



Captive chimpanzees share diminishing resources

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Abstract

Wild chimpanzees routinely share high-value resources such as meat obtained through hunting and fruit procured from raiding crops. Although it is predicted that the proximate mechanisms for sharing behaviour are the result of reciprocity, interchange and mutualism, examinations of these factors in captivity have not mirrored the degree to which they are found in the wild. The goal of the current study was to investigate how a group of seven captive chimpanzees responded when a highly desirable and monopolizable resource diminished over the course of eight months. To do this we measured the amount of time that was spent sharing food at an artificial termite mound as well as the relationship between dyads that spent time sharing. Our results contradicted our predictions that rates of aggression would increase and the number of individuals fishing at the termite mound would decrease when resources diminished, as we observed no difference in either variable over time. We did, though, find an increase in the amount of sharing as the number of baited holes decreased. We also found a correlation between the strength of dyadic relationships outside of the study and the amount of time that individuals spent sharing with each other.

Keywords

sharing, social tolerance, chimpanzee.

1. Introduction

As a social species, chimpanzees (*Pan troglodytes*) must routinely balance the costs and benefits of intraspecific competition with those of cooperation

(Muller & Mitani, 2005). If a resource becomes increasingly monopolizable, as would occur when a preferred food source becomes scarce, competition between individuals is predicted to increase (Wittig & Boesch, 2003). For example, in Gombe National Park, Tanzania, higher population densities lead to high rates of aggression between resident female chimpanzees and immigrant females over access to food resources (Pusey & Schroepfer-Walker, 2013). Although aggression is common, wild chimpanzees are well known for their ability to demonstrate social tolerance and mitigate competition. Chimpanzees in Tai National Forest share meat from hunts even when only a small amount is caught (Boesch & Boesch, 1989) and chimpanzees at Bossou share high-value fruit that was risky to obtain (Hockings et al., 2007). Wittig et al. (2014) found higher levels of oxytocin, in individuals who had recently shared food than in those who had recently spent time grooming. Given that oxytocin is thought to be important for social bonding, these results indicate that activities such as food sharing could be important for forming and maintaining social relationships.

Although such prosocial tendencies have been routinely investigated in captive chimpanzees, results from these studies often fail to replicate the high levels of cooperation and sharing that have been observed in the wild. Studies that aim to examine cooperation and sharing behaviours in captive chimpanzees show that subjects fail to maintain reciprocal cooperation, do not transfer food to a partner at no cost to themselves and make choices based on side preference rather than whether a subject in an adjacent enclosure receives food (Silk et al., 2005; Vonk et al., 2008; Yamamoto & Tanaka, 2009; but see Horner et al., 2011). These results have led to the conclusions that chimpanzees perform better within competitive rather than cooperative experimental paradigms and do not respond prosocially to the presence of a social partner (Hare & Tomasello, 2004; Yamamoto & Tanaka, 2009); conclusions that contradict behaviour observed in the wild.

One explanation for this discrepancy may be that most captive studies separate chimpanzee subjects from their social groups and utilize social dyads that are accustomed to working together (but see Crick et al., 2013). Since chimpanzees live in dynamic social groups, factors such as reproductive opportunities, reciprocal exchanges and relationship quality are likely critical for determining when and with whom they cooperate or share food (Nishida, 1968; van Lawick-Goodall, 1968; de Waal, 1989; Mitani & Watts, 2001). Although choosing affiliative pairs for dyadic experiments may ensure low lev-

els of social tension and allow for high levels of control, it does not reflect the complete social milieu encountered by chimpanzees living in large groups.

According to Noë & Hammerstein (1995), partner choice is the most common way for an individual to gain resources through cooperation. Therefore, chimpanzees that are given the opportunity to work within a group setting, and to choose the individuals with whom they interact, are able to exhibit more natural decision-making processes than those working in pre-determined dyads. In addition, studies that use tolerant pairs lack the ability to examine how measures of prosocial and agonistic behaviours outside of a testing situation may correlate with the ways in which individuals choose their own social partners. Eppley et al. (2013) for example, examined group-wide food sharing in captive chimpanzees and found that an interaction between relationship quality and begging persistence significantly determined with whom a food possessor would share.

