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RESEARCH ARTICLE

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The effects of social context and food abundance on chimpanzee feeding competition

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Feeding competition is thought to play a role in primate social organization as well as cognitive evolution. For chimpanzees (*Pan troglodytes*), social and ecological factors can affect competition, yet how these factors interact to affect feeding behavior is not fully understood; they can be difficult to disentangle in wild settings. This experiment investigated the differential effects of food quantity, the presence of a co-feeding partner, and the contestability of a food patch on feeding rate. We presented tolerant pairs of chimpanzees from a semi-captive social group with an apparatus comprising a matrix of transparent tubes between two adjacent rooms, of which, either all (abundant condition) or only a small proportion (scarce condition) were baited with peanuts. Dyads were either grouped into the competitive treatment, in which peanuts were accessible from both sides of the apparatus simultaneously, or the non-competitive treatment, in which the peanuts were pre-divided; half of the tubes were accessible to one chimpanzee from one side, and the other half were accessible only from the opposite side of the apparatus. We compared dyadic tolerance levels with individual feeding rates across quantity conditions and between competitive treatments. While tolerance and food quantity had no effect on feeding rate, partner presence significantly increased feeding rate relative to individual feeding. This increase was much larger when the dyads directly competed over the peanuts than when they were co-feeding on a pre-divided set of peanuts. Thus, in a co-feeding situation, the presence of another individual and, to an even larger extent, the contestability of the food source play a larger role in chimpanzee feeding behavior than dyadic tolerance or food quantity. These findings highlight the relative impact of social facilitation and direct competition on co-feeding behavior between pairs of chimpanzees.

KEYWORDS
chimpanzee, co-feeding, competition, food abundance, social facilitation

1 | INTRODUCTION

Competition over limited resources is a ubiquitous challenge to overcome in the lives of social animals. When humans and other animals compete for resources, the nature and degree of competition can be influenced by various characteristics of the resource itself, such as quantity and distribution, as well as the social and ecological environment in which such goods are acquired (e.g., Begon, Townsend, & Harper, 2006; Gardner, Ostrom, & Walker, 1990). Such is the importance of food competition on animal social organization that optimal group size and structure are determined by a trade-off between the benefits associated with sharing ecological costs, and the drawbacks associated with competition over depletable resources (Brown, 1982). Therefore the nature of food competition for a given species—as measured by feeding rate (e.g., White & Wrangham, 1988), food encounter rates (Sterck, Watts, & van Schaik, 1997) or, more restrictively, as a function of agonistic social interactions between members of the same species (Christian, 1970)—can impact group organization. According to the ecological model, in addition to predation, the distribution of food can explain interspecies differences in dominance hierarchies, coalitions, and the quality of social relationships across the primate order (Sterck et al., 1997).

Chimpanzees, some of our closest living relatives, have highly social lives for which competition with group mates plays an important role (for a review see Schmelz & Call, 2016). A motivation to out-compete conspecifics appears so fundamental to chimpanzee lives that competition has been credited with helping to shape the evolution of their cognitive abilities (Hare, 2001). Indeed, when tested for cognitive performance, chimpanzees have shown more skillful performance in competitive than in cooperative tasks (Hare & Tomasello, 2004). The aim of this research is to differentiate the effects of the social and ecological context of a feeding bout on chimpanzee (*Pan troglodytes*) competitive behaviors, namely food intake rate and accuracy. Specifically, this experiment assesses to what extent chimpanzee feeding behavior is affected by the presence of a co-feeding partner (social facilitation), the accessibility of food by both partners simultaneously (contestability), the relative scarcity of food (quantity), and whether these effects are moderated by the relationship quality (tolerance) of co-feeding partners.

In their natural habitat, chimpanzees have a flexible fission-fusion social system which is often cited as a social adaptation to minimize intra-group competition by allowing groups to split into smaller feeding parties in response to seasonal fruit shortages (Asensio, Korstjens, Schaffner, & Aureli, 2008; Aureli et al., 2008; e.g., Doran, 1997; Furuichi, 2009; see also: Symington, 1988; Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996). This is, however, not a behavioral pattern observable within a specific feeding bout, but rather over longer time scales (Basabose, 2004). With a focus on how behavior is affected by competition within specific feeding bouts, evidence has been found for increased competition among wild chimpanzees while feeding from small patches in comparison to large patches of fruit, leading to the conclusion that "the relative severity of feeding competition compared to the possible benefits of sociality will vary with the distribution and abundance of food" (White & Wrangham, 1988, p. 148). Indeed, competition has been shown to be higher for scarce in comparison to abundant resources in humans as well (e.g., Gault, Meinard, & Courchamp, 2008; John, Melis, Read, Rossano, & Tomasello, 2017).

