Ape Duos and Trios: Chimpanzee Cooperation Under Free Partner Choice

Because there has been doubt about the level of cooperation that chimpanzees (Pan troglodytes) can achieve, the present study sought to push the boundaries. Would the apes, without any pre-training or restrictions in partner choice, successfully engage in joint action? We were also the first to offer them an opportunity to cooperate not only in duos, but also trios. Captive chimpanzees were given a chance to cooperate with multiple partners of their own choosing. All members of the group (N=11) had simultaneous access to an apparatus that required two (dyadic condition) or three (triadic condition) individuals to pull in a tray baited with food. Without any training, the chimpanzees spontaneously solved the task a total of 3,565 times in both dyadic and triadic combinations. Their success rate and efficiency increased over time, whereas the amount of pulling in the absence of a partner decreased, demonstrating that they had learned the task contingencies. They preferentially approached the apparatus when kin or nonkin of similar rank were present, showing a preference for socially tolerant partners. The forced partner combinations typical of cooperation experiments cannot reveal these abilities, which demonstrate that in the midst of a complex social environment, chimpanzees spontaneously initiate and maintain a high level of cooperative behavior.

1 Ape Duos and Trios: Chimpanzee Cooperation Under Free Partner Choice

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9 Abstract

Because there has been doubt about the level of cooperation that chimpanzees (*Pan troglodytes*) 10 11 can achieve, the present study sought to push the boundaries. Would the apes, without any pre-12 training or restrictions in partner choice, successfully engage in joint action? We were also the 13 first to offer them an opportunity to cooperate not only in duos, but also trios. Captive chimpanzees were given a chance to cooperate with multiple partners of their own choosing. All 14 15 members of the group (N=11) had simultaneous access to an apparatus that required two (dvadic condition) or three (triadic condition) individuals to pull in a tray baited with food. Without any 16 17 training, the chimpanzees spontaneously solved the task a total of 3,565 times in both dyadic and 18 triadic combinations. Their success rate and efficiency increased over time, whereas the amount 19 of pulling in the absence of a partner decreased, demonstrating that they had learned the task 20 contingencies. They preferentially approached the apparatus when kin or nonkin of similar rank 21 were present, showing a preference for socially tolerant partners. The forced partner 22 combinations typical of cooperation experiments cannot reveal these abilities, which demonstrate 23 that in the midst of a complex social environment, chimpanzees spontaneously initiate and 24 maintain a high level of cooperative behavior.

25 Key Words: Cooperation, Chimpanzee, Pan troglodytes, Partner Choice, Tolerance

26 Introduction

27 Cooperation, joint action by two or more individuals to achieve a goal, is often regarded 28 as less puzzling than altruistic behavior, in which one individual benefits another at a cost to 29 himself or herself. While this may be true in an evolutionary sense, on a proximate level, 30 cooperation often consists of a series of potentially complex decisions including a choice of partners. When multiple potential partners are available, an individual faces many questions: 31 32 Whom to cooperate with? Has that individual been a good partner in the past? How much to 33 invest in this partner and what to expect in return? Will cooperation yield more benefits than solitary action? 34

These questions highlight the complexity of cooperative behavior, and yet for such a 35 complex phenomenon it is surprisingly ubiquitous across a wide variety of taxa (Dugatkin 1997; 36 37 Gadakar 2006). This paradox has inspired research examining the emergence and maintenance of cooperative behavior at both the ultimate and proximate levels of explanation. In particular, 38 39 cooperation among nonhuman primates has attracted considerable research because of the 40 evolutionary implications of such research for human behavior and the ubiquity of cooperation 41 among wild primates, including coalition formation, food sharing, group hunting, and territorial 42 defense (Mueller & Mitani 2005; Mitani 2006; de Waal & Suchak 2010). Nevertheless, we know 43 little about the proximate mechanisms of primate cooperation. Do primates coordinate their 44 actions in space and time? Do they keep track of favors given and received? Do they understand 45 whether and how their partners contribute to successful outcomes? Or do they just simultaneously 46 pursue the same goal? Conceivably, the appearance of cooperation could be created by parties focused entirely on their own individual gain (Stanford 1998). Given the ambiguity of the field 47 48 data, experimental studies of cooperation have focused on elucidating the underlying cognitive 49 and social mechanisms.