In this study we investigated how increasing food competition influences social tolerance in a group of zoo-housed chimpanzees ($N = 7$) by examining whether or not they share a high-value food source that diminishes over time. The data we present here comes from a study that was originally designed to determine how chimpanzees cope with environmental variability while fishing from holes at an artificial termite mound (Bonnie et al., 2012). Because of the close proximity of the holes and the fact that they can be easily monopolized, activities at the termite mound require high levels of tolerance. While conducting our primary analyses, we discovered that our subjects shared fishing holes regularly. Social tolerance can be measured by the tendency toward prosocial behaviours and food sharing is a particularly good indication that a social partner is accepted (de Waal, 1997a; Melis et al., 2006; Hare et al., 2007). Therefore, we examined social tolerance by measuring rates of sharing at the termite mound as well as changes in affiliation and aggression as the number of baited holes decreased. We also investigated relationship characteristics to determine whether they influenced who shared with whom. Although chimpanzees have exhibited high levels of social tolerance at the artificial termite mound when all holes were baited with a food reward (Lonsdorf et al., 2009), we hypothesized that as the availability of resources in our experiment declined the chimpanzees would spend less overall time fishing and would show less social tolerance, as indicated by a decrease in sharing activity, at the mound (Prediction I). We also predicted that the number of individuals fishing at the baited termite mound and

the number of dyads sharing baited holes would decrease as the number of baited holes decreased (Prediction II) and that competition over fewer baited holes would cause overall rates of agonism to increase in the group (Prediction III). However, since chimpanzees often mitigate social stress through prosocial behaviours such as grooming (Nieuwenhuijsen & de Waal, 1982; Baker, 1992; Caws & Aureli, 2003; Palagi et al., 2004), an alternative to prediction III was that we would see an increase in affiliation as the number of baited holes decreased. During the study, the integrity of the social group was maintained so that all individuals in the group had access to each other. We then used data from a long-term observational study to investigate how social behaviours correlated with sharing at the termite mound.

2. Methods

For this study we define sharing as the “joint use of monopolizable food items” (Stevens & Gilby, 2004, p. 603). This includes both active transfers of food as well as passive food sharing, which takes place when the possessor tolerates the consumption of part of a controlled food item by another individual (Boesch & Boesch, 1989; Gilby, 2006; Hockings et al., 2007). While both types of sharing have been documented in chimpanzees, passive food sharing is most prevalent (Hauser et al., 1993; Nishida & Turner, 1996) and it was the only type of sharing that was possible in our study given the design of the artificial termite mound. Following Lonsdorf (2005), we considered a subject to be fishing when he or she made contact with a hole using a tool, interacting and/or modifying a tool, licking the tool after obtaining food, poking or prodding a bait hole using fingers or toes, and inspecting the mound using visual or olfactory senses. Two or more subjects were considered sharing when they both exhibited fishing behaviours at the same hole (see Figure 1).

2.1. Subjects and housing

The subjects were a group of seven chimpanzees (3 males and 4 females; Table 1) housed at the Regenstein Center for African Apes (RCAA) at Lincoln Park Zoo, Chicago, IL, USA. All animals were captive born. The exhibit had an indoor/outdoor design; the indoor exhibit measured 124 m² and the outdoor exhibit measured 613 m². Access to the outdoor yard was temperature dependent, and during the course of the study, the group had outdoor access at varying times depending on weather conditions. The indoor exhibit,



Figure 1. Two chimpanzees sharing a hole while fishing at an artificial termite mound. Photo courtesy of Lincoln Park Zoo.

where the artificial termite mound was located, contained climbing structures of varying heights, deep-mulch bedding and was visible to the general public during daytime hours. Daily meals of fresh produce and biscuits were scattered through the exhibit twice daily, but never within 1 h of testing.

2.2. Apparatus

The artificial termite mound (hereafter ‘the mound’) was a hollow structure with a concrete crust approximately 274 cm wide and 205 cm tall. Eight

Table 1.

Individual and kinship details of the study subjects.