Crucially, however, chimpanzee competition in wild settings has been traditionally measured as a stable food removal rate based on the estimated size of the feeding patch (e.g., tree) and the number of individuals in the feeding party (e.g., White & Wrangham, 1988). This measure assumes a constant feeding rate for all individuals present throughout the duration of all feeding bouts, and ignores other potential activities at a feeding site such as socializing and resting (Isabirye-Basuta, 1988). Wild studies which have successfully taken into account specific individual feeding rates from focal observations report evidence of decreasing feeding rate during specific feeding bouts (Chapman, Wrangham, & Chapman, 1995). The limitation of this method is that visual access to specific food intake bouts is often extremely limited in chimpanzees' natural habitats, such that quantities per minute are difficult to verify. Additionally, this evidence fails to differentiate between satiation and a decrease in physical accessibility of food as a result of patch depletion (Chapman et al., 1995). Thus, it remains difficult to confirm whether chimpanzees alter their feeding rate as a result of food quantity and further, whether changes in individual feeding rate are a result of aspects of the social context, food quantity, or some combination of these factors, as they are inherently confounded in wild studies on feeding competition.

If competition over food resources does indeed vary as a function of food availability at a specific patch, then chimpanzees must be capable of differentiating patches with a high quantity of food (abundant) from patches with a low quantity of food (scarce). It has been argued that chimpanzees express sensitivity to food quantity by varying their food call production, for example, by producing more long-distance pant hoots at the discovery of abundant food patches in comparison to more scarce food patches (Ghiglieri, 1984; Wrangham, 1977). This effect has been replicated experimentally (Hauser & Wrangham, 1987). By showing that chimpanzees indeed call more for larger quantities of discovered food, these studies provide evidence that chimpanzees can discriminate differences in food quantity, even when relative differences are small (Beran, 2001; Boysen & Berntson, 1995).

Other factors affecting the nature of food competition are the physical size, distribution, and density of food patches, which directly affect how accessible food items are to competitors. Food that is physically monopolizable—i.e., densely clumped or large in size—such that individuals can prevent others from accessing it, leads to contest competition. Alternatively, food that is highly divisible and thus accessible to all competitors leads to scramble competition (van Schaik, 1989). Food call production experiments provide evidence that chimpanzees are sensitive to changes in the contestability of food items when quantity is held constant, calling less for monopolizable food items than for highly divisible items (Hauser, Teixidor, Fields, & Flaherty, 1993), indicating a sensitivity to the distinction between contest and scramble competition in chimpanzees.

In addition to the quantity or contestability of the food resource, the social environment may play a role in determining food competition among chimpanzees at specific food patches. Specifically, the nature of the relationship between feeding partners may play a role in moderating food competition, potentially over and above ecological factors (e.g., Eppley, Suchak, Crick, & de Waal, 2013; Evans et al., 2012). When a group of chimpanzees accessed baited food from holes on an experimental mound that steadily decreased in abundance over time, agonistic interactions around the food resource did not increase as the resource diminished, yet dyadic likelihood to groom or affiliate outside the experimental context was highly correlated with the probability to co-feed from the same increasingly scarce baited holes

(Calcutt, Ross, Milstein, Lonsdorf, & Bonnie, 2014). Thus, affiliative dyadic relationships may help to mediate competition over scarce resources. For example, tolerance in chimpanzees, defined as the propensity that individuals' will share a common food source (Melis, Hare, & Tomasello, 2006b), appears to moderate the strength of the dominance difference between partners and as such is an effective social predictor for collective action (Schneider, Melis, & Tomasello, 2012) and cooperation to obtain shared food rewards (Melis, Hare, & Tomasello, 2006b; Suchak, Eppley, Campbell, & de Waal, 2014).