50 Most experimental work on cooperation has examined cooperation within pre-arranged 51 pairs. Coordinated lever-pressing studies required two monkeys to simultaneously press levers or 52 pull handles to receive food (Chalmeau 1994; Chalmeau et al. 1997; Visalberghi et al. 2000). 53 These studies demonstrated conditioned responses without any apparent understanding of the 54 contingencies: both individuals continually and rapidly pressed the lever and occasionally did so 55 simultaneously by coincidence (Visalberghi et al. 2000). In contrast, when two individuals were 56 required to pull in a weighted tray too heavy for one individual, several primate species 57 demonstrated an ability to coordinate pulling rather than instrumental conditioning (de Waal & 58 Berger 2000; Crawford 1937; Cronin et al. 2005; Mendres & de Waal 2000). Subjects 59 demonstrated an understanding of the need for a partner: a juvenile chimpanzee (*Pan troglodytes*) 60 would recruit a partner through gestures (Crawford 1937), cotton-top tamarins (Saguinus 61 *oedipus*) pulled more when a partner was present than when a partner was absent (Cronin et al. 62 2005), and brown capuchin monkeys (*Cebus apella*) were unsuccessful if they could not see each 63 other, suggesting visual coordination (Mendres & de Waal 2000). The high degree of success in 64 these tasks, as compared to lever-pressing studies has been attributed to the intuitive nature of 65 pulling in a tray baited with food (Mendres & de Waal 2000). In weighted tray tasks, individuals 66 can clearly see the results of their actions and receive kinesthetic feedback about the role of their 67 partner.

Similarly, primates are quite successful at cooperative string-pulling tasks, which require two individuals to simultaneously pull a loose string threaded around an apparatus to jointly bring in a tray of food (Hirata 2003, as cited in Hirata & Fuwa 2007). These studies differ from the weighted tray and lever-pressing studies in that responding before a partner causes the string to release, rendering both subjects unable to solve the task. The critical test is a delay test in which one individual arrives at the apparatus before the other. Understanding of the cooperative nature of the task requires this individual to wait for the second individual before pulling. This is precisely what has been found in several mammals (chimpanzees: Hirata & Fuwa, 2007; Melis et
al 2006a; hyenas (*Crocuta crocuta*): Drea & Carter 2009; elephants (*Elephas maximus*): Plotnik
et al. 2011). Not all species pass this critical test: two bird species able to pull simultaneously,
failed to wait for their partner in the delay task (rooks (*Corvus frugilegus*): Seed et al. 2008;
parrots (*Psittacus erithacus*): Péron et al. 2011).

Most experimental studies eliminate partner choice. This limitation holds for virtually all primate studies (e.g. Crawford 1937; Hirata & Fuwa 2007) but also for experiments on nonprimates, such as elephants or birds (Seed et al. 2008; Plonik et al. 2011; Peron et al. 2011). An exception is the work by Melis et al. (2006b; 2008), which allowed a choice between two potential partners and demonstrated that chimpanzees differentiate partners based on social tolerance and past success. Yet, the partner choice presented in these experiments was still greatly limited compared to the options within an open group setting.

