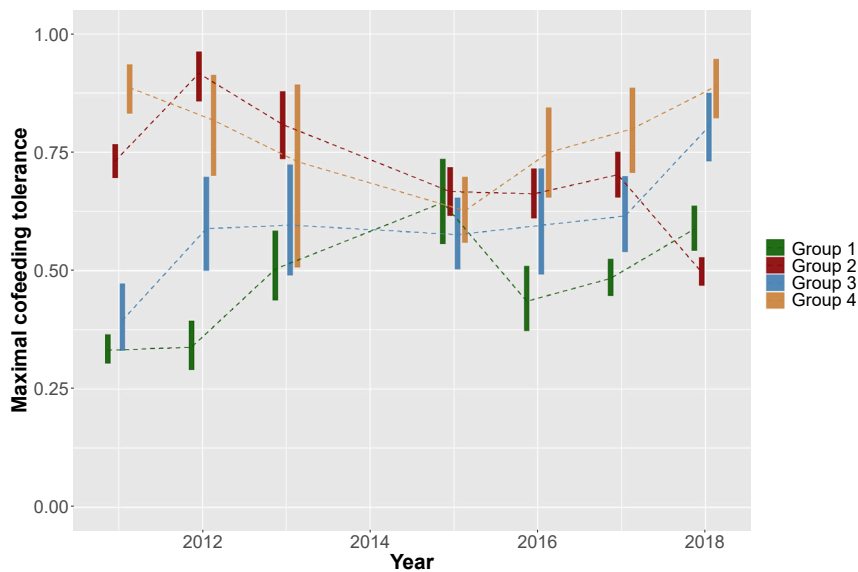


Figure 2. Time series of cofeeding tolerance in four groups of chimpanzees

Each bar plots the central 90 percent credible interval of maximal cofeeding tolerance (i.e., initial cofeeding tolerance) in each group of chimpanzees in each year. Bars are jittered around year for visual clarity, but all empirical observations were matched in time. We observe substantial variation in cofeeding tolerance, both across groups and within groups across years. See also [Figures S1–S6](#) and [S8–S13](#), [Tables S3](#) and [S4](#), and [Video S1](#).

cofeeding tolerance. Further details about these and additional counter-factual predictive simulations can be found in [Transparent methods](#) section “Counter-factual predictive simulations”.

An individual-level network analysis of dyadic cofeeding tolerance

For a subset of peanut swing sessions, we were able to code the identities of all individual chimpanzees present at the food zone at each scan ($n=1,264$ individual observations). As a follow-up of our findings regarding the influence of group-level demographics on cofeeding tolerance (see [Demographic correlates of cofeeding tolerance](#)), we explored the propensities of individuals of specific sex/age categories to be in the food zone, expressed both in individual and dyadic terms ($n=9,280$ dyadic observations). To account for repeated observations of individuals and dyads, we used Stan code from [Pisor et al. \(2019\)](#) to implement the social relations model ([Kenny and La Voie, 1984](#); [Koster et al., 2020](#)). See [Transparent methods](#) section “The social relations model” for complete details on this model.

Our network analysis of coresidence in the food zone indicates that, at the individual level, females with infants under age 3 are somewhat less likely than other individuals to reside in the food zone across scans. At the dyadic level, females with infants under age 3 are less likely to coreside in the food zone with adult or adolescent males, while adult females without infants are more likely to coreside with adult males. See [Figure 4](#) for additional discussion.

Generalizability of the assay

Finally, we compared estimates of maximal cofeeding tolerance taken in 2018 using both the peanut swing and the juice pipe methodologies. We find that, under either assay, the rank order of groups by maximal cofeeding tolerance is identical (see [Transparent methods Figure S13](#)). The cross-group differences, however, are starker under the juice pipe assay than the peanut swing. Moreover, the estimates are more precise under the juice pipe procedure.

DISCUSSION

In this study, we measured the cofeeding tolerance levels of four groups of chimpanzees longitudinally over the course of eight years to explore whether cofeeding tolerance is a stable group-level characteristic and which demographic factors, if any, might influence group-level cofeeding tolerance levels over time. We find that cofeeding tolerance in these groups of chimpanzees is a highly flexible construct that displays

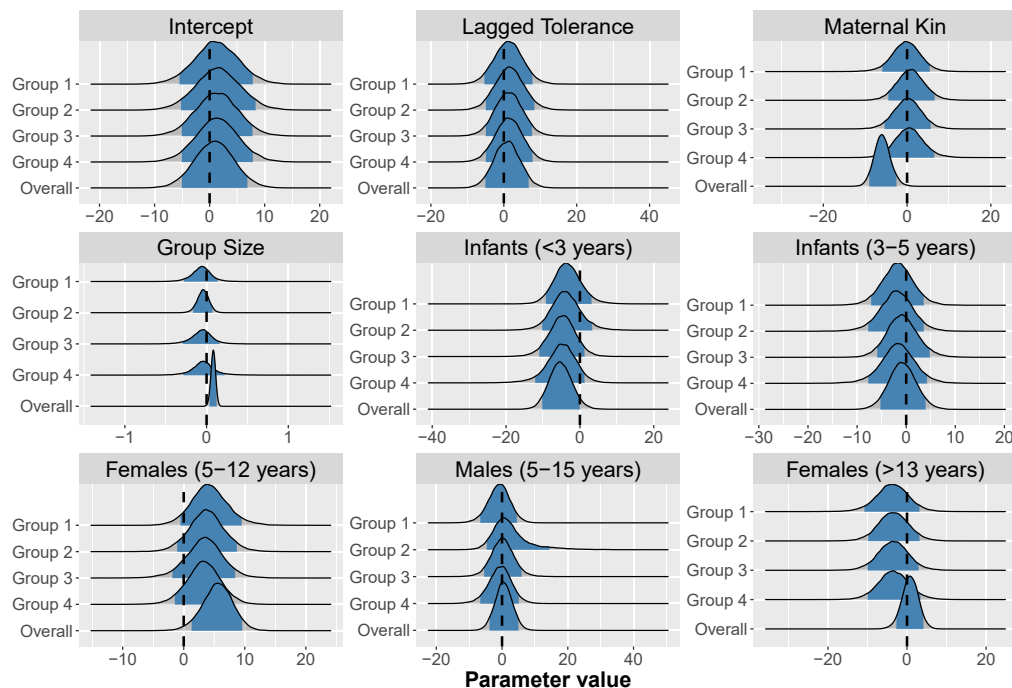


Figure 3. Density plots of covariates

Density plots of the effects of various covariates on maximal coveeding tolerance, with central 90% credible intervals in blue. The group-specific plots show the within-group effects of a change in a covariate on the maximal coveeding tolerance in that group (i.e., all parameters are random effects by group). The overall plots (the bottom plot in each panel) show the between-group effects (i.e., when the same parameters are shared across all groups). Note that for the covariates “infants (<3 years)” and “females (5-12 years)” very little of the central 90% credible intervals overlap with 0, indicating reliable within- as well as between-group effects. For the parameters “group size” and “maternal kin”, this is only the case for the between-group effects. See also [Figure S8](#).

an appreciable amount of variation over time. These changes do not represent random fluctuations but correspond closely to changes in the demographic composition of each group.

The frequency of infants under three years of age had a negative within- and between-group influence on coveeding tolerance. Our finer-scale social network analysis reveals that females with infants under three years of age were indeed somewhat less likely to be present in the food zone than females without young infants. Females with young infants were especially less likely to be in the food zone when adult and adolescent males were present. This is presumably due to the mothers of young infants refraining from being in close proximity to other individuals, especially males, so as to minimize aggressive behaviors directed toward themselves and their offspring ([Lowe et al., 2019](#); [Otali and Gilchrist, 2006](#)). We expect this kind of situationally dependent coveeding avoidance behavior to have a strong temporal component, decreasing as the infants grow older and are less vulnerable and then increasing again with the birth of new, highly vulnerable infants.

In the literature, much of the male-female aggression observed in chimpanzees is assumed to be sexually motivated (i.e., selectively directed toward parous and maximally sexually swollen females) ([Muller et al., 2007, 2009](#)); but see ([Stumpf and Boesch, 2010](#)) for conflicting findings), and more common in adult than adolescent males ([Muller et al., 2009](#)). Non-sexually motivated male-female aggression, however, has been shown to be most frequent in adolescent and young adult males ([Muller et al., 2009](#)) and is hypothesized to be motivated by young males’ attempts to climb the dominance hierarchy ([Muller et al., 2009](#); [Nishida, 2003](#)). This could explain why females with small infants were most strongly deterred by adolescent males.

The frequency of juvenile and adolescent females within the population was found to have both within- and between-group effects. Groups with larger numbers of juvenile and adolescent females showed higher levels of coveeding tolerance. This could possibly reflect an effect of females in estrous, who are known

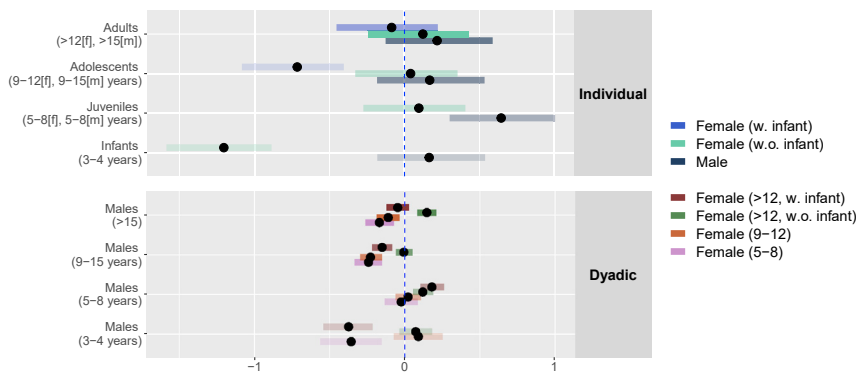


Figure 4. Estimates from the social relations model

Each bar plots the central 90 percent credible interval of the regression coefficients giving the change in log-odds of a cofeeding tie as a function of the indicated variable. Bars with little or no overlap with 0 indicate reliable positive or negative effects of the respective variable. Bars are clustered by age category on the left axis, with color showing unique estimates by sex within each age category and shading indicating sample size. In the top frame, we plot individual-level random effect estimates for the interaction of sex and age category on residence in the food zone. In the bottom frame, we plot random effect estimates for dyads composed of females with or without infants under 3 years old (indicated by color) and males of various age categories (indicated by rows). Adult females with infants under age 3 and young females are less likely to coreside in the food zone with adult or adolescent males, while adult females without infants under age 3 are more likely to coreside with adult males. Females, with or without infants, are more likely to coreside with male ages 5 to 8 than with males of other age classes.

to show increased gregariousness (Matsumoto-Oda, 1999) and to also attract males (Hashimoto et al., 2001; Matsumoto-Oda, 1999). While we do not have sufficient data on the females' states of estrous over the eight years, our age categories of juveniles and adolescents likely contained females already in estrous (female chimpanzees are known to reach menarche earlier in captivity (Atsalis and Videan, 2009; Coe et al., 1979). Since older females are more likely to either have a more permanent form of contraceptive or be pregnant or nursing (for more details on Chimfunshi's breeding policies, see the [Transparent methods](#) section "Study site and subjects"), the age categories of juveniles and adolescents may best account for cycling females without dependent young. Groups with higher numbers of juvenile and adolescent females might therefore have more females in estrous, increasing the overall number of individuals willing to be in close proximity while cofeeding. However, since this effect was not found at the individual level—i.e., adolescent and juvenile females were not more likely than females of other age categories to cofeed in our experiment or to coreside with adult males—this interpretation should be treated with caution, and we suggest that future research should further investigate the possible direct and indirect effects of female behavior on group-level cofeeding tolerance.