Beyond relationship quality, the potential moderating effects of the presence and co-action of a partner in close proximity cannot be ruled out as an explanation for differences in feeding behavior. According to the drive theory of social facilitation (Guerin, 2010; Zajonc, 1965), the presence of conspecifics increases arousal, thereby affecting behavior in the context of task performance. Social facilitation is often referred to as a co-action effect, or, more specifically to "an increase in the frequency or intensity of [behavioral] responses . . . when shown in the presence of others engaged in the same behavior at the same time" (Clayton, 1978). Mechanisms promoting social facilitation are thought to be evolutionarily significant because behavior affected by the presence of a conspecific will have a tendency to optimize the exploitation of resources and protection from predators (Clayton, 1978), the two most often cited factors of the advantages of group living (e.g., Rubenstein, 1978). Social facilitation is suggested to increase fitness via various mechanisms including competition perception arousal, evaluation apprehension (Geen & Gange, 1977), and socially stimulated information acquisition in conditions of resource uncertainty (Galef & Giraldeau, 2001). For example, some authors have speculated that the mechanisms underlying socially facilitated behavior may vary within a species as a function of the current relative resource abundance at a given time (Lanjouw, 2002). Indeed, many animal species, from domestic chicks (Gallus domesticus; Tolman, 1964) to capuchin monkeys (Cebus apella; Dindo, Whiten, & de Waal, 2009; Galloway, Addessi, Fragaszy, & Visalberghi, 2005), have been shown to increase food intake when in the presence of conspecifics relative to feeding alone, even in the absence of competition. Experimental evidence shows that chimpanzees increase food intake rate when in proximity to a conspecific engaged in the same extraction task of their own (Engelmann, Herrmann, & Tomasello, 2016). Humans also increase their food intake rate when feeding with others (De Castro & Brewer, 1992), this effect being even stronger for meals shared with family than with other acquaintances (De Castro, 1994; but, see also: Herman, Roth, & Polivy, 2003) indicating the potential for relationship quality to moderate social facilitation effects, even outside the context of competition.

Given the potential for social facilitation to affect feeding rate while chimpanzees forage in proximity to one another, it is important to differentiate the effects of direct competition over mutually accessible foods from socially facilitated responses, when feeding rate is used as a measure of competition. Partner presence and food contestability can both affect feeding rate, yet because both involve the physical proximity of a conspecific during feeding these effects cannot be teased apart in observational studies, but must instead be experimentally examined. Moreover, the effects that food abundance or relationship quality have on socially facilitated or competitive feeding responses is not clear. Thus, the present study was designed to assess the differential effects of direct competition and social facilitation, as well as the moderating effects of food abundance, and the relationship of feeding partners on co-feeding behavior as compared to feeding alone.

Based on previous work we predicted chimpanzee feeding rate (a time-based estimate) would increase from the abundant condition to the scarce condition (Begon et al., 2006). We also predicted an increase in feeding rate due to partner presence, when comparing individual baseline rates with feeding rates in the non-competitive condition, in line with previous findings (Engelmann et al., 2016). Third, we predicted that feeding rates would increase from the non-competitive to the competitive treatment because direct competition over food has been shown to play a crucial role in chimpanzee social lives (Hare & Tomasello, 2004). Because social relationship quality has been shown to potentially moderate the effects of competition and social facilitation (Calcutt et al., 2014) we predicted differential feeding responses for dyads as a function of social tolerance index. Likewise for food abundance, we predicted that our quantity conditions would have a moderating effect on the competition between dyads such that low quantity trials in the competitive treatment would reveal higher feeding rates than high quantity non-competitive trials.

2 | METHODS

2.1 | Ethics

The present study was non-invasive and strictly adhered to the legal requirements of the country in which it was conducted. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology as well as the Uganda Wildlife Authority and the Uganda National Council for Science and Technology. Animal husbandry and research complied with the "PASA Primate Veterinary Healthcare Manual" and the policies of Chimpanzee Sanctuary & Wildlife Conservation Trust, Uganda.

2.2 | Subjects

We tested 20 semi-captive chimpanzees (11 males, 9 females, estimated 10–23 years old, mean age: 15.85) at Ngamba Island Chimpanzee Sanctuary, Lake Victoria, Uganda. All subjects came to the sanctuary as unrelated orphans as a result of the illegal bushmeat trade, were raised by humans together with peers (and in most cases with surrogate chimpanzee mothers) and lived together in one social group. The vast majority of subjects had access to a large tract of primary forest (38.5 hectares) throughout the day. All chimpanzees came back from the forest every evening and spent the night in indoor enclosures (average 35 m^2) with hammocks. Two of these adjacent indoor enclosures were used as testing rooms (14.5 m^2 each). All participants voluntarily participated in the study and were never deprived of food or water for any reason. In addition to the food available in the forest and the four species-appropriate meals they were provided, all subjects received peanuts in their night rooms, used as our testing rooms. Water was available ad libitum from the night rooms.