87 Studies that have allowed open partner choice have generally not found high degrees of cooperation (Burton 1997; Chalmeau 1994; Chalmeau & Gallo 1996; Chalmeau et al. 1997; Fady 88 89 1972; Petit et al 1992). In fact, the only species to succeed on such a task were Tonkean 90 macaques (Macaca tonkeana; Petit et al. 1992). Although chimpanzees and capuchins succeed at 91 dyadic pulling tasks (Melis et al. 2006a; Mendres & de Waal 2000), and are known for 92 cooperative behavior in nature (Muller & Mitani 2005), both species failed to establish 93 cooperation in studies offering free partner choice (Chalmeau 1994; Chalmeau & Gallo 1996; 94 Chalmeau et al. 1997). Two possibilities are raised by these results: first, tolerance may be so 95 constrained in the group setting that it prevents cooperation without experimenter interference. 96 Although this idea is supported by the fact that the highly tolerant Tonkean macaques are the only 97 species that succeeded at the task (Petit et al 1992), if true partner choice is available, individuals should simply be able to avoid intolerant partners. A second possibility is that the design of the 98 99 tasks, with one small, highly monopolizable food source as the reward contributed to a contest

100 competition in which there was not an overall net benefit for all participants (e.g. Chalmeau101 1994, Chalmeau et al 1997).

102 In the current study we allow all individuals access to the apparatus while choosing their 103 own partners. To find out which partners chimpanzees prefer to cooperate with, we carried out 104 experiments in a large outdoor enclosure with the entire group present. All chimpanzees could 105 potentially participate in the cooperative task. We explored several determinants of partner 106 choice. If social closeness were the primary constraint on partner choice (Melis et al. 2006a), then 107 chimpanzees should work mostly with kin or nonkin affiliates. Closeness in dominance rank may 108 also play a role in cooperation, since closely ranked individuals have similar abilities and needs 109 and may be in the best position to benefit each other (de Waal & Luttrell 1986; Mueller & Mitani 110 2005). Cercopithecine monkeys and chimpanzees who are close in rank tend to interact more than 111 those at greater rank distances (Silk 1982; de Waal 1991; Mueller & Mitani 2005). Rank distance 112 may also play an important role when there is competition for resources (e.g. de Waal 1986), as 113 individuals who are close in rank tend to be more tolerant of each other's presence near a 114 clumped resource. If the presence of the group in the current cooperation task engenders 115 competitive tendencies, then rank distance is expected to affect partner choice. Finally, an 116 alternative hypothesis unrelated to social relationships is that chimpanzees will preferentially 117 choose to work with those with whom they have enjoyed previous successes (Melis et al. 2006b). 118 In addition to allowing partner choice, the current study further deviates from the previous 119 work by testing both dyadic and triadic cooperation. In nature, chimpanzee cooperation often 120 requires working with more than one other individual, including coalitions, group hunting and 121 territorial defense (Mueller & Mitani 2005). In Kibale National Park in Uganda, for example, 122 chimpanzees hunt in groups and an increasing number of hunters leads to increased success even though this effect plateaus at six individuals (Mitani & Watts 1999). 123

124 Methods

126 Subjects were 11 chimpanzees (1 male, 10 females, Table 1) kept in a large outdoor enclosure at the Field Station of the Yerkes National Primate Research Center (YNPRC). The 127 128 group's 711m² enclosure contained a large climbing structure and several enrichment items 129 (barrels, tires, etc.) and was adjacent to indoor sleeping quarters. Testing occurred in the outdoor 130 enclosure with the entire group present and did not require separating individuals from the group. 131 During testing, subjects had access to the indoor sleeping quarters. Chimpanzees were fed two daily meals consisting of fruits, vegetables and grains at approximately 8h30 and 15h00 and had 132 133 access to water and primate chow *ad libitum*. All food used in this study was supplemental to the 134 chimpanzees daily intake and at no time was food or water restricted. The chimpanzees were not 135 distressed and were free to stop participating at any time. All procedures were approved by 136 Emory University's Institutional Animal Care and Use Committee (IACUC), protocol #YER-137 2000180-53114GA. The Yerkes National Primate Research Center is furthermore fully 138 accredited by the Association for Assessment and Accreditation of Laboratory Animal Care 139 (AAALAC).