Strier et al. (Strier et al., 2014) identify two types of behavioral traits: constraining traits—which are temporally stable and respond slowly to change—and responding traits—which are temporally and locally variable. They found that grouping pattern (e.g., stable core or fission-fusion) was a responding trait among 22 primate species and highly dependent on demographic changes (Strier et al., 2014). Given the variation we have observed in chimpanzees' group-level cofeeding tolerance, our results suggest that the propensity to join in close proximity to others in the vicinity of depleting, valuable food resources is another such responding trait, reflecting the context-dependent nature of chimpanzees' social behavior.

However, not all of the inter-group variation could be explained by demographic variables, and there was reliably more variation between groups than across years. As such, our results also imply a certain amount of group-level stability in social tolerance levels. This group effect could reflect an additional influence of group-specific factors, such as learned behavioral styles (van Leeuwen et al., 2018) or the more emergent phenomenon of so-called "collective/group personalities" (Wright et al., 2019; Bengston and Jandt, 2014). Group-level differences have been found for the personality trait "sociability" among chimpanzees (Koski, 2011) and may be affected by socioenvironmental factors such as group size and key individuals (Wright et al., 2019; Bengston and Jandt, 2014; Koski and Burkart, 2015; Cronin et al., 2014).

Cronin et al. (Cronin et al., 2014) compared cofeeding tolerance with two additional measures: the evenness of the distribution of food resources (calculated with Pielou's measure of J [Pielou, 1977]) and the average association indices in the social group outside of an experimental context. In one cross-sectional study, these measures of sociality were associated with one another (Cronin et al., 2014). It remains unknown, however, how different measures of sociality compare in their temporal stability: some aspects of sociality might be temporally stable and others much more dynamic. A recent study by van Leeuwen et al. (van Leeuwen et al., 2018) investigated (non-food related) spatial proximity, grooming proclivities, and party size among the four groups in Chimfunshi and found consistent differences in group-level sociality such that the groups with relatively high rates of spatial associations were also characterized by stronger grooming bonds and larger party sizes. These differences, however, displayed a high level of consistency over the course of the three years in which the data were gathered (2011-2013), suggesting that they could represent temporally stable differences in sociality at a group level (e.g., cultures). The aspects of sociality analyzed in van Leeuwen et al. (van Leeuwen et al., 2018) were based on individuals' choices of whom to associate with and who to groom, likely reflecting their relationships with group members, which are known to be relatively stable among chimpanzees (Gilby and Wrangham, 2008; Kossi et al., 2012; Lan-gergraber et al., 2009). The cofeeding measure that is the focus of the current study, on the other hand, reflects the upper limit of individuals' willingness to be with conspecifics, in a competitive situation. It is possible that willingness to cofeed, as a responding trait, is a more flexible and transient behavioral characteristic than is dyadic bonding.

We also found group size to have a positive effect and the frequency of maternal kin to have a negative effect on cofeeding tolerance when comparing between groups. However, we did not find an effect of these predictors on changes in cofeeding tolerance over time within groups. This is due to the lower within-group variation as opposed to between-group variation in these variables in our data. It is possible that between-group differences in these variables are causally related to difference in cofeeding tolerance, but given our study design, it is difficult to rule out confounding.

In our final year of data collection, we introduced a secondary measure of cofeeding tolerance, the juice pipe. Both assays reveal the same inter-group pattern of cofeeding tolerance levels, validating our previous measure, the peanut swing. The juice pipe was shown to be an improvement in measuring cofeeding tolerance, as it ensures a stable resource level within each session and reduces the variance in food zone size across sessions, resulting in more precise and reliable measurements of cofeeding tolerance. As such, the juice pipe represents an improved paradigm for future studies on cofeeding tolerance, when resources allow.

Social tolerance is often discussed as a species-specific trait and, as such, has been used to describe and characterize many different species. Our study, however, demonstrates that social tolerance levels within a species—as measured with a cofeeding paradigm—can vary substantially, both among groups as well as within groups over time. This said, our results do not preclude the possibility of a species-level component to social tolerance. The cofeeding tolerance levels we illustrate here do not span the full set of possible values, and so it is conceivable that the typical range of cofeeding tolerance values in chimpanzees differs from the typical ranges of other species, for example, bonobos (see Cronin et al., 2015). Species can also be characterized by different extents of variability, possibly reflecting different levels of behavioral flexibility (Kamilar and Baden, 2014). To address these possibilities, however, we would require data sets of measurements over multiple years from multiple groups. Our study highlights the need for future research to consider not only inter-group variation but also intra-group variation over time. A full comprehension of the breadth of intraspecific variation will allow us to better understand the extent to which social tolerance is a necessary precondition for successful group living.

Limitations of the study

There is, to date, a lack of research focused on comparing and integrating different theories and operationalizations of social tolerance (see DeTroy et al., Manuscript submitted for publication), which limits the generalizations that can be made from our findings on cofeeding tolerance in chimpanzees to other measures of social tolerance in other species. Future research would benefit from studies systematically comparing a variety of measures of social tolerance and sociability in multiple species with longitudinal data.

A further factor which could have influenced cofeeding tolerance in chimpanzees that we did not consider is rank stability. There were three changes in alpha male over the course of the eight years (in groups 1, 2, and 3), with two additional ongoing challenges (in groups 3 and 4) during our final year of measurement. While there are not enough instances of such rank changes to support formal statistical modeling, such social changes warrant further attention as rank stability has been shown to affect sociability in wild and captive chimpanzees (Gilby and Wrangham, 2008; Hemelrijk and Ek, 1991; Koyama et al., 2017; Preis et al., 2019a).

Our results are also based on chimpanzees living with supplemented human care. While our study groups live in large outdoor enclosures, enabling individuals to display natural fission-fusion dynamics for the majority of the day (see van Leeuwen et al., 2018, 2019), they are provisioned twice a day. As a result—and contrary to the natural conditions of wild chimpanzees—the four groups experience a constant and stable level of resource availability. In wild settings, increased resource availability has been posited to have led to increased female sociability in a comparison of two neighboring wild chimpanzee populations (Wakefield, 2013) and to explain the differences in social tolerance between Sumatran and Bornean orangutans (Schuppli et al., 2017). Seasonal differences in resource availability have also been shown to be a good predictor for party size among wild chimpanzees (Fawcett, 2000). Research comparing cofeeding tolerance in wild and captive redfronted and ringtailed lemurs has found captive populations of both species to have higher levels of cofeeding tolerance, a result attributed to higher food availability in captive populations (Fichtel et al., 2018). On the other hand, among Japanese macaques, provisioning has been observed to decrease social tolerance, presumably because it causes group members to gather in competitive situations more often than they would under natural conditions (Kaigaishi et al., 2019; Hill, 1999).

Our data show that while resource availability may play a role in cofeeding tolerance, it is not the sole influencer, as we observe substantial cross-group variation in cofeeding tolerance even when resource availability is held experimentally fixed. Similar findings have been shown in studies of wild chimpanzees (Lehmann and Boesch, 2004). By working with multiple chimpanzee groups in the same captive context, we can investigate the effects of lesser studied sources of variation in cofeeding tolerance—such as the demographic composition of the group—without our estimates being confounded by differences in resource access. Future research would benefit from investigating how the effects of resource availability interact with the effects of demographic variables.

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Sarah E. DeTroy (sarah_detroy@eva.mpg.de).

Material availability

This study did not generate new unique reagents.

Data and code availability

Code and data for diagnostics and analysis replication are available at the Open Science Framework repository https://osf.io/meq59/?view_only=3cda5b91921a4178b6286955da16538c.

METHODS

All methods can be found in the accompanying [Transparent Methods supplemental file](#).

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.isci.2021.102175>.

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AUTHOR CONTRIBUTIONS

S.E.D., E.J.C.v.L., and D.B.M.H. designed research; S.E.D., E.J.C.v.L., and K.A.C. performed research; C.T.R. analyzed data, S.E.D., E.J.C.v.L., C.T.R., K.A.C., and D.B.M.H. wrote this paper. All authors gave final approval for publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental information

**Cofeeding tolerance in chimpanzees depends
on group composition: A longitudinal
study across four communities**

**Sarah E. DeTroy, Cody T. Ross, Katherine A. Cronin, Edwin J.C. van Leeuwen, and Daniel
B.M. Haun**

Transparent Methods

Supplemental Tables

Table S1: Demographics per group by year. Related to Table 1. Number of group members in demographic categories, males in parentheses. Age groups according to [Nishida et al. \(2003\)](#). Non participant infants: ≤ 3 years; Participant infants: 3-4 years; juveniles: 5-8, male adolescents: 9-15, female adolescents: 9-12, male adults: ≥ 16 , female adults: ≥ 13 .