2.3 | Materials

The test apparatus comprised 36 horizontal Plexiglas® tubes situated between the bars of two adjacent rooms configured in a 6 × 6 matrix (see Figure 1 for apparatus layout). Tubes measured 9 cm in length with 4 cm inner diameter. Two parallel Plexiglas® panels housed the tubes and stabilized the matrix from either side of the bars, allowing subjects to see into each tube from any angle as well as between and through all tubes to the adjacent room. Subjects could access baited peanuts from the middle of each tube (placed in the central 1 cm of tubes, approximately 4 cm from either edge) using 1–3 fingers or, in some cases, an upper lip. In the non-competitive treatment, three of the six rows were blocked on either side using 4 cm diameter Plexiglas® circles, preventing access to the peanuts to one side of the apparatus but not the other side. Blocked circles were colored around the outer edges using highlighter markers to visually distinguish them from non-blocked tubes. Rows were blocked in an alternating pattern such that accessible and non-accessible rows were spaced one after another. This pattern had an inverse order for subjects on either side of the apparatus. In this way, 50% of the peanuts were available to one subject and the other 50% were available to the other subject.

2.4 | Design and procedure

All subjects participated in a familiarization phase and a tolerance pre-test before moving on to the test conditions.

2.5 | Familiarization

Prior to testing, each subject was familiarized alone with the apparatus. In familiarization sessions, all tubes were baited with one peanut each. All subjects were given the opportunity to explore the apparatus individually, without the influence of nearby conspecifics. For all subjects, the apparatus was set up in the non-competitive treatment state with alternating rows blocked on either side. The door between the two test rooms was open, allowing full access to all baited peanuts throughout familiarization trials. This method allowed all subjects experience with extracting peanuts, and with blocked tubes, from both sides of the apparatus. Subjects were given one trial per session, with three consecutive sessions, in which they could extract the peanuts on both sides of the apparatus until all peanuts were gone.

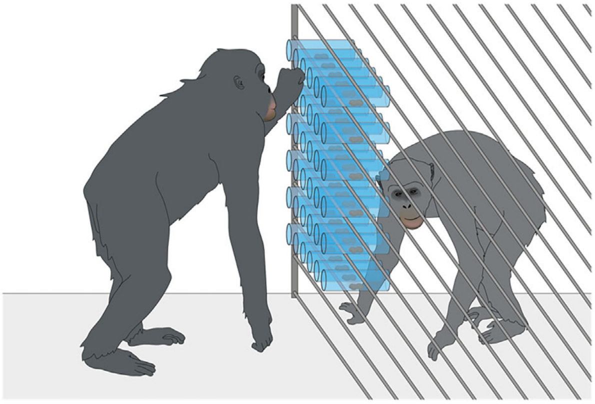

FIGURE 1 Apparatus setup in open competitive state

2.6 | Tolerance pre-test

After individual familiarization, subjects were tested on a tolerance co-feeding task to ascertain dyadic tolerance levels. We predicted that only chimpanzee pairs who would naturally be inclined to feed in close proximity to one another would be affected by social facilitation and direct competition. Thus, the aim was to test dyads who would be most likely to feed in close proximity outside of the experimental context. For this reason, pairings of maximal tolerance were selected based on caretaker recommendations. Caretakers were asked which individuals would be most likely to feed within an arm's reach of one another during group feeding times in their daytime forest enclosure. In cases for which caretaker recommendations did not yield a clear pair match, pairings were based on previous tolerance data involving many of the same individuals (e.g., Melis, Hare, & Tomasello, 2006a). Dyads were presented with a matrix of 24 banana pieces and 40 peanuts arranged on the ground in a grid divided exactly in half between two adjacent rooms. Tolerance criterion was met when both subjects co-fed on the matrix within 1-m proximity for more than 5 s, on at least three of four consecutive sessions. The separating bars were wide enough for a full chimpanzee arm extension, allowing for one subject to displace the other, thereby monopolizing the entire array of food by one individual, as would be expected of non-tolerant pairs. Subjects were allowed entrance to the two adjacent rooms, one per room, at the same time. All 10 dyads passed criterion and thus proceeded to the test phase of the study.