140

TABLE 1 ABOUT HERE

141 Apparatus

142 The apparatus required that one chimpanzee (in the dyadic condition) or two chimpanzees 143 (in the triadic condition) remove a barrier in order for another chimpanzee to simultaneously pull 144 in a tray baited with food (Figure 1). The second barrier and the corresponding pull bar were only present in triadic tasks, providing a clear cue to the chimpanzees that a third individual was 145 needed. Once the tray was pulled in all the way (approximately 30 cm) food rewards dropped into 146 147 a funnel, which delivered them directly to each of the chimpanzees that solved the task. The rods to pull down the barriers and pull in the tray were sufficiently far apart (~ 1.6 m) so that one 148 149 individual could not participate in both roles at the same time. If a barrier rod was pulled and

released before the tray was pulled in, the barrier rose back into place. Hence, a lone individual could not remove the barrier and pull in the tray; simultaneous action by multiple chimpanzees was required. Food rewards (one grape, two raisins, a small slice of sweet potato or a small slice of banana) varied randomly from trial to trial to maintain the chimpanzees' interest; for each trial all chimpanzees received the same reward.

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155

FIGURE 1 ABOUT HERE

156 Procedures

Test Sessions. A trial began when the tray was baited with food. Following successful trials, the 157 158 experimenter waited for the chimpanzees to release the rods and then reset the tray back in the 159 starting position and re-baited the tray. The tray was re-baited as long as the chimpanzees present 160 were not pulling; they did not need to leave and re-approach between trials. If the chimpanzees 161 did not solve the task within 5 minutes, the trial was considered a failure, the food removed, and a 162 one-minute time out commenced prior to re-baiting. Each session lasted 1 hour and consisted of 163 as many trials as could be accomplished in that time period. Since dominant individuals could 164 monopolize the apparatus early in the session, a longer session allowed more individuals to 165 interact with the apparatus. Only one session was run per day.

166 Test Phases.

167 <u>Phase 1a: Dyadic cooperation acquisition</u>. There were 28 dyadic cooperation tests, which

required two chimpanzees to work together to pull in the tray (one to hold down the barrier

and a second to pull in the tray). As there was no training, and none of the chimpanzees had

170 participated in cooperative pulling tasks before, we waited for a significant majority (9 out of

171 11 chimpanzees, binomial test p = 0.02) of the chimpanzees to reach at least 20 successes

before moving onto the next phase.

- 173 <u>Phase 1b: Triadic cooperation acquisition</u>. Following Phase 1a a second barrier was added so
- that three chimpanzees were required to solve the task. There were 28 triadic cooperation
- tests, to allow for direct comparison to the acquisition of dyadic cooperation.

Phase 2: Alternating, proficiency tests. In order to see if proficiency and experience with
 triadic cooperation influenced partner choice, we began alternating dyadic and triadic
 sessions. There were 38 alternating sessions, or 19 of each dyadic and triadic.

179 Behavioral Coding

180 Each trial was videotaped from two angles (an overview from above, taken from an 181 observation tower, and a front view) using HD digital video cameras. Additionally, one 182 experimenter had a digital voice recorder to record a narrative of any social interactions that 183 occurred during testing. Success or failure of each trial, which chimpanzees solved the task, and 184 which chimpanzees received rewards were recorded in-person and later confirmed from video. 185 Latency to succeed and the number of pulls before success were also recorded from video. 186 Pulling included any movement of the barrier as well as any bodily pulling motion. A second rater coded a subset of the videos and the two ratings were highly correlated for both latency 187 (r=0.99, p < 0.001) and pulling (r = 0.85, p < 0.001). Agreement was also excellent for the 188 189 identities of the chimpanzees participating in the task (Cohen's Kappa = 0.89) and success at the 190 task (Kappa = 1).

Long-term affiliation was calculated from data collected as part of routine observations from 2010-2011 (5220 min, described in de Waal 1989). Every 10 minutes a scan sample of affiliative behavior was collected including: grooming, sitting in close proximity, sitting within arm's reach, and play. These data were used to form a sociometric matrix from which adjusted residuals were calculated, a measure comparing observed and expected values (Everitt, 1977). These adjusted residuals were used as a quantitative measure of long-term affiliation in the current study. In addition to routine observations, pant-grunts, a unidirectional submissive vocalization, were recorded *ad libitum* from 2010-2011 and used to determine the linear dominance hierarchy.