ID	Sex	Date of birth (dd/mm/yyyy)	Relatedness
Hank	Male (alpha)	30/11/1990	Unrelated
Cashew	Female	18/08/1984	Mother of Kipper
Kathy	Female	02/09/1990	Mother of Chuckie
Nana	Female	20/01/1994	Unrelated
Chuckie	Female	24/09/1999	Daughter of Kathy
Optimus	Male	09/01/1999	Unrelated
Kipper	Male	22/01/2000	Son of Cashew

holes, each approximately 15 cm deep, were evenly distributed on the mound and easily monopolized by a single individual. Each hole could be attached to polyvinyl chloride (PVC) receptacles through the interior of the mound. The exterior of the mound was only visible to the apes, and therefore keeper staff could easily access the inside of the mound without entering the chimpanzees' enclosure. Before each session, research staff filled PVC tubes with ketchup (532 ml) and keeper staff accessed the interior of the mound to attach the tubes to each bait hole. The chimpanzees acquired and used natural vegetation (hay, trees, branches, etc.) from their outdoor enclosure as tools to extract ketchup from the mound (hereafter referred to as 'fishing'). The testing apparatus was available to the group as a whole without human intervention. No animals were trained to complete the task or given a demonstration of any portion of the task. Prior to the present study, the chimpanzees had intermittent access to the mound from July 2004 to June 2008 during which the group became proficient at fishing (Lonsdorf et al., 2009).

2.3. Procedure

During the study period, from 28 July 2008 to 20 March 2009, the mound was baited each weekday from 12:00–13:00. In the baseline condition, we baited all eight holes with ketchup, as had been done for prior experiments (Lonsdorf et al., 2009). After 10 days, we removed one tube and capped the opening, leaving 7 baited holes. One additional tube was removed every 10 days until all holes were capped, leaving zero baited holes. The study consisted of 17 such time periods, which are herein referred to as phases. The order of holes capped was determined by calculating the most preferred hole for each phase. After one 10-day phase during which all tubes were empty, we added one baited tube back into the mound every 10 days using the same methodology described above, until all eight holes were baited. Each phase was 10 days in length, except in rare circumstances when there were technical difficulties (mean number of days per phase = 8.7). The research staff involved in collecting live data and video scoring was blind to which holes were capped for the entire study (see Bonnie et al., 2012 for details).

2.4. Video scoring

For each experimental session, we used a ceiling-mounted security camera located outside of the exhibit to capture all occurrences of behaviours at the mound and/or within a 1 m perimeter around the mound from 12:00–13:00. The security camera was connected to a DVD-R that was set to record

each 1-h session. DVDs were then scored using Noldus Observer Video-Pro 5.0 (Noldus Information Technology, Wageningen, The Netherlands) by four trained researchers who achieved an inter-observer reliability of >85% accuracy. The study consisted of 170 observation hours divided into 17 phases, each consisting of 10 1-h sessions. For each session, we scored, in seconds, the duration of fishing behaviours and the hole at which the fishing behaviours occurred for every focal subject, including when 2 subjects were fishing at the same hole.

2.5. Analysis

2.5.1. Fishing and sharing durations

We did not include phase 9, in which no holes were baited, in the analysis but for each of the remaining 16 phases, we calculated every individual's fishing duration per phase by summing the total time that an individual spent fishing in that phase. Likewise, we calculated an individual's sharing duration by summing an individual's time spent sharing in that phase. To analyse whether the amount of time that each individual spent sharing a hole at the mound changed relative to the number of baited holes and the amount of time spent fishing (Prediction I); we ran general linear mixed models (GLMMs) in SAS (Version 9.2) with duration of sharing as the response variable. The predictor variables were duration of fishing and a categorical variable for the number of baited holes available, hereafter referred to as 'hole availability': 1–2 baited holes = low; 3–5 baited holes = medium; 6–8 baited holes = high. We included a random effect for each subject to account for repeated measures on individuals.

2.5.2. Number of individuals and dyads fishing

In order to determine whether a reduction in the number of baited holes was associated with a decrease in the number of individuals fishing at the baited mound (Prediction II) we documented individual presence at the mound during every day of each phase as well as which dyads were sharing. We then used a repeated-measures ANOVA to examine whether fewer individuals fished at the mound as the number of baited holes decreased. We used a Pearson Correlation to investigate whether fewer dyads shared holes at the mound when fewer holes were baited and confirmed these results by calculating a 95% confidence interval via bootstrapping which was assessed using 2000 replicates.