2.7 | Test conditions

Individuals were tested in only one dyad for the full experimental cycle. To avoid carry-over or learning effects of experience on behavior, each dyad was randomly assigned to either the competitive or the non-competitive group, such that all dyads experienced only one of the two treatments. Group composition was balanced for between-group tolerance, such that the aggregate group tolerance levels approached equal distribution. With this design, we aimed to compare feeding behavior under scramble competition (represented by the competitive state) with feeding behavior in the in the same physical and social context but in the absence of scramble competition (the non-competitive condition state). Within each treatment group, dyads were presented with the scarce and abundant condition test cycles, with order of conditions counterbalanced across dyads. All subjects were presented first with an individual (solo) feeding trial in either the scarce or abundant condition. Solo trials consisted of a single subject entering their room without the presence of their dyadic partner, who was located neither in the adjacent room, nor in the vicinity of the testing rooms. Individuals only had access to their side of the apparatus across both competitive and non-competitive treatments during solo trials. The first solo trial was followed by two dyadic trials in the same scarce or abundant condition. Each subject then received a post-dyadic solo trial, for a total of four trials in each quantity (i.e., scarce or abundant) condition. In the abundant condition, all 36 tubes were baited and in the scarce condition only 8 tubes were baited, in a consistent pattern of two clumped squares diagonally terminating in the center (see Figure 2).

Dyads then repeated this process of four trials for the remaining quantity condition, for a total of eight trials, with one trial per day. Each subject was randomly assigned one of the two rooms and experienced all test trials from this same room throughout the experiment. Across all conditions, baited tubes contained three peanuts each. Subjects began all trials from two over-head tunnel hatches, each with entrance into one of the two adjacent experimental rooms, equidistant to the apparatus. Trials began when dyads were simultaneously given access to the experimental rooms and ended when all available peanuts had been consumed.

2.8 | Coding & analysis

All videos were coded to determine the two main dependent variables for each subject: feeding rate and feeding accuracy. All experimental trials were first coded for total individual feeding time per trial, measured from the time each subject entered (by inserting a finger or lip) the first tube upon approach of the apparatus, and ended at the time the last peanut was extracted from the apparatus.

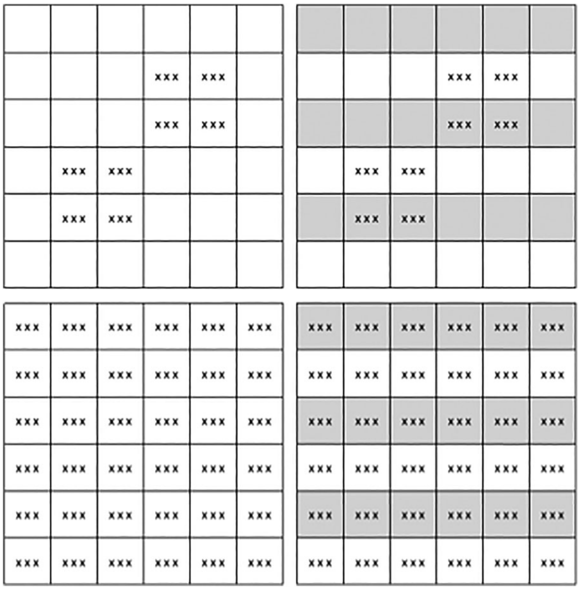

FIGURE 2 Layout of baited tubes in four test states. “x”s indicate baited peanuts. Top left: scarce condition, competitive layout. Top right: scarce condition, non-competitive layout. Gray rows indicate blocked tube rows. Bottom left: abundant condition, competitive layout. Bottom right: abundant condition, non-competitive layout

To determine individual feeding rate, videos were coded for individual net tubes entered (total number of tubes from which at least one peanut had been extracted per individual, per trial). Individual feeding rate was therefore calculated as the net tubes entered per individual and per trial divided by individual feeding time (duration). To assess feeding accuracy, videos were also coded for individual gross tube entries (total number of tube entries per individual, per trial, whether entries resulted in peanut extraction or not). Feeding accuracy was measured as the ratio of the net tubes successfully fed from per trial over the gross tube entries per trial. The accuracy response variable thus represented the proportion of successful (i.e., at least one peanut was retrieved) tube entries out of all total tube entries per trial. Tolerance trials were also coded for duration of 1-m proximity co-feeding as well as total overall dyadic feeding time, the ratio of which determined tolerance index. All data were coded by the experimenter; 20% of all coded videos, representing equal proportions of each condition, were re-coded by a second coder, blind to the predictions of the study. Inter-rater reliability correlations indicated a high degree of agreement between coders for experimental feeding duration ($r = 0.96$), net tubes ($r = 1.0$), and for 1-m proximity co-feeding duration ($r = 0.95$) as well as overall dyadic feeding duration ($r = 0.85$) in tolerance trials.