200 Analyses

201 Understanding of the task. To test whether the chimpanzees learned about the need for and role of 202 the partner, we compared behavior during the acquisition phases to the proficiency phase. Within-203 subjects mixed measures ANOVAs were run to compare differences between phases and partner 204 conditions (dyadic and triadic) for latency, efficiency, and pulling. Latency and efficiency 205 (number of pulls to success) were both measured from the time the succeeding pair or triad 206 arrived at the apparatus until the time of success, when they obtained the food. We compared the 207 pulling rate (pulls per minute) of each individual when the correct number of partners was at the 208 bar "ready" to pull versus when there were not enough partners present. This is a very strict 209 criterion as chimpanzees who momentarily stepped away from the apparatus or were approaching 210 but not yet within reach of the bar were not considered to be "present." In the dyadic condition 211 we compared the pulling rate when a partner was present versus absent and in the triadic 212 condition we compared the pulling rate when all three partners were in place to when only two or 213 one partners were in place. We compared these rates between the acquisition and proficiency 214 phases to check for developing understanding of the need for a partner over time. All pulls, even 215 those that occurred in the absence of success were included in this analysis. All acquisition 216 analyses were run using SPSS Statistics 20.0 (IBM, inc.).

Partner Choice. We explored which chimpanzees chose to approach the apparatus when otherchimpanzees were already there as potential partners. When a chimpanzee was present at the

apparatus, he or she had 10 potential partners that could approach. If another individual 219 220 approached, they were scored as a 1, whereas individuals who did not approach were scored as 0. 221 This was done by session, so if a chimpanzee was never at the apparatus during a given session, 222 they were excluded from the analysis for that session (since they had to be at the apparatus in 223 order for someone to approach to work with them). All triads were broken down into their corresponding dyads for the purpose of analysis. Partner choice analyses are limited to the 224 225 proficiency phase only as we could confirm at that point the chimpanzees knew they needed a 226 partner.

227 To determine which factors influenced partner choice, we ran a generalized linear mixed 228 model (GLMM), with approach as a binomial dependent variable. Kinship, long-term affiliation, 229 rank distance between the two individuals, recent success (total number of successes for that pair 230 during the current phase) and relative past success (the percentage of that individual's success 231 from the previous phases with that partner) were included in various combinations as fixed terms. The advantage to using two different measures of past success is that if past success is the key to 232 233 partner choice, we can determine whether the chimpanzees gauge success based on cumulative 234 rewards obtained (which could result in partner choice by reinforcement) or if they judge partners 235 based on their relative effectiveness at the task (which would reflect a more sophisticated 236 evaluation of available partners). Models examined each fixed effect independently as well as 237 interactions between the effects. None of the fixed effects were correlated with each other. We 238 also ran a full model which contained all of the fixed effects and a null model that contained only 239 the random effects for all phases. Dvadic and triadic sessions were analyzed separately and in 240 total we examined 14 models for each. Identity of the chimpanzee already present at the 241 apparatus, identity of the chimpanzee that approached, and session were included as random 242 effect to control for repeated sampling, frequency of presence at the apparatus, frequency of 243 approach, and interdependence between dyads. We used an ANOVA to determine which model

had the most explanatory power by comparing the Akaike's information criterion (AIC) for all of the possible models. Once the best model was identified, we used a Markov chain Monte Carlo simulation of 10,000 interactions to obtain significance values. All partner choice analyses were run using R statistical software (2012), with the lme4 package.