Year	Group	Total	Non-participant infant	Participant infant	Juvenile	Adolescent	Adult	Maternal kin
2011	1	23 (10)	0 (0)	4 (1)	2 (1)	4 (3)	13 (5)	17
2011	2	42 (12)	2 (1)	6 (3)	8 (3)	7 (3)	19 (2)	38
2011	3	14 (6)	2 (1)	0 (0)	2 (1)	0 (0)	10 (4)	7
2011	4	13 (8)	1 (1)	1 (1)	1 (1)	5 (2)	5 (3)	5
2012	1	24 (10)	1 (1)	2 (0)	4 (2)	4 (3)	13 (5)	18
2012	2	44 (15)	4 (4)	3 (1)	8 (4)	10 (4)	19 (2)	40
2012	3	14 (6)	2 (1)	0 (0)	2 (1)	0 (0)	10 (4)	7
2012	4	13 (8)	1 (1)	1 (1)	1 (1)	4 (2)	6 (3)	5
2013	1	24 (10)	2 (0)	0 (0)	6 (2)	4 (3)	12 (5)	18
2013	2	46 (15)	7 (5)	0 (0)	10 (4)	10 (4)	19 (2)	42
2013	3	12 (4)	0 (0)	2 (1)	1 (0)	1 (1)	8 (2)	7
2013	4	11 (8)	1 (1)	0 (0)	2 (2)	3 (2)	5 (3)	3
2015	1	23 (8)	2 (1)	1 (0)	5 (1)	4 (2)	11 (4)	16
2015	2	47 (16)	7 (5)	1 (1)	6 (3)	10 (4)	23 (3)	43
2015	3	10 (4)	1 (0)	1 (0)	1 (1)	1 (1)	6 (2)	4
2015	4	12 (9)	1 (1)	1 (1)	1 (1)	3 (3)	6 (3)	3
2016	1	25 (9)	4 (2)	2 (0)	2 (0)	6 (3)	11 (4)	19
2016	2	46 (15)	5 (3)	3 (2)	4 (2)	9 (5)	25 (3)	42
2016	3	10 (4)	1 (0)	0 (0)	2 (1)	1 (1)	6 (2)	4
2016	4	12 (9)	1 (1)	1 (1)	1 (1)	2 (2)	7 (4)	3
2017	1	24 (8)	3 (1)	1 (0)	1 (0)	7 (2)	12 (5)	18
2017	2	49 (18)	8 (5)	1 (0)	4 (4)	11 (6)	25 (3)	45
2017	3	10 (4)	1 (0)	0 (0)	2 (1)	1 (1)	6 (2)	4
2017	4	11 (9)	0 (0)	1 (1)	1 (1)	2 (2)	7 (5)	3
2018	1	25 (9)	4 (2)	1 (1)	2 (0)	6 (1)	12 (5)	20
2018	2	52 (18)	8 (4)	3 (1)	5 (4)	9 (5)	27 (4)	48
2018	3	10 (4)	0 (0)	1 (1)	2 (1)	1 (1)	6 (2)	4
2018	4	11 (9)	0 (0)	0 (0)	2 (2)	2 (2)	7 (5)	3

Table S2: Peanut swing and juice fountain sessions per group by year. Related to Figure 2. Identity coded sessions are in parentheses.

Year	G1	G2	G3	G4	Season
2011	9(0)	9(0)	8(0)	11(0)	cold-dry
2012	2(0)	2(0)	2(0)	2(0)	post-rainy
2013	2(2)	2(2)	2(2)	2(2)	cold-dry
2014	-	-	-	-	-
2015	3(3)	6(6)	10(10)	10(10)	post-rainy
2016	4(4)	5(5)	2(2)	5(5)	post-rainy
2017	8(8)	6(6)	6(6)	8(8)	cold-dry
2018	8(2)	8(2)	8(2)	8(2)	cold-dry
2018 [juice fountain]	13(0)	13(0)	10(0)	10(0)	cold-dry

Table S3: ICC-estimates: Peanut swing. Related to Figure 2. ICC-estimates for reliability coding pairs.

Coding-Pair	ICC(2,1)-Estimate	95% Confidence Interval
Peanut Swing		
Coder1-Coder2	0.95	0.921, 0.967
Coder1-Coder3	0.815	0.732, 0.872
Coder1-Coder4	0.967	0.933, 0.984
Coder1-Coder5	0.523	0.226, 0.733

Table S4: ICC-estimates: Juice pipe. Additional data related to SI Figure 13. ICC-estimates for reliability coding pairs.

Coding-Pair	ICC(2,1)-Estimate	95% Confidence Interval
Juice Pipe		
Coder1-Coder6	0.989	0.975, 0.995
Coder1-Coder2	0.959	0.925, 0.977

Supplemental Figures

Figure S1: The two experimental paradigms. Related to Figure 2. The food zone used to classify cofeeding tolerance is illustrated with green rectangles.

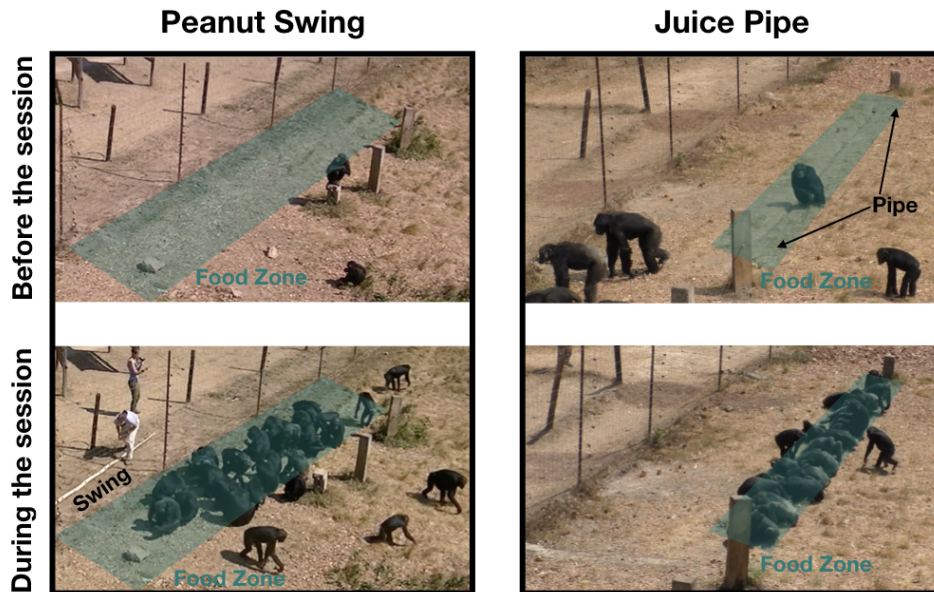


Figure S2: Traceplot of μ from the varying effects model. Related to Figure 2.

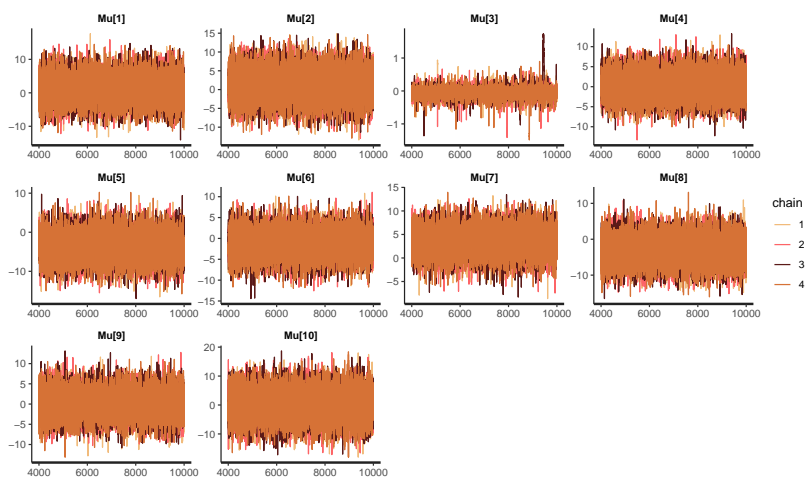


Figure S3: Traceplot of μ from the pooled model. Related to Figure 2.

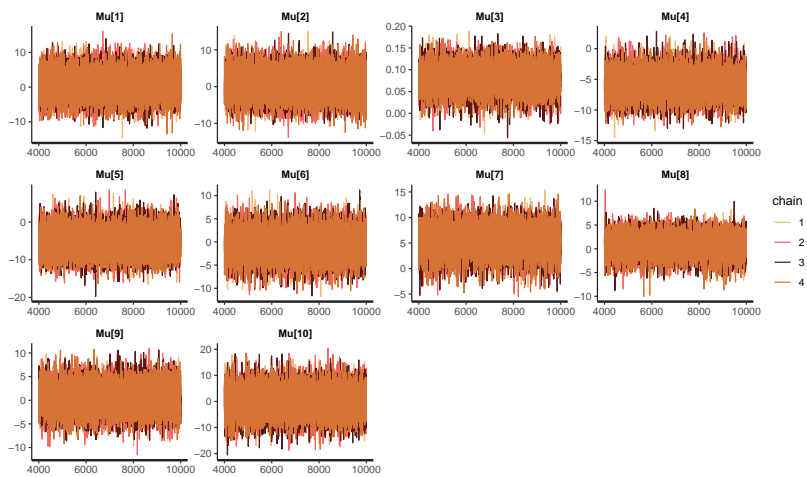


Figure S4: Traceplot of μ from the juice pipe model. Additional data related to SI Figure 13.

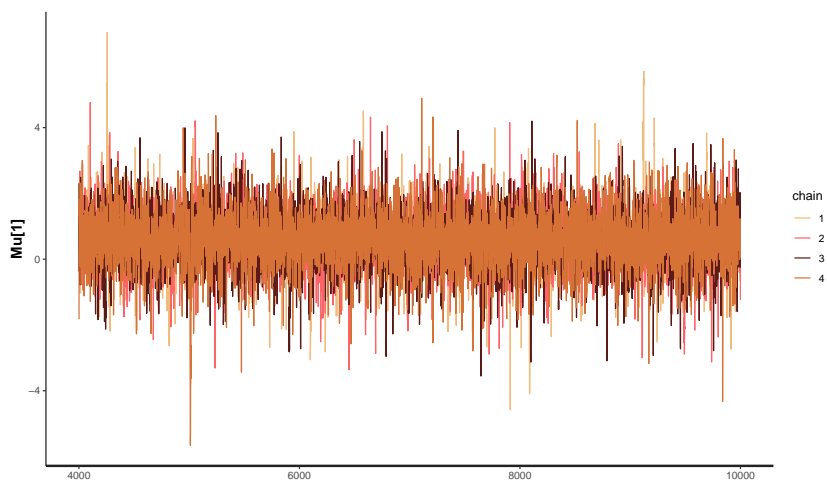


Figure S5: Pooled effects model fit. Related to Figure 2. Violin plots (in blue) of posterior estimates of cofeeding tolerance, $\theta_{[y,g,m]}$, by group, year, and measurement scan. Jittered raw observations are superimposed in red.