2.5.3. *Agonistic and affiliative behaviour*

We analysed Prediction III by examining whether there was a change in agonistic or affiliative behaviour as the number of baited holes changed. To do this we extracted frequencies of agonistic and affiliative behaviours for each dyad during a time period over which the baiting of the mound could have influenced social behaviour. We refer to this as the bait period. Since the mound was baited daily at 12:00 pm, we analysed frequencies of behaviour from 11:00 am to 2:00 pm. We then compared these frequencies to a control period, which was considered to be 10:00 am to 11:00 am and 2:00 pm to 4:00 pm. We obtained an average of 13 h of behavioural observation for both the bait period and control period with a range of 11.3–18.5 (bait period) and 11.6–17.6 (control period).

To examine whether phase influenced social behaviour we averaged the frequencies of affiliation and agonism across all dyads for each phase. We then analysed the differences between phases as well as between bait and control periods for both agonistic and affiliative behaviours. To do this we used a Univariate ANOVA with number of holes baited and time period as fixed factors. The analyses for Predictions II and III were performed using IBM SPSS Statistics version 21.

The behavioural data was extracted from ongoing behavioural monitoring research conducted at RCAA since July 2004 (Ross et al., 2010). In brief, during 10-min focal follows, research staff recorded behaviour every 30 s onto a handheld computer (Pocket Observer 2.0, Noldus Observer, Noldus Information Technology). All research staff attained inter-observer reliability of over 85% prior to data collection and collected 185.5 h of behavioural data. Here, we define affiliative behaviours as: groom, receive groom, embrace, reassurance, mock biting, leading/pulling away, lip-smacking gestures and play. We define agonism as: giving and receiving contact and non-contact aggression as well as displacements, crouching and fear grinning.

The same behavioural monitoring data was also used to examine whether each dyad's duration of sharing during the study corresponded with that dyad's rates of affiliative behaviour outside the context of fishing. To measure this we calculated both a dyadic affiliation index and a dyadic sharing index in order to control for individual differences in affiliation and sharing (Pepper et al., 1999; Gomes et al., 2009). To create the dyadic affiliation index we divided the total frequency of affiliative behaviours for a dyad by the sum of both individuals' affiliative behaviours with all group members plus the

total frequency of affiliative behaviours for the dyad. In order to evaluate the amount of time each individual shared with different group members, we calculated a dyadic sharing index by dividing the total sharing time for a dyad by the sum of both individuals' time spent sharing with all group members plus the total sharing time for that dyad.

3. Results

3.1. Fishing and sharing durations

Figure 2 illustrates the group's mean percentage of time spent sharing (line) in relation to the mean percentage of time that was spent fishing (columns). We found via GLMM that sharing was significantly affected by duration of fishing ($F_{100,1} = 53.80$, $p < 0.0001$) as well as fishing duration by hole availability interaction ($F_{100,2} = 18.67$, $p < 0.0001$) (Prediction I). These results indicate that significantly more sharing occurred relative to amount of time spent fishing during low hole availability (when 1 or 2 holes were baited) than during high hole availability (6, 7 or 8 holes were baited). This contradicts our expectation for Prediction I, as it indicates that there was a

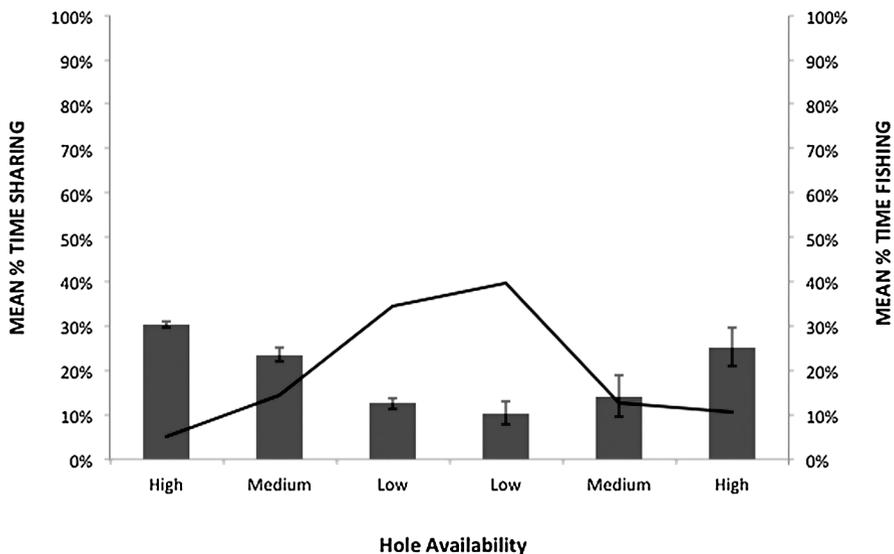


Figure 2. The y-axis shows the group's mean percent fishing time, for each category representing hole availability, in relation to the total available time (columns). The line represents the percent of this fishing time that was spent sharing.

significant increase in the amount of time that each individual spent sharing a hole at the mound when fewer holes were baited relative to the amount of time spent fishing.