248 **Results**

249 Understanding of the task

For both dyadic and triadic tests, at least four different chimpanzees spontaneously solved 250 251 the task within the first 2 hours of exposure without any training. Overall, 10 of the 11 252 chimpanzees solved the task at least once during both the dyadic and triadic tests for a total of 253 2,462 dyadic successes and 1,103 triadic successes. The total number of successes by each 254 individual across the entire study is displayed in Figure 2. One female, Mai, failed to solve the 255 task in either dyadic or triadic tests and in fact ceased making pulling attempts before the 256 proficiency phase. Since her overall pulling rates were more than two standard deviations below the group mean, she was eliminated from the analysis. 257

258

FIGURE 2 ABOUT HERE

259 Latency to success was significantly lower in the proficiency phase than in the acquisition 260 phase (Mixed Measures ANOVA: $F_{1,7}$ = 21.29, P = 0.002). Similarly, extraneous pulling, i.e. pulls 261 that did not lead to success, dropped significantly from the acquisition to the proficiency phase. 262 The chimpanzees succeeded with significantly fewer pulls per success (e.g. higher efficiency) 263 during the proficiency phase (Mixed Measures ANOVA: $F_{1,7}$ = 16.83, P = 0.005, Figure 3). For 264 both of these measures there was no significant difference between dyadic and triadic tests (latency: $F_{1,7} = 0.11$, P = 0.75; extra pulling: $F_{1,7} = 0.18$, P = 0.68), demonstrating increased 265 effectiveness of cooperation regardless of how many chimpanzees were needed for the task. 266 FIGURE 3 ABOUT HERE 267

268 In order to assess whether the chimpanzees developed an understanding of the need for a 269 partner, we compared pulling rates when the correct number of individuals were present and 270 sitting ready at the bars to pull to when an insufficient number was present. In the dyadic test 271 sessions there was a significant effect of partner presence; chimpanzees pulled more when a partner was at the other bar then when no partner was present (Mixed Measures ANOVA: $F_{1,9}$ = 272 39.53, P < 0.001; Figure 4). There was also a significant phase by partner presence interaction: 273 the ratio of pulls when a partner was present as compared to pulls when a partner was absent was 274 greater in the proficiency phase than in the acquisition phase ($F_{1,9} = 14.11$, P = 0.005). Finally, 275 276 there was an overall effect of phase, such that individuals had higher overall pulling rates in the 277 proficiency phase than in the acquisition phase, however this increase was primarily observed when a partner was present ($F_{1,9} = 9.76$, P = 0.01). 278

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FIGURE 4 ABOUT HERE

In triadic tests, the trends were similar but less pronounced. There was a main effect of partner presence: when two other partners were present the chimpanzees pulled more than when there was only one or zero partners present ($F_{1.12,10.99}$ = 11.62, p = 0.006, Greenhouse-Geisser corrected due to lack of sphericity). Unlike dyadic tests, however, the phase by number of partners interaction was no longer significant ($F_{1.07, 9.59}$ =0 .962, p = 0.36, Greenhouse-Geisser corrected due to lack of sphericity) and there was no longer a main effect of phase ($F_{1.9}$ = 2.49, p= 0.15).

Most of the chimpanzees spontaneously developed a bias for a particular position at the apparatus. In the dyadic task, three chimpanzees had significantly more success (as determined by a binomial test P < 0.05) at the barrier than the tray position, two chimpanzees had no preference and five chimpanzees had significantly more success at the tray than the barrier the fact that there were two barrier positions available and only one tray position.

293 Partner choice

There were a total of 45 possible dyadic combinations and 120 possible triadic combinations among all of the adults who solved the task (N = 10). In total, 29 unique dyads and 32 unique triads manifested actual cooperation in the experiments.

Applying GLMM, we examined factors that might influence whether or not one individual approaches another already present at the apparatus. Across both dyadic and triadic tests, there was a significant influence of the tested random effects (intercept; dyadic: Z = -4.30, P < 0.001; triadic: Z = -5.11, P < 0.001; random effects included identity of the approacher and individual already there and test session number). Given the high variability of individual participation in the task, it is not surprising that most of the variance of the random effects comes from individual identities rather than the session number (Table 1).