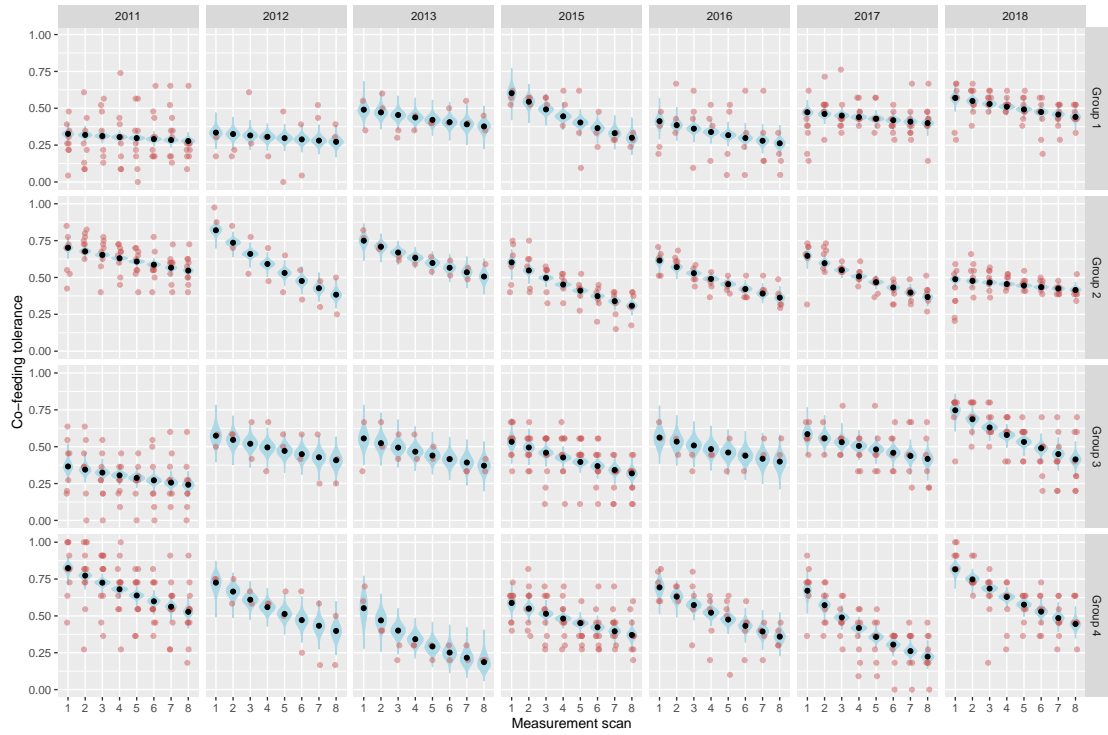


Figure S6: Varying effects model fit. Related to Figure 2. Violin plots (in blue) of posterior estimates of cofeeding tolerance, $\theta_{[y,g,m]}$, by group, year, and measurement scan. Jittered raw observations are superimposed in red.

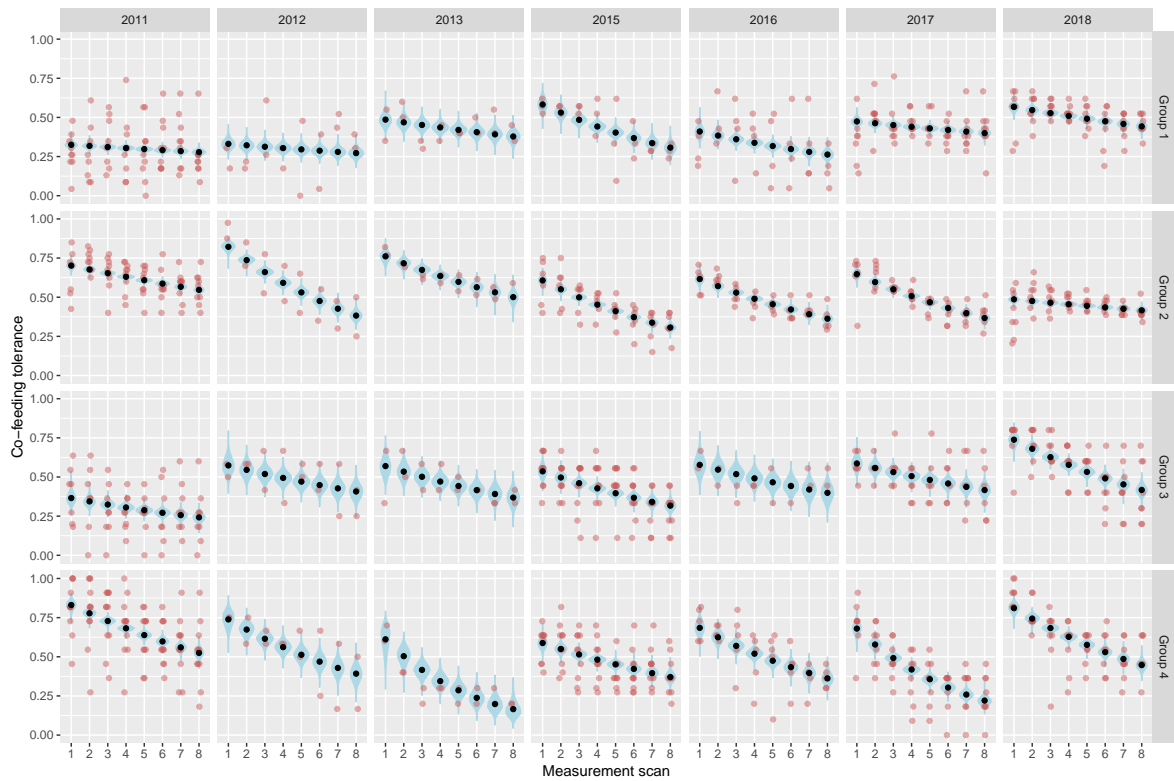


Figure S7: Juice pipe model fit, 2018. Additional data related to SI Figure 13. Violin plots (in blue) of posterior estimates of cofeeding tolerance, $\theta_{[y,g,m]}$, by group and measurement scan. Jittered raw observations are superimposed in red.

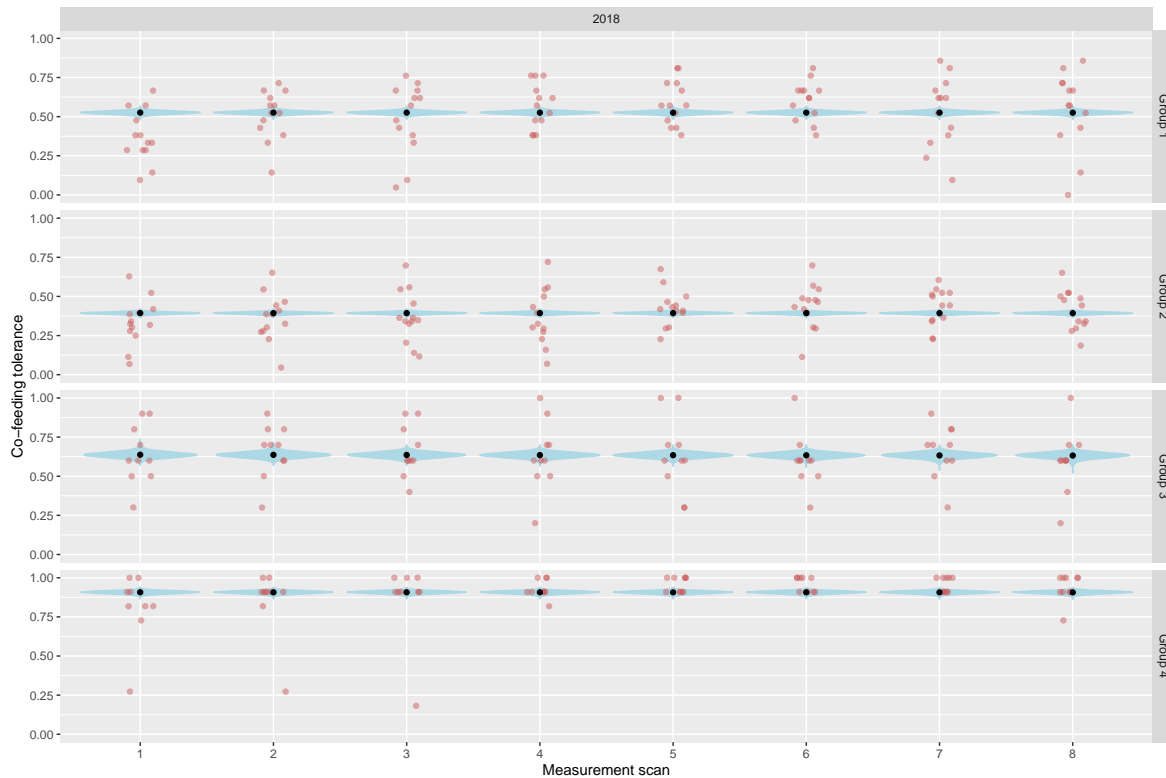


Figure S8: Coefficients of variation. Coefficient of variation (CV) in maximal cofeeding tolerance across groups by year (Frame A), across years by group (Frame B), and the contrasts between the average CV across groups and the average CV across years (Frame C). Related to Figures 2 and 3. The bottom density plot on Frame C shows that there is reliably more variation across groups within years than across years within groups.

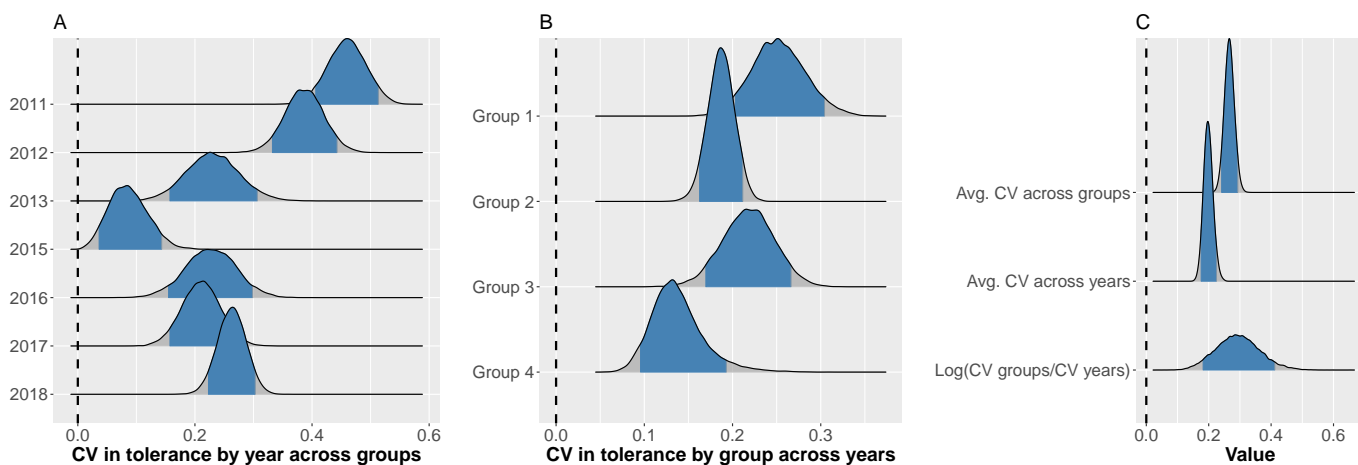


Figure S9: Time-Series of cofeeding tolerance in four groups of chimpanzees (same as Figure 2 from main text). Each bar plots the central 90 percent credible interval of maximal cofeeding tolerance (i.e., initial cofeeding tolerance) in each group of chimpanzees in each year. Bars are jittered around year for visual clarity, but all empirical observations were matched in time. We observe substantial variation in social tolerance, both across groups, and within groups across years.