3.2. Number of individuals and dyads fishing

Contrary to our expected result for Prediction II, the average number of subjects fishing at the mound did not decline as the number of baited holes decreased. Significantly fewer subjects, though, fished per day in the later phases of the study than in the earlier phases ($F_{7,12} = 4.13$, $p = 0.001$). It is likely that this effect was due to a loss of interest in the baited mound since the number of baited holes was increasing during these phases.

We failed to find a significant correlation between the number of dyads sharing a hole at the mound and the number of holes that were baited (Pearson Correlation ($r = 0.468$, $N = 16$, $p = 0.068$, two-tailed)). According to a Shapiro–Wilk test these data were normally distributed ($p = 0.171$) and the bootstrapped confidence interval included zero (-0.084 to $+0.776$), confirming that our results were not significant. Overall it was possible for a total of 21 different dyads to share holes. In this experiment we found that an average of 16 dyads per phase shared holes with a range of 10–21 dyads. This suggests that a wide variety of dyads jointly fished at the same hole and that no single pair of individuals drove the results of the sharing interactions.

3.3. Agonistic and affiliative behaviour

We found no significant differences in the frequency of agonistic ($F_{7,111} = 0.663$, $p = 0.703$) or affiliative ($F_{7,111} = 0.782$, $p = 0.604$) behaviours during bait periods as the number of baited holes changed over time (Prediction III). We did find a significant effect of time period on frequency of affiliation ($F_{1,111} = 6.671$; $p = 0.01$) where the subjects engaged in more affiliation during control periods than during bait periods but did not find an effect on frequency of agonism ($F_{1,111} = 2.097$, $p = 0.151$). There was also a significant association between the dyadic affiliative index and the dyadic sharing index (Figure 3), where dyadic partners who groomed and engaged in other social behaviours more frequently outside of the fishing task shared for more time at the mound ($r = 0.556$, $p = 0.009$). In order to determine whether the two mother-offspring dyads substantially contributed to the correlation between relationship and sharing, we analysed the data both with and without these pairs. Excluding these pairs did not change the significance of the correlation between sharing and affiliation ($r = 0.945$, $p < 0.000$).

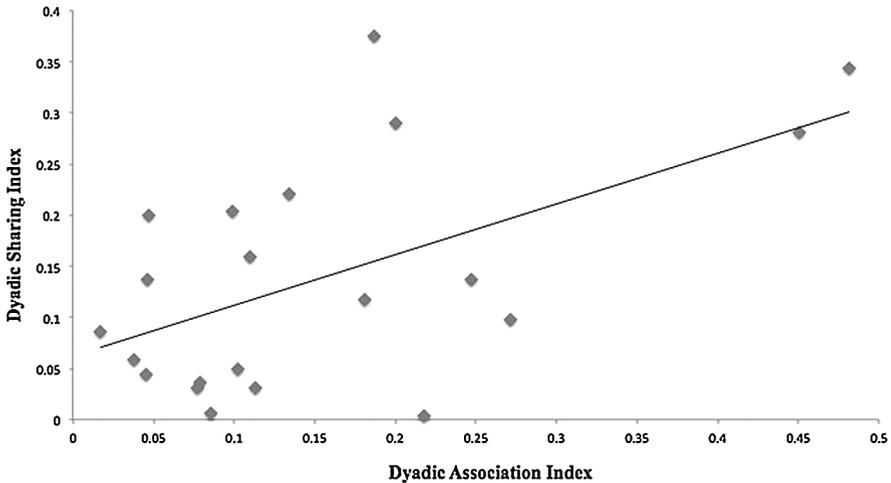


Figure 3. Correlation between the dyadic affiliation index, measured while outside the context of fishing, and the dyadic sharing index while fishing at the mound.