The analysis was conducted in R (version 3.0.2; R Core Team, 2016) using the lme4 package (Bates, Maechler, Bolker, & Walker, 2014). Variance Inflation Factors we derived using the function vif of the R-package car (Fox & Weisberg, 2011). The sample size for these analyses were 160 feeding rates, and 160 feeding accuracies, determined for 20 subjects arranged in 10 dyads and tested in a total of 80 sessions.

To test whether our response variable, individual feeding rate per trial, was influenced by our social or quantity conditions, by our competitive treatment, or by the tolerance index of the dyads, we used a Generalized Linear Mixed Model (GLMM; Baayen, 2008). The test predictors (Mundry, 2014) with fixed effects included the factors quantity (levels: scarce and abundant), social condition (levels: solo and dyadic), and competitive treatment (levels: competitive and non-competitive) as well as the quantitative predictor tolerance index. Based on the prediction that feeding rates may vary with the tolerance level of the dyad tested, and that tolerance may have a differential effect across varying quantities, social states, and competitive treatments we also included the three two-way interactions between tolerance and quantity, social condition, and competitive treatment. The model also included a three-way interaction between social condition, competitive treatment, and quantity, based on the prediction that the effect of feeding with a partner present may be differentially affected by whether or not the food is under direct competition and by the relative amount of food available. For example, we predicted differential changes in feeding rate between solo and dyadic feeding when dyads encountered a large amount of pre-divided food, as compared to a relatively small amount of food under direct competition. The model included fixed effects of session and order of quantity conditions as control predictors.

To avoid pseudo-replication we included random intercepts for subject (which included both the individual and the partner), dyad, and session (nested within dyad). Since each individual was a member of one dyad only we assigned it to the respective dyad regardless of whether it was tested in the dyadic or solo condition. In order to keep the type I error rate at the nominal level of 5% we included random slopes (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) of session within subject and dyad as well as those of quantity and social condition (both manually dummy coded) and their interaction within subject and dyad. Note that with regard to the random slopes this model is maximal as recommended by Barr et al. (2013); however, we did not include the correlations among random slopes and intercepts in order to avoid an overly complex model and because neglecting these correlations does not compromise type I error rates (Barr et al., 2013).

Because individual feeding rate was right skewed and included a considerable proportion of tied observations we fit the model with the net number of tube entries as the response, using a Poisson error structure and log link function and included the log-transformed individual feeding duration as an offset term (McCullagh & Nelder, 1989). Prior to fitting the model we z-transformed session number and tolerance index to a mean of 0 and standard deviation of 1 (Schielzeth, 2010). Variance Inflation Factors (VIFs; Field, 2005) were derived from a standard linear model including only the fixed main effects. The largest VIF for the model was 1.34 indicating that collinearity was not an issue. The model was also determined to be stable by excluding subjects, dyads, and sessions, one at a time from the data. The estimates derived from the respective subsets of the data were subsequently compared with those obtained for the full data set, which indicated no influential levels of the random effects to exist. Overdispersion was not problematic (dispersion parameter: 0.69).

To determine whether the test predictors collectively had an effect on feeding rate, we conducted a full-null comparison (Forstmeier & Schielzeth, 2011), whereby the null model lacked all test predictors, leaving only fixed control and random effects. We compared the two models using a likelihood ratio test (R function anova with argument test set to "Chisq"; Dobson, 2002). Significance of individual predictors was determined using subsequent likelihood ratio tests (R function drop1; Barr et al., 2013) comparing the full model with a model lacking the respective predictor to be tested. From the final model, we conducted pairwise comparisons (Wald Z test) to determine specific differences between the individual factors.

We also analyzed the effect of all above predictors, interactions, fixed & random effects on feeding accuracy using a GLMM with binomial error structure and logit link function. Model stability checks revealed no problems, the VIFs revealed no collinearity issues (highest VIF = 1.34), and over-dispersion was not problematic (dispersion parameter: 0.65). We transformed variables and compared the full, null, and reduced models using the same methods described above.