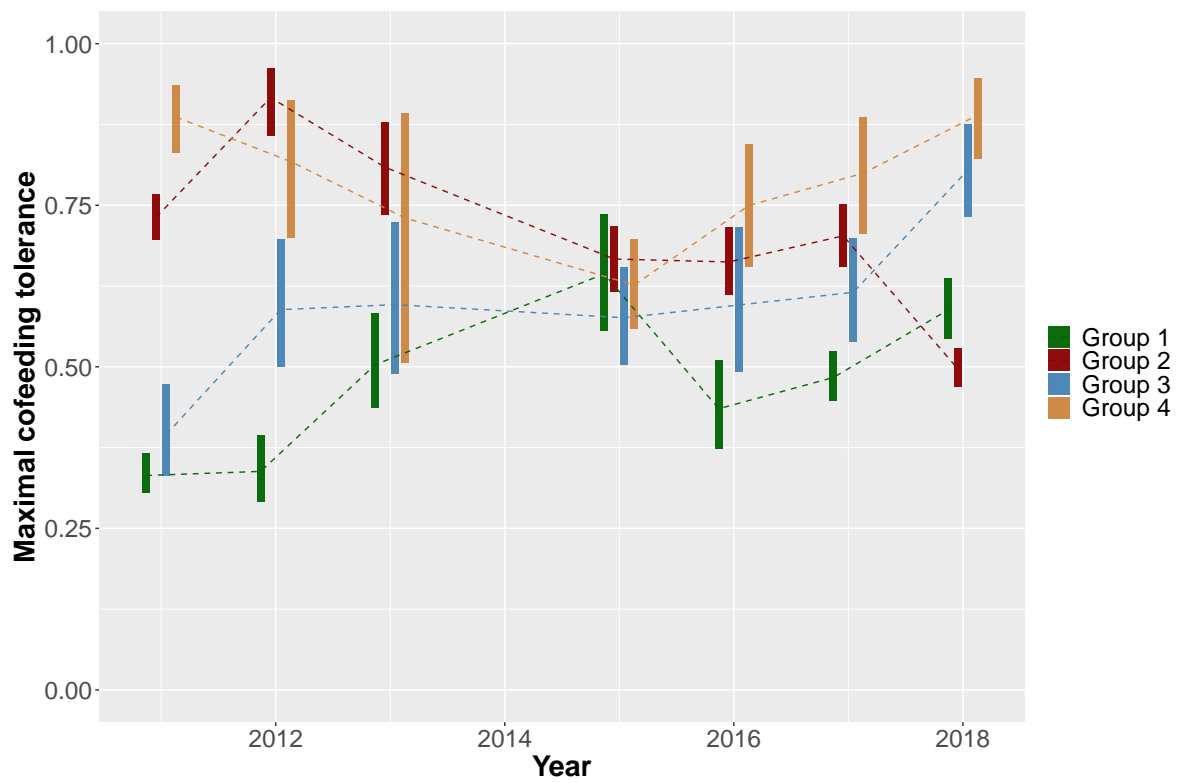


Figure S10: Counter-factual predictions of cofeeding tolerance using real demographic data. Related to Figure 2. Time-series of counterfactually predicted average cofeeding tolerance in the same groups, using real demographic data, D . Each bar plots the central 90 percent credible interval of maximal cofeeding tolerance (i.e., initial cofeeding tolerance) in each group of chimpanzees in each year. Bars are jittered around year for visual clarity.

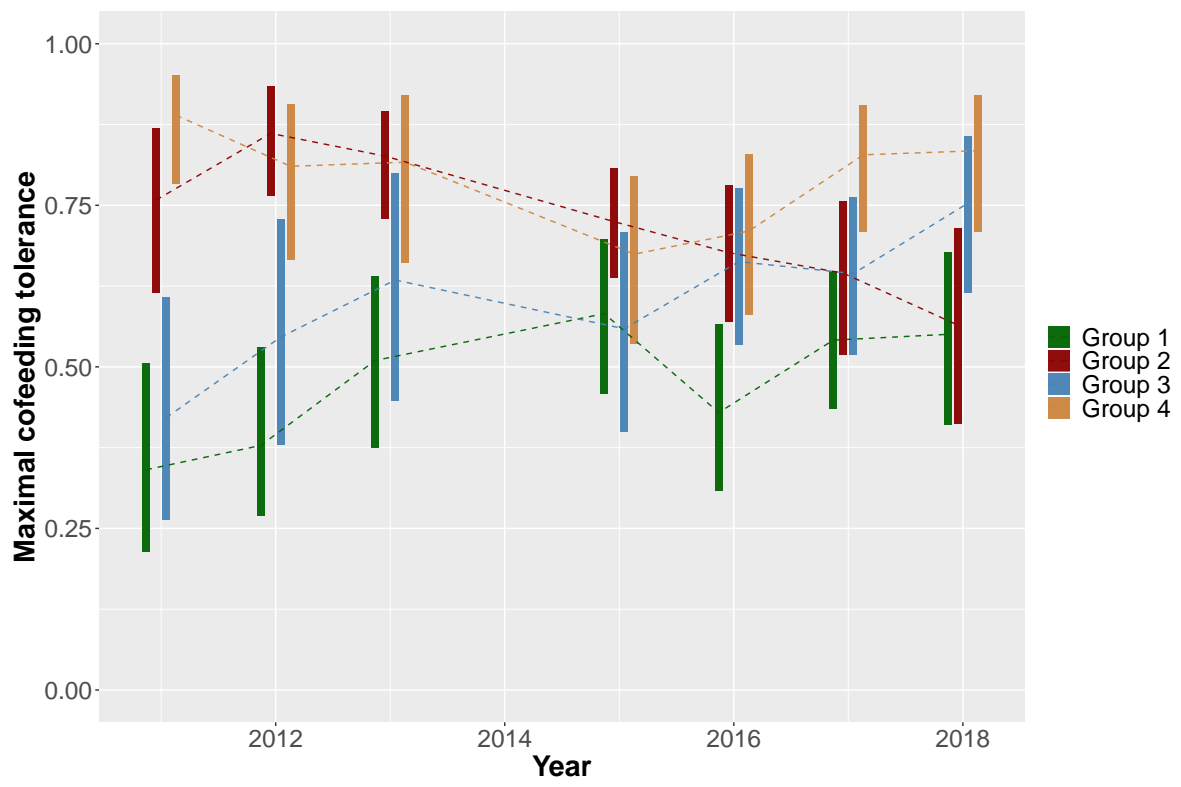


Figure S11: Counter-factual predictions of cofeeding tolerance using group-specific, time-averaged demographic data. Related to Figure 2. Time-series of counterfactually predicted average cofeeding tolerance in the same groups, using group-specific, time-averaged demographic data \hat{D} . Each bar plots the central 90 percent credible interval of maximal cofeeding tolerance (i.e., initial cofeeding tolerance) in each group of chimpanzees in each year. Bars are jittered around year for visual clarity.

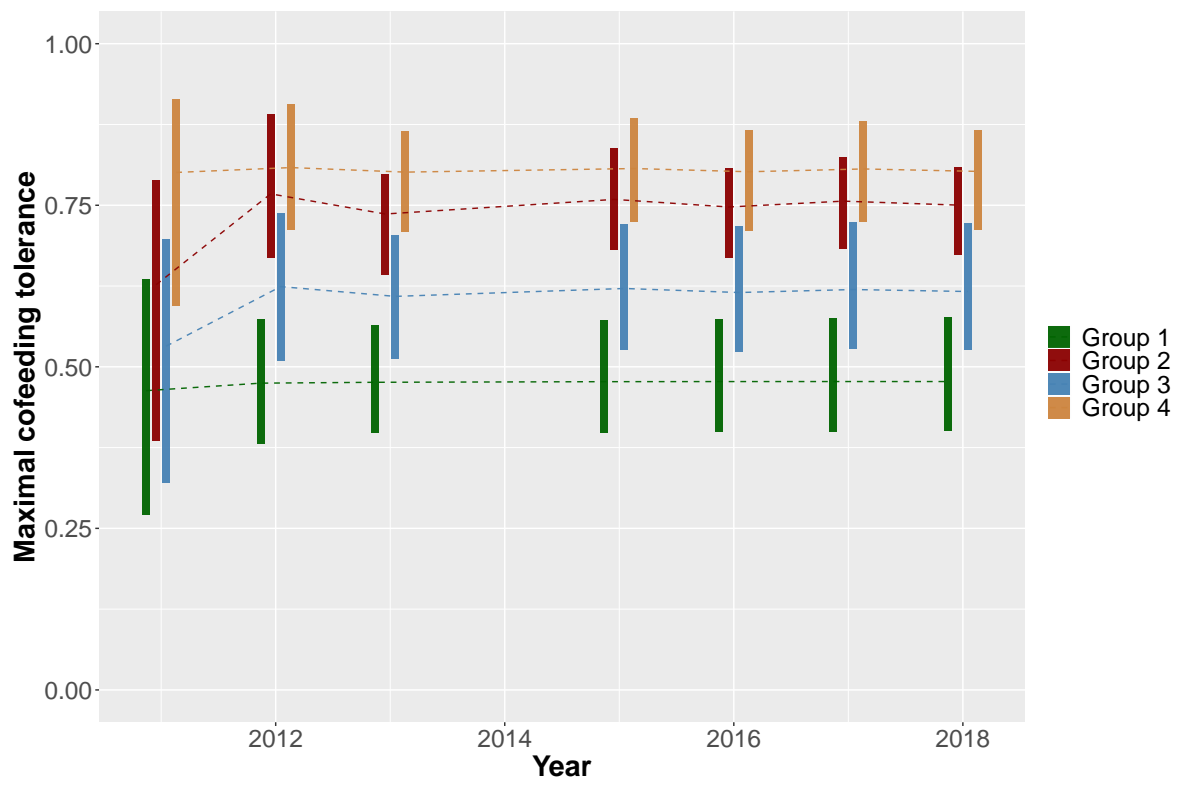


Figure S12: Counter-factual predictions of cofeeding tolerance using group- and time-averaged demographic data. Related to Figure 2. Time-series of counterfactually predicted average cofeeding tolerance in the same groups, using group- and time-averaged demographic data \hat{D} . Each bar plots the central 90 percent credible interval of maximal cofeeding tolerance (i.e., initial cofeeding tolerance) in each group of chimpanzees in each year. Bars are jittered around year for visual clarity.