4. Discussion

We investigated social tolerance in chimpanzees by measuring the amount of time that chimpanzees spent sharing a food resource that diminished over time. This study differs from previous sharing studies in that most measured food distribution over the course of hours. Our study, though, investigated how chimpanzees react to the slow decline of a resource over days and months. This more closely resembles variations of food availability in the wild (McGrew, 1979; Wrangham et al., 1998; Deblauwe, 2009). Although chimpanzees often share resources in the wild (van Lawick-Goodall, 1968; de Waal, 1989; Nishida et al., 1992), competition over food can increase social tension and aggression (Wittig & Boesch, 2003; Kahlenberg et al., 2008). Because of this we predicted that competition and agonism would increase as the number of baited holes at an artificial termite mound decreased and anticipated that this would cause fewer dyads to share holes at the mound.

Our results indicated that as the number of baited holes decreased, the chimpanzees shared holes for a greater amount of their time spent fishing, and there was no increase in agonism in the group. We did find that affiliation was higher during control periods than during bait periods. This could indicate that the chimpanzees were engaging in affiliative behaviours during

control periods to mediate the tension produced by the reduction of desirable resources at the mound during bait periods. However, this result may simply reflect the chimpanzees' time budget while the mound was baited, since, during bait periods, they were most likely engaged in fishing activities instead of social behaviours.

We found no correlation between the number of baited holes and the number of dyads sharing for each phase. Furthermore, one or two affiliative pairs monopolizing holes at the termite mound did not drive our results, as a range of different dyads shared holes during each phase, and the inclusion or exclusion of mother-infant pairs did not affect the results. The overall findings in this study are notable because while chimpanzees regularly share resources in the wild, it has been difficult for researchers to replicate these behaviours in captivity.

Although sharing has been studied in captive chimpanzees (de Waal, 1989, 1997b; Crick et al., 2013), our study revealed that chimpanzees can transition from an abundance of a highly desired, monopolizable food to a scarcity of the same food with no increase in agonism. In contrast to previous results in chimpanzees, bonobos do voluntarily share food with other individuals (Hare & Kwetuenda, 2010), indicating that some ape species willingly choose to eat with a conspecific even when it results in less food for them. The variety of situations in which different ape species do and do not share remains a fruitful area for future research.

The low rates of agonism and the ability to share a diminishing resource in this study could have been mitigated by the relationship between affiliative behaviour within dyads and their time spent sharing. Although levels of social tolerance correlate to amount of food sharing, these results may also indicate reciprocity or mutualism. The influence of reciprocity in food sharing, according to Jaeggi & Gurven (2013a, b), rivals the effects of kinship and tolerated scrounging indicating that it is a significant driver of prosocial behaviours. Given that our food resource was not divisible, we were unable to measure reciprocity in a meaningful way. However, the correlation between sharing and affiliative behaviour outside of the context of fishing suggests this may be a contributing factor.

Another mechanism by which sharing is thought to take place is the avoidance of harassment from group members (Wrangham, 1975; Stevens & Gilby, 2004). Both Gilby (2006) and Crick et al. (2013) found that the more a subject begged from an individual in possession of food, the more

likely they were to receive food in return. Although we did not specifically code for changes in harassment behaviours at the termite mound, anecdotally we saw few, if any, instances of stealing tools or begging during the study.

The level at which food items can be controlled, could also be a factor in how often subjects share, as more monopolizable food items take less energy to guard (Hauser et al., 1993; Stevens, 2004). In this study, although the ketchup itself could not be divided, the holes from which it came from could easily be monopolized. We did not find, though, that our subjects chose to defend the holes at which they were positioned. The most common tactic was for two or even three chimpanzees to sit around one hole and take turns inserting their tools to retrieve ketchup.

Overall our findings add to literature suggesting that social tolerance in chimpanzees enables them to respond flexibly to changing circumstances without resorting to aggression (Aureli & de Waal, 1997). This illustrates that even in circumstances with a scarce and monopolizable resource chimpanzees are able to share rather than compete. Chimpanzees share these capabilities with humans, their closest genetic relative, who are thought to benefit from unique levels of social acceptance with high cognitive abilities and increased opportunities for social learning (Fehr & Fischbacher, 2003; Burkart et al., 2009). Further studies that investigate cooperation and sharing at the group level will help to elucidate the mechanisms by which both chimpanzees and humans make social decisions and regulate agonistic versus tolerant behaviours.

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