3 | RESULTS

Means and distributions of the experimental feeding rate response can be found in Table 1. The feeding rate full-null comparison revealed significance (likelihood ratio test: $\chi^2 = 28.56$, df = 11, $p = 0.003$), indicating that the test predictors as a collective had a significant effect on the feeding rate (see supplementary material for full and final model output). Reduced model comparisons indicated that all interactions were non-significant (all $p > 0.34$) and were therefore dropped from the final model, with the exception of a significant two-way interaction between the competitive treatment and the social condition ($\chi^2 = 12.67$, df = 1, $p < 0.001$; see Figure 3). Likelihood ratio tests revealed non-significant effects for tolerance ($\chi^2 = 0.11$, df = 1, $p = 0.74$) and quantity ($\chi^2 = 0.005$, df = 1, $p = 0.94$). Pairwise comparisons for factors involved in the significant interaction revealed that feeding rate significantly increased from feeding alone (solo) to co-feeding (dyadic) in both the non-competitive treatment group ($z = 2.67$, $p = 0.008$) and the competitive treatment group ($z = 9.72$, $p < 0.001$). Feeding rate in the dyadic competitive group was significantly higher than in the dyadic non-competitive group ($z = 3.89$, $p < 0.001$). Thus, feeding rate increased from solo feeding to dyadic feeding in each of the competitive treatment groups, however, this increase in feeding rate was significantly larger in the competitive treatment group than in the non-competitive treatment group ($z = 4.66$, $p < 0.001$).

The feeding accuracy full-null model comparison was not significant (likelihood ratio test: $\chi^2 = 10.88$, df = 11, $p = 0.45$) and no further testing was done. Feeding accuracy appeared to remain unaffected by tolerance, our social and quantity conditions, and competitive treatment (See supplementary material for full accuracy model output).

4 | DISCUSSION

We investigated the effect of food abundance, food contestability, dyadic tolerance, and partner presence itself on the feeding rate of co-feeding chimpanzee dyads. Our results highlight the importance of certain aspects of the social context for chimpanzees engaged in co-feeding with conspecifics. Specifically, the presence of others engaged in the same feeding task in close proximity and the contestability of the food resource appear to have a much stronger influence on feeding rate than the tolerance of the co-feeding pair and

TABLE 1 Mean (standard deviation) of all solo and dyadic net tubes feeding rates for the non-competitive and competitive groups in both scarce and abundant conditions

	Non-competitive mean (SD)	Competitive mean (SD)
Solo abundant	0.30 (0.05)	0.28 (0.11)
Dyadic abundant	0.42 (0.12)	0.68 (0.27)
Solo scarce	0.40 (0.21)	0.34 (0.10)
Dyadic scarce	0.46 (0.19)	0.76 (0.21)

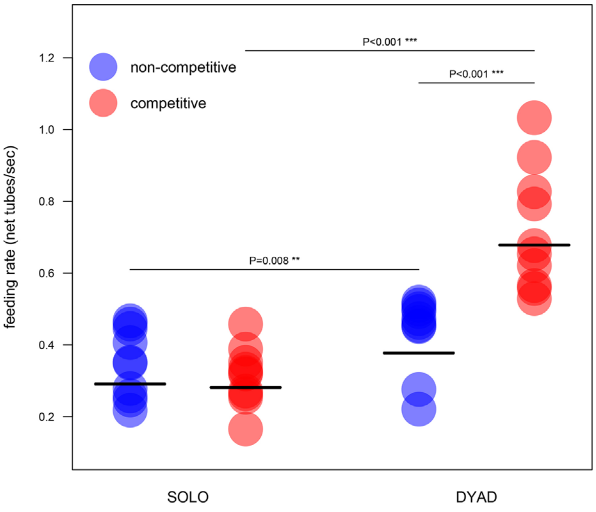

FIGURE 3 Feeding rates for solo and dyadic conditions in the non-competitive (blue) and competitive (red) treatments. Points show the observed feeding rates and black lines show the values fit by the model. Quantity conditions were pooled because no effect for quantity was found

the quantity of the food resource available. Our results also indicate that in chimpanzees, directly competing over a divisible food resource affects feeding behavior over and above the simple socially facilitated effect of the presence of a partner in a feeding situation. The latter findings corroborate previous experimental results showing a socially facilitated increase in food extraction rate in chimpanzees due to the presence of a partner in close proximity engaged in the same food extraction task (Engelmann et al., 2016). As predicted, social facilitation played a role in co-feeding to the extent that the presence of a conspecific feeding from the other side of the apparatus—even when no contest for peanuts was involved—increased peanut feeding rate.