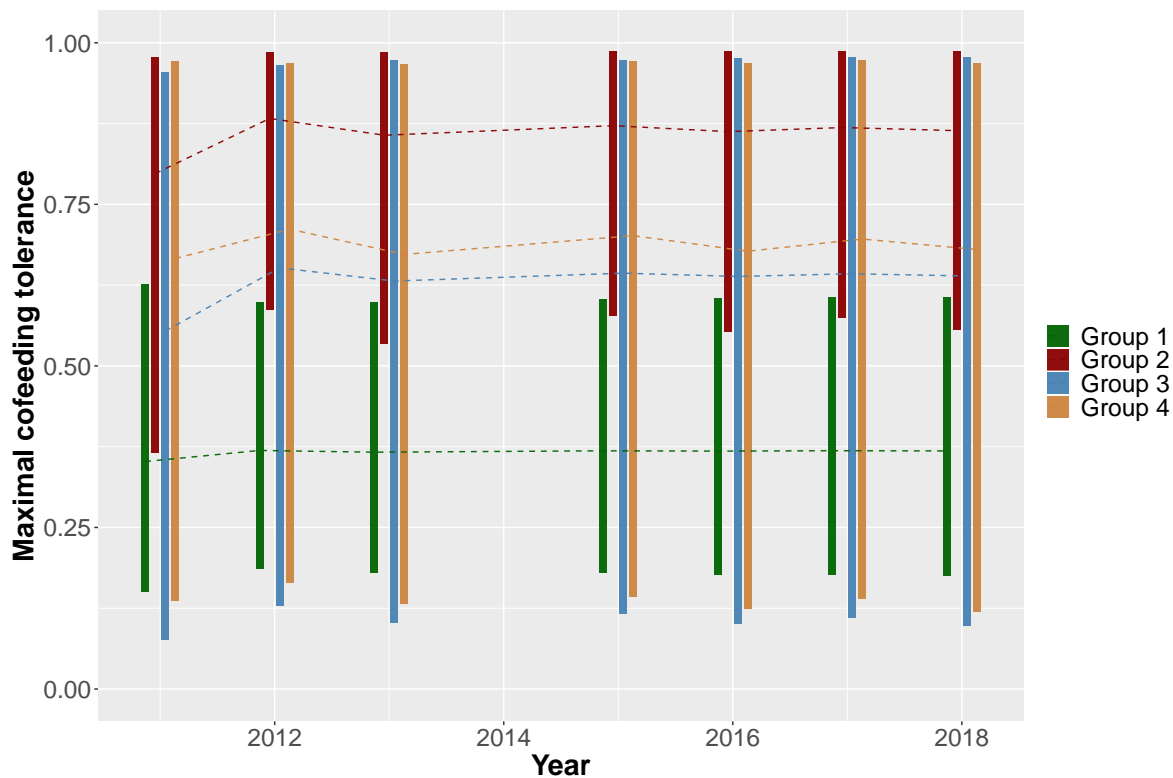
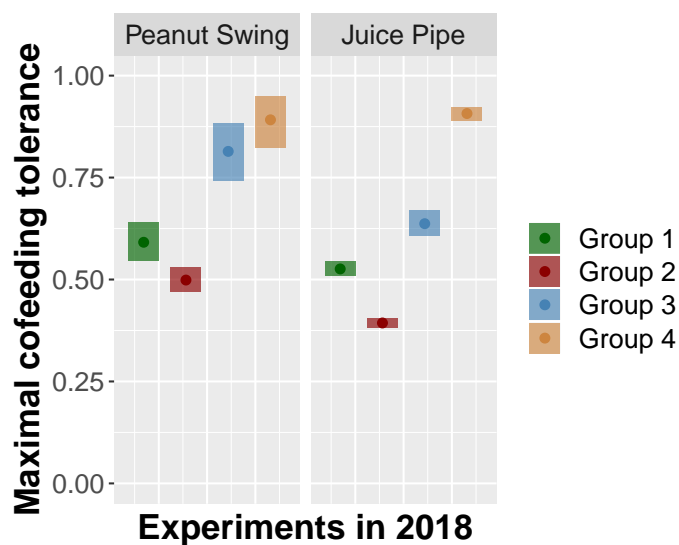


Figure S13: Comparison of the peanut swing and juice pipe. Related to Figure 2. A comparison of maximal cofeeding tolerance estimates in 2018 using both the peanut swing and the juice pipe. Vertical bars plot 90 percent credible intervals.



1. Study site and subjects

This study took place at the Chimfunshi Wildlife Orphanage Trust (Chimfunshi), a non-profit wildlife sanctuary in the Copperbelt region of Northern Zambia (S12°23', E29°32') in miombo woodland forests suitable for chimpanzees (Ron and McGrew, 1988). The study was conducted at the Project Area of Chimfunshi in which approximately 100 chimpanzees, separated into four groups, live in woodland enclosures measuring between 19 and 77 hectares. For demographic details across the study period, see Table S1. The groups consist of chimpanzees that have been rescued from various conditions, as well as sanctuary-born individuals. The chimpanzees remain in their enclosures during day and night, except for 2 hours midday when they are called inside indoor holding facilities for additional feeding and medical checkups. Reproductive management consists of a combination of oral birth control and subcutaneous implants for females, and vasectomies for males. Despite these efforts there have been several births each year. Data collection procedures were approved by the Chimfunshi Research Advisory Board before the start of the study. Additional information can be found in Cronin et al. (2014).

2. Cofeeding tolerance assay: The peanut swing

Our main measure of cofeeding tolerance was a group feeding paradigm devised by Cronin et al. (2014), which operationalizes social tolerance as the proportion of the group (3 years and older) simultaneously gathered within a group-size dependent food zone (see Figure S1). Cronin et al. (2014) used the age of three as an inclusion criterion because most infants under three years of age are carried by their mothers for the majority of the day and seldom forage for food on their own. The food zone was created by distributing peanuts within the enclosures using a device referred to as *the peanut swing*. The peanut swing consisted of a bamboo trunk cut in half lengthwise and filled with peanuts. We determined the length of the bamboo by the size of the group, with one meter per five chimpanzees three years and older (henceforth: “subjects”). The number of peanuts was determined by multiplying the number of subjects by 12. A group with, for example, 20 subjects would have a 4 meter long peanut swing filled with $20 \cdot 12 = 240$ peanuts, which, once delivered, would create a food zone approximately 4 meters long and 1 meter wide with approximately 60 peanuts per square meter.

The exact manner of distributing the peanuts varied slightly between the first year of measurement and the following years. In the first year the peanuts were dropped into the enclosure from the bamboo-trunk with a releasing mechanism; for a more detailed description, see Cronin et al. (2014). As this delivering mechanism was time-intensive to construct and difficult to utilize, the swing was simplified in the following years and the bamboo-trunk was used to simply throw the peanuts into the enclosure through the enclosure fence. The corresponding peanut-covered surface did not differ in any noticeable way between the two methods of distribution.

We conducted measurements each year between 2011-2018, except for 2014. Data were either collected in the post-rainy season (March-May) or the cold-dry season (June-August) (see Table S2). The individual measurements were conducted either in the morning before the midday feeding break (10:00am-11:30am) or in the afternoon (1:30pm-4:30pm). Before the start of the experiment, the chimpanzees were called to ensure that all group members were aware of the experiment and could participate. When at least 90 percent of the group were within eyesight, the peanuts were distributed by either dropping or tossing them into the enclosure. Video recording from two vantage points began before the start of the test and continued for at least two minutes. Sessions that were interrupted by events such as management-induced additional feeding sessions, visiting tourists, or passing vehicles (which typically distracted the chimpanzees) were discarded. We collected a total of 158 valid peanut swings for the four groups between 2011-2018, with between 2-11 measurements per group per year (see Table S2).

From 2012 to 2016, peanut swing sessions were gathered opportunistically, often as a covariate in studies focusing on specific groups. Based on the very low variation within groups in 2011 (see Cronin et al., 2014), we initially aimed at gathering a minimum of 2 sessions per group, with more data being gathered from the groups that were the focus of other research projects. After preliminary analyses in 2017 revealed a larger than expected variation in cofeeding tolerance, we increased the number of sessions per group to a minimum of 6.

Our measure of interest was the proportion of the group that simultaneously gathered in the food zone. All individuals within one meter of the food zone (and hence capable of reaching the peanuts) were considered as being present. Sessions were coded at 15-second intervals for the first 2 minutes after the peanuts were delivered, which led to 8 measurements per session. In all sessions, the peanuts were eaten within 2 minutes. All coding was conducted from video using a VLC player and transcribed into an Excel spreadsheet. For a subset of 89 sessions, we were able to code the identities of the individuals within the food zone at each of the 8 measurements.

The fact that the peanuts can be eaten quickly leads to a phenomenon whereby groups with high initial social tolerance can deplete more peanuts rapidly, leading to a quicker rate of disbandment and lower apparent measures of social tolerance at later measurement scans (e.g., scans after the first minute of foraging). We deal with this phenomenon

statistically by using a dynamic depletion model, but we also developed a novel experimental paradigm—the juice pipe—to eliminate the effect empirically.

3. Secondary assay: The juice pipe

The juice pipe consists of a metal pipe (3/4 inches in diameter) that is cemented into the ground within the enclosures with only the top half protruding. The top half of the pipe is perforated and connected with rubber hoses to a large vessel outside the enclosure containing juice. This setup creates a sprinkler-like juice dispenser. Holes are drilled at a distance of 12.5cm, resulting in 8 holes per meter. The length of the pipe used in each enclosure is again determined by the size of the group; one meter per four individuals and two holes per individual. This design theoretically allows two chimpanzees on either side to share one meter of pipe. We consider this to be an appropriate space for two adult chimpanzees to comfortably share, if socially tolerant of one another.

The juice pipe was devised to demonstrate the generalizability of our main measure and to address several sub-optimal features of the peanut swing. The first sub-optimal feature of the peanut swing is that there is a necessary decline in the number of peanuts over the course of a measurement session, leading to dynamically changing resource levels within each session (we currently deal with this phenomenon statistically). The second sub-optimal feature is that individuals can quickly collect peanuts and then leave the zone, thereby avoiding the cofeeding situation. Finally, the actual food zone can vary slightly from session to session, depending on how the peanuts, by chance, fall onto the ground. The juice pipe eliminates the issues introduced by all three of these features. By providing a steady flow of juice, we were able to ensure that the resource amount stayed constant during the course of the session, and that it could not be gathered and carried away from the zone. Additionally, since the pipe was permanently installed within the enclosure, the feeding zone also did not vary between sessions.