304 Once individual identity was controlled for, the same model had the best fit for both 305 dyadic and triadic sessions. It included kinship, affiliation as well as the interaction of these factors with rank distance (dyadic: AIC = 601.44, χ^2 = 9.68, df = 0, P < 0.001; triadic: AIC = 306 1199.22, $\chi^2 = 4.12$, df = 0, P < 0.001; Table 2). The interaction between kinship and rank 307 308 distance was significant (dyadic sessions: Z = 3.80, P < 0.001; triadic sessions: Z = 2.67, P =309 0.007), reflecting the reluctance of chimpanzees to approach individuals much higher ranking 310 than themselves, unless these individuals were relatives. Additionally, for the dyadic sessions, there were main effects of kinship (Z = -2.07, P = 0.04) and rank distance (Z = -3.86, P < 0.001) 311 but these effects were not found not in triadic sessions (kinship: Z = -1.05, P = 0.30; rank 312 distance: Z = -.58, P = 0.56). Affiliation and the interaction between affiliation and rank distance 313 were not significant in either the dyadic or triadic sessions. 314

TABLE 2 ABOUT HERE

The effect of rank distance indicates that individuals of similar rank were likely to approach each other. There was no overall effect of rank on task performance, i.e. individuals of high rank did not have more successes than individuals of lower rank (Spearmans' rank correlation between individual rank and number of successes; $r_s = 0.07$, N = 10 individuals, P =0.44).

Finally, approaches tended to be reciprocal—that is, the more frequently individual A approached B at the apparatus, the more frequently B approached A (dyadic: $r_s = 0.42$, N = 90, P< 0.001; triadic: $r_s = 0.56$, N = 90, P < 0.001). Note that the p-values reported here are exact twotailed p-values obtained from 10,000 random permutations so as to address interdependence between dyads.

326 Discussion

Without any specific training, the chimpanzees in this study spontaneously solved the cooperation task and were extremely successful under both dyadic and triadic conditions. The high success rate, with a total of 3,565 completed cooperative acts (an average of 38 per one hour test session), confirms observations of cooperation in nature: chimpanzees are capable of cooperating in more complex open environments than typically tested. The current study contrasts with previous work in a number of ways. First, in many

333 studies the chimpanzees required extensive training (Crawford 1937), or had been individually

familiarized with the apparatus before cooperative testing (Melis et al. 2006a; 2006b). In the only

previous study without pre-training, 5 out of the 6 chimpanzees showed no understanding of the

task and were just as likely to pull when a partner was present versus absent (Chalmeau 1994). In

the current study, the chimpanzees had no experience with a pulling apparatus of any kind prior

338 to the dyadic acquisition phase. However, it might be argued that the dyadic acquisition phase 339 served as pre-training for the triadic phase. If so, we would expect to see high rates of pulling 340 when only one other partner was present in the triadic phase of testing. This was not the case, 341 however: the chimpanzees pulled the most when both partners were present, less when one 342 partner was present and the least was when no other partner was present. The low frequency of pulling when an insufficient number of partners were present demonstrates an understanding of 343 the triadic nature of the task, which manifested itself right at the beginning of the triadic 344 345 acquisition phase.

346 Despite the chimpanzees' demonstrable sensitivity to partner presence in both the dyadic 347 and triadic phase, pulling in the absence of a needed partner never fully disappeared. Incomplete 348 extinction of such pulling was probably due to continuing conditioning effects as well as the 349 conservative measure of partner presence employed: the partner had to be at the bar, ready to pull. Therefore, any pulls made as a partner was approaching or nearby were counted as pulling 350 351 when a partner was "not ready." It is possible that the chimpanzees viewed a partner approach as 352 a signal to start the task. Moreover, pulling was an extremely low cost behavior. The energy 353 expended on pulling might simply not have been great enough to deter extraneous pulling.

354 One of the surprises of this study was the high level of success without any pre-training. 355 Previous work has shown that more intuitive tasks, where individuals are pulling food towards 356 them (e.g. Mendres & de Waal 2000), are learned faster and showed greater understanding than 357 non-intuitive tasks where pulling is not mechanically connected to food delivery. Thus primates 358 participating in weighted tray