That peanut quantity did not lead to discernible differences in feeding behavior could be an indication that food scarcity or abundance does not affect co-feeding behavior in chimpanzees. This finding substantiates recent experimental work with chimpanzees and children which found, at least in chimpanzees and 4-year-old children, no evidence of heightened value-attributions toward items presented as scarce versus abundant, even in the context of competitors (John et al., 2017). On the other hand, 6-year-old children in the same study paradigm did show a strong scarcity preference, especially in the context of competitors, leading the authors to conclude that this preference develops uniquely in human ontogeny and is not shared by chimpanzees. In line with these findings scarcity, as measured in this study, does not appear to affect feeding behavior in chimpanzees when compared to other social factors such as partner presence and, to an even greater extent, food contestability.

One alternative interpretation of this finding is that the relative difference between our scarce and abundance conditions, in which 8 and 36 tubes were baited, respectively, lacked the perceptual salience to produce behavioral changes. Chimpanzees are capable of distinguishing between different quantities of food, even when the differences themselves are small (Beran, 2001; Boysen & Berntson, 1995), yet it is possible that the relative difference between scarcity and abundance must be larger than was manipulated in this study for food quantity differences to affect feeding behavior. For example, there is a salient difference between the perceptual scarcity of a small patch of ripe fruits surrounded by a large tree full of inedible fruits, and the perceptual abundance of a full tree crown of ripe fruits so plentiful as to be impossible for a sub-group of chimpanzees to consume them in one feeding bout. The scarce and abundant conditions used here could not have reflected such a large relative difference. A second alternative interpretation is that relative scarcity affects competition in captive and semi-captive populations less than it may in wild populations. For food-provisioned populations of chimpanzees, the effects of social facilitation and contestability (direct competition over divisible foods) may be more influential for co-feeding behavior when compared to the relative scarcity or abundance of a food patch.

Dyadic tolerance, as measured in co-feeding pre-tests for dyads tolerant enough to feed simultaneously in close proximity, also appeared to have no effect on co-feeding response across conditions. This could be due again to the relative importance of competition over other features of co-feeding scenarios. However, it is also possible that the range of tolerance levels tested in this experiment was not variable enough to discern differences as a result of tolerance. It is possible that a wider range of dyadic tolerance than was measured in this study would result in different co-feeding responses across our competitive treatments or abundance conditions. Little can be said, however, about dyadic competition between dyads not tolerant enough to co-feed from the apparatus, as was the case for one of our original female pairs. This dyad passed the tolerance pre-tests yet declined to co-feed from the apparatus during experimental trials and was subsequently removed from the study. Thus, it is likely that once a dyad is tolerant enough to co-feed at close proximity, they will show feeding behaviors in line with the results reported here. Because the dyads that took part in the study were highly tolerant, the effects of food displacement, a dominance-based form of food monopolization, were minimized. As a result, the findings of this study offer a closer look at how scramble competition, as represented by the competitive treatment, affects chimpanzee feeding behavior with tolerant partners.

This study supports the well-established notion that competition is a highly influential force for chimpanzees (e.g., Bräuer, Call, & Tomasello, 2007). Co-feeding behavior is differentially affected by the presence of a partner and whether the food is contestable. These two factors are not easily dissociable in wild studies on feeding competition in chimpanzees, which are limited with respect to feeding rate measurements and cannot isolate the effects of partner presence and contestability while keeping the food source or quantity constant (e.g., Chapman et al., 1995). The results of this study suggest that when chimpanzees co-feed on patches of ripe fruits in the wild, the size of the patch itself and the tolerance of co-feeding dyads may not have an immediately observable effect on the competition between individuals. However, individuals will feed faster when a feeding partner is not only present but also able to access the same food items simultaneously, and therefore compete over them. The interaction between social facilitation and competition over contestable foods stresses the importance of the social context for chimpanzees while co-feeding, as food contestability and distribution indicates how much can be monopolized and how much can potentially be taken by others.

Future experimental research on co-feeding competition should examine the distinction between the effects of direct competition and social facilitation by expanding upon this paradigm with further exploration into the role of group size, which is particularly relevant for chimpanzees in non-fission-fusion captive settings. By expanding this paradigm beyond the dyadic interaction, we will gain further understanding of the interplay between the social and ecological context on co-feeding behavior in chimpanzees.

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ETHICAL APPROVAL

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

CONFLICT OF INTEREST

The authors have none to report.

DATA AVAILABILITY

The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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