The juice zone itself consisted of the pipe with an additional 0.5m on either side of it. This was estimated to be the distance at which a standing or sitting individual could lean down and access the juice with its mouth (see Figure S1). A group with 20 subjects would therefore have a juice zone of 5 meters long and 1 meter wide with 40 holes emitting juice. The juice provided to the chimpanzees was a mixture of juice concentrate of various flavours (always the same flavour across the study groups) and water (always diluted to a ratio of at least 10 parts water to 1 part juice).

The water-pressure varied slightly between groups, as the longer pipes with more holes in G1 and G2 needed a higher pressure than the shorter pipes with fewer holes in G3 and G4. To achieve a comparable level of water-pressure, we increased the height of the juice container in G1 and G2. During our study, two of the four groups succeeded in digging up and removing parts of the device: G4 after their first session and G2 after their 7th session. In both cases, the setup was successfully reinstalled.

The rest of the experimental procedures followed those of the peanut swing exactly, with the exception that the session was started by switching on the juice pipe and ended by switching it off two minutes after the juice had started flowing from all of the holes (as there was a small time-lag between the time point of when juice started flowing out of the holes at the beginning of the pipe, closest to the vessel, and those at the end of the pipe). We conducted 13 sessions each in Group 1 and Group 2, and 10 sessions each in Group 3 and Group 4 (see Table S2). During the first 9 sessions of the experiment, the water delivery system in G1 and G2 was broken and the chimpanzees were given water by hand multiple times a day. While none of the individuals displayed any sign of dehydration (personal communication with the on-site veterinarian), we expected that not having unlimited access to water throughout the day could have increased motivation to participate in the experiment as well as increased the potential for aggressive interactions while at the pipe. Therefore, we decided to increase the number of sessions in G1 and G2 to 13 sessions, in order to be able to analyse sessions both with and without unlimited access to water. As there were no observable qualitative difference in the cofeeding patterns or aggression rates between these sessions, we included the full dataset into our analyses.

The cofeeding coding procedure was based on the same methodology as was used in the peanut swing study. As with the peanut swing, individuals under 3 years of age were not included in the analysis. The only change was the slightly narrower definition of the food zone.

4. Reliability coding

At least twenty percent of the sessions were coded by a second individual to assess the primary coding reliability. There was a total of 6 coders, 5 of whom also served as reliability coders. Cronin et al. (2014) reported a high agreement between the two coders for the 2011 data (Spearman $r^2 = 0.950$, $P < 0.001$). For the remaining sessions, intraclass correlation coefficients (ICC) and their 95% confidence intervals were calculated with the R-package `irr` based on a two-way, single rater, absolute agreement model (Koo and Li, 2016). The ICC estimate over all peanut swing sessions and coding pairs was excellent: $ICC(2,1) = 0.955$, 95% confidence interval: 0.943, 0.964. Similarly, for the juice pipe

data, the ICC estimate over all sessions and coding pairs was excellent: $ICC(2,1) = 0.975$, 95% confidence interval: 0.96, 0.984.

The ICC estimates for each unique coding pair were all excellent (for a complete overview see Tables S3 and S4) with the exception of Coder 3 and Coder 1 who had a “good to moderate” agreement: $ICC(2,1) = 0.815$, 95% confidence interval: 0.732, 0.872, and Coder 5 and Coder 1 who had a “moderate to poor” agreement $ICC(2,1) = 0.523$, 95% confidence interval: 0.226, 0.733. In both cases, the main coders Coder 3 and Coder 5 had spent only a comparatively short time in the field site with the chimpanzees (i.e., ~ 2 months). We therefore recoded two sessions coded by Coder 3 (these two sessions were coded from videos of poor quality which led to the coder misidentifying the size and position of the food zone) and all eleven sessions coded by Coder 5. These sessions were recoded by Coder 1, who had direct experience with all groups from 2015–2018 and also had the most extensive experience coding the sessions. The results reported here are based on the full data set including the recoded data.

5. Video availability and quality

Video footage of the experimental sessions is available for all years besides 2018. The majority of the video recordings of the peanut swing and juice fountain sessions from 2018 were lost during a break-in in early 2019. At this point, both the primary and the reliability coding had been completed, but the identities of the individuals had not yet been coded. Additionally, the video quality of the sessions recorded in 2011 and 2012 is very poor, making the coding of individual identities unfeasible. In total, 89 out of 158 peanut swing sessions could be coded for the identities of individuals (see Table S2 for details).

6. Ethical statement

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*.

7. Statistical methods

7.1. A statistical model for the peanut swing data generating process

To model the cofeeding tolerance of chimpanzees, we build a statistical model that explicitly follows the structure of the experimental setup. The experiment was repeated several times in each year, in each group. We thus estimate effects unique to the interaction of group and year. Measurements of cofeeding in each experimental session were taken at fixed time-points after the introduction of peanuts. We explicitly account for the effects of peanut depletion on inferred cofeeding tolerance with a dynamic consumption model within each experimental session.

Outcome-level data are modeled with a specialized Binomial regression:

$$F_{[y,g,m,s]} \sim \text{Binomial}(N_{[y,g,s]}, \theta_{[y,g,m]}) \quad (1)$$

where: $F_{[y,g,m,s]}$ gives the count of chimpanzees (3 years and older) within the bounds of the food zone in year y , in group g , at measurement scan m , in experimental session s , $N_{[y,g,s]}$ gives the count of individuals (3 years and older) in the population in year y , in group g , during experimental session s , and $\theta_{[y,g,m]}$ gives the parameters of interest: the estimates of cofeeding tolerance specific to the respective year, group, and measurement scan.

We note that $\theta_{[y,g,m]}$ varies structurally by measurement scan, m . Since each scan, m , is done at equal intervals after the peanuts are added to the food zone (and consumed peanuts are not replaced), there is an overall negative trend in $\theta_{[y,g,m]}$ at each scan m , since chimpanzees presumably leave the food zone as food availability declines. Food availability (and hence our measure of cofeeding tolerance) is expected decline at a rate that is proportional to the density of cofeeders. In other words, groups with high initial cofeeding tolerance will deplete the peanut supply more quickly. This approach therefore provides a more refined estimate of cofeeding tolerance than the previous approach of averaging scans within a session.

To control for the structural interaction between food availability and initial cofeeding tolerance, we note that the food consumption dynamics can be approximated using the differential equation: $\partial X/\partial t = \omega X$, i.e., where the rate of change in X (e.g., cofeeding) is proportional to the level of X . This implies that X at time t can be expressed as:

$X(t) = X(0)e^{-\omega t}$, where $X(0)$ is the initial quantity of X and ω is a decay rate. Translating this dynamical model of resource depletion to our measure of social tolerance yields the following definition for $\theta_{[y,g,m]}$:

$$\theta_{[y,g,m]} = \underbrace{\text{logistic}(\kappa_{[y,g]})}_{\text{Maximal cofeeding tolerance}} \exp\left(- \underbrace{\exp(\phi_{[y,g]})}_{\substack{\text{Decay rate of apparent cofeeding} \\ \text{tolerance due to consumption}}} \underbrace{m}_{\text{Time step}}\right) \quad (2)$$

In Eq. 2, we use the logistic function to constrain maximal cofeeding tolerance to the unit interval, and the exponential function to constrain the decay parameter to be positive. Jointly, these constraints ensure that all values of $\theta_{[y,g,m]}$ lie on the unit interval, while also allowing the use of a multi-level model to estimate variation in maximal cofeeding tolerance as a function of covariates:

$$\kappa_{[y,g]} \sim \text{Normal}(D_{[y,g]}\beta_{[g]}, \sigma) \quad (3)$$

Here $\beta_{[g]}$ is a group-specific parameter vector giving the effects of various predictor variables. The row vector of data $D_{[y,g]}$ is composed of such covariate information—e.g., a constant 1, the lagged outcome (i.e., $\kappa_{[y-1,g]}$), group size, maternal kin frequency, and the frequencies of the different sex/age categories—from chimpanzee group g in year y . Finally, σ measures the unexplained variation of the κ random effects. Variation in maximal cofeeding tolerance can then be compared across groups and years by making calculations based on $\text{logistic}(\kappa_{[y,g]})$.

We also allow ϕ to depend on year and group:

$$\phi_{[y,g]} \sim \text{Normal}(\psi, \varsigma) \quad (4)$$

The parameter ψ gives the mean value of the decay parameter and ς controls variation in the decay parameter across years and groups.

We consider two basic models. In the first, we use a standard multi-level modeling design to estimate effects unique to each group:

$$\beta_{[g]} \sim \text{Multivariate Normal}(\mu, \Omega) \quad (5)$$

In the second, we fix the coefficients to be constant across groups:

$$\beta_{[g]} = \mu \quad (6)$$

To complete the models, we specify priors on the top-level parameters. First we note that the covariance matrix can be decomposed:

$$\Omega = \text{Diag}(\Sigma)\rho\text{Diag}(\Sigma) \quad (7)$$

which allows priors to be placed independently on the scale parameters Σ and correlations ρ . The prior on ρ is given using an LKJ prior of 2.5 on the Cholesky factor (see details in Stan code). The scale parameters have weak priors (Gelman, 2006):

$$\Sigma \sim \text{Folded Cauchy}(0, 2.5) \quad (8)$$

$$\varsigma \sim \text{Folded Cauchy}(0, 2.5) \quad (9)$$

$$\sigma \sim \text{Folded Cauchy}(0, 2.5) \quad (10)$$

and the location parameters have priors:

$$\mu \sim \text{Normal}(0, 5) \quad (11)$$

$$\psi \sim \text{Normal}(0, 5) \quad (12)$$

Additionally, the zero-th year social tolerance vector $\kappa_{[0]}$ has weak normal priors:

$$\kappa_{[0]} \sim \text{Normal}(0, 5) \quad (13)$$

7.2. The social relations model

As a check on the role of demographic variables on cofeeding tolerance, we conduct a social network analysis of cofeeding ties using individual-level data. To account for repeat observations of individuals and dyads, we use the social relations model (Kenny and La Voie, 1984; Koster et al., 2020) coded in `Stan` (see Pisor et al., 2019) and modified slightly for the data types of this current study.

Let $C_{[y,i,j]} \in \mathbb{N}$ be the number of measurement scans in year y in which individuals i and j were observed to have been in the food zone at the same time, and $N_{[y,i,j]} \in \mathbb{N}$ be the total number of scans in year y in which individuals i and j could have been in the food zone at the same time. We can model these outcomes using a binomial regression model:

$$C_{[y,i,j]} \sim \text{Binomial}(N_{[y,i,j]}, \text{Logistic}(\theta_{[y,i,j]})) \quad (14)$$

To parameterize the model, we first define intermediate variables. The effects of covariates linked to a focal individual are defined as:

$$\psi_{[y,i]} = \lambda_{[i]} + \beta_{[A(y,i), S(y,i)]} \quad (15)$$

The effects of covariates linked to alters are defined as:

$$\phi_{[y,j]} = \pi_{[j]} + \beta_{[A(y,j), S(y,j)]} \quad (16)$$

And, the effects of covariates linked to dyads are defined as:

$$\kappa_{[y,i,j]} = \delta_{[i,j]} + \gamma_{[1]} Z_{[y,i,j]} + \dots \quad (17)$$

We can then define $\theta_{[y,i,j]}$ as:

$$\theta_{[y,i,j]} = \iota + \psi_{[y,i]} + \phi_{[y,j]} + \kappa_{[y,i,j]} \quad (18)$$

Here: $A(y, i)$ is the age category of individual i in year y and $S(y, i)$ is the sex category of individual i (male, female without infant, or female with infant) in year y . The parameter array β thus contains random effects for the interaction of age category and sex category. The term Z is a matrix of dyadic variables. We use a series of such matrices with data on the nature of the dyad, with the effect of each variable given by a coefficient, γ . The parameters λ and π are both vectors and serve as individual-level random effects for focal and alter, respectively. The parameter matrix δ is a dyad-level random effect. Lastly, the term ι is an intercept coefficient.

To complete the model, we use the pooling structure outlined in *Statistical Rethinking* (McElreath, 2020):

$$\begin{pmatrix} \lambda_{[i]} \\ \pi_{[i]} \end{pmatrix} \sim \text{MV Normal} \left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_\lambda^2 & \sigma_\pi \sigma_\lambda \rho \\ \sigma_\lambda \sigma_\pi \rho & \sigma_\pi^2 \end{pmatrix} \right) \quad (19)$$

which, computationally, is better to implement by defining:

$$\begin{pmatrix} \lambda_{[i]} \\ \pi_{[i]} \end{pmatrix} = \begin{pmatrix} \sigma_\lambda \\ \sigma_\pi \end{pmatrix} \circ \left(L * \begin{pmatrix} \hat{\lambda}_{[i]} \\ \hat{\pi}_{[i]} \end{pmatrix} \right) \quad (20)$$

$$\sigma_\lambda \sim \text{Exponential}(1.5) \quad (21)$$

$$\sigma_\pi \sim \text{Exponential}(1.5) \quad (22)$$

$$\hat{\lambda}_{[i]} \sim \text{Normal}(0, 1) \quad (23)$$

$$\hat{\pi}_{[i]} \sim \text{Normal}(0, 1) \quad (24)$$

$$L \sim \text{LKJ Cholesky}(2) \quad (25)$$

where L is a Cholesky factor from the decomposition of the 2×2 correlation matrix with a correlation parameter, ρ , on the off-diagonal.

We use this same approach for the dyad-level random effects:

$$\begin{pmatrix} \delta_{[i,j]} \\ \delta_{[j,i]} \end{pmatrix} = \begin{pmatrix} \sigma_\delta \\ \sigma_\delta \end{pmatrix} \circ \left(L_\delta * \begin{pmatrix} \hat{\delta}_{[i,j]} \\ \hat{\delta}_{[j,i]} \end{pmatrix} \right) \quad (26)$$

$$\sigma_\delta \sim \text{Exponential}(1.5) \quad (27)$$

$$\hat{\delta}_{[i,j]} \sim \text{Normal}(0, 1) \quad (28)$$

$$L_\delta \sim \text{LKJ Cholesky}(2) \quad (29)$$

Applied to this data set, ρ , and its counterpart, ρ_δ , will go to unity, since ties are always coded reciprocally.

7.3. Software environment

Data analysis was handled entirely in R (version 3.5.0, [R Core Team, 2016](#)). Statistical models were coded in Stan and fit using the RStan package (version 2.19.2, [Stan Development Team, 2020](#)). Code and data for diagnostics and analysis replication are available at the Open Science Framework repository https://osf.io/meq59/?view_only=3cda5b91921a4178b6286955da16538c

7.4. Model fit and diagnostics

We diagnosed model fit and Markov Chain Monte Carlo performance using trace plots, \hat{R} , and reported effective samples ([Gelman et al., 2013](#)). In each of the three models, we fit 4 chains for 4,000 warmup and 6,000 sampling iterations each. In each case, \hat{R} values for all model parameters were less than 1.01 and effective sample size was $>1,600$ (normally much greater), and no error messages or warnings from Stan were thrown. Traceplots of the main regression parameters indicate excellent mixing and apparent convergence of all chains to the same posterior region. See Figures [S2-S4](#).

7.5. Posterior predictive checks

We checked the fit of our statistical models by plotting model predictions against the raw data. Figures [S5-S7](#) illustrate these posterior predictive checks. Across models, groups, years, and measurement scans, we observe good predictive accuracy, with model predictions generally falling in the middle of the data range. Our use of a dynamical model of resource depletion in our measure of social tolerance (for the peanut swing) allows for an accurate fit of the apparent declines in social tolerance due to the declining availability of peanuts. Note the downward trends in cofeeding frequency over measurement scans in the raw data (red) and model predictions (blue) in Figures [S5-S6](#). Note also that the use of the juice pipe paradigm negates the need for such a complex statistical model, since the raw data (red) in Figure [S7](#) show no evidence of decline over measurement scans. Our statistical model, however, still performs well in this case, recovering the fact that the decay rate parameter in this experimental setup is approximately zero in all groups. As such, our model still makes accurate predictions, as noted by the tight correspondences of the model predictions (blue) and raw data (red) in Figure [S7](#).

7.6. Variation in cofeeding tolerance across years and groups

Variation in cofeeding tolerance across years and groups is quantified in Figure [S8](#). Specifically, Figure [S8\(A\)](#) plots the coefficient of variation in maximal cofeeding tolerance across groups within years. We find that there is reliably greater across-group variation in cofeeding tolerance in some years (i.e., 2011 and 2012) than in other years (i.e., 2015 and 2016). Figure [S8\(B\)](#) plots the coefficient of variation in maximal cofeeding tolerance across years within groups. There is evidence that some groups (i.e., Group 1) show greater temporal variability in cofeeding tolerance than other groups (i.e., Group 2 or 4). Figure [S8\(C\)](#) then shows: 1) the average coefficient of variation in maximal cofeeding tolerance across groups—obtained by averaging the estimates in Figure [S8\(A\)](#), the average coefficient of variation in maximal cofeeding tolerance across years—obtained by averaging the estimates in Figure [S8\(B\)](#), and finally the log of the ratio of these terms. The fact that the log ratio lies reliably on the positive side of zero is evidence of greater inter-group differences within years than intra-group differences across years in maximal cofeeding tolerance.

7.7. Counter-factual predictive simulations

Our regression analysis suggests that demographic variables can explain much of the variation in maximal cofeeding tolerance. To investigate this relationship in more detail, we plot the results of a series of counter-factual simulations that illustrate how demographic variation affects predicted maximal cofeeding tolerance.

To begin, we reproduce Figure 3 from the main text as Figure [S9](#), which plots the time-series of maximal cofeeding tolerance by group conditional on the observed demographic variables (along with their group-specific effects) *and* the observed cofeeding data.

Next, in Figure S10, we plot the time-series of predictions of maximal cofeeding tolerance by group conditional on *only* the observed demographic variables and their estimated group-specific effects—i.e., we calculate $\text{logistic}(D_{[y,g]}\beta_{[g]})$ from Eq. 3 above using posterior estimates of β and the observed demographic data D . The results of this simulation can be interpreted as illustrating the predicted time-series of maximal cofeeding tolerance if we were to counter-factually redo the experiment in the same groups of chimpanzees, experiencing the same time-series of demographic changes. Note that the credible regions in Figure S10 are wider than those in Figure S9, reflecting the greater uncertainty we have about these estimates.

Next, in Figure S11, we plot the time-series of predictions of maximal cofeeding tolerance by group conditional on counter-factual demographic variables and group-specific random effects. In this case, the observed demographic data, $D_{[y,g]}$, are replaced with group-specific averages of the observed demographic data over time—i.e., for each element e in the row vector $D_{[y,g]}$, we define $\hat{D}_{[y,g,e]} = \frac{1}{Y} \sum_{y=1}^Y D_{[y,g,e]}$. This makes the demographic variables invariant over time, but lets them vary by group. We then calculate $\text{logistic}(\hat{D}_{[y,g]}\beta_{[g]})$ from Eq. 3 using posterior estimates of β and the counter-factual demographic data \hat{D} . The results of this simulation can be interpreted as illustrating the time-series of predicted maximal cofeeding tolerance if we were to counter-factually redo the experiment in the same groups of chimpanzees while keeping the group-specific demographic compositions constant over time. Note that in Figure S11, we now observe almost no change in estimates over time. Thus, the difference in predicted cofeeding tolerance between Figure S11 and Figure S10 is indicative of the predicted effects of demographic changes on cofeeding tolerance outcomes under our model.

We still see inter-group differences in predicted tolerance levels, partially due to the differing initial demographic characteristics across groups. In Figure S12, we again plot the time-series of predictions of maximal cofeeding tolerance by group conditional on counter-factual demographic variables and their group-specific effects, but in this case, the group-specific averages of the observed demographic data over time are themselves averaged, $\hat{\hat{D}}_{[y,g,e]} = \frac{1}{G} \sum_{g=1}^G \hat{D}_{[y,g,e]}$, yielding demographic variables that are fixed across groups and years. We then calculate $\text{logistic}(\hat{\hat{D}}_{[y,g]}\beta_{[g]})$ from Eq. 3 using posterior estimates of β and the counter-factual demographic data $\hat{\hat{D}}$. The results of this simulation can be interpreted as illustrating the time-series of predicted maximal cofeeding tolerance if we were to counter-factually redo the experiment in the same groups of chimpanzees with identical demographic compositions that remain constant over the eight years.

Note that in Figure S12 we see reduced inter-group differences in predicted tolerance levels. Now that inter-group variation in demographic variables has been counter-factually removed, the credible regions for the groups overlap, and are generally wider. Nevertheless, we still observe some inter-group differences—for example, Group 1 appears the least tolerant and Group 2 the most tolerant, and the credible regions for these groups are fairly well separated. From this simulation analysis, we can conclude that demographic variation across groups can explain much, but not all, of the variation in maximal cofeeding tolerance across groups. There is some evidence that groups differ in their tolerance levels in ways that are not reducible strictly to the demographic differences accounted for here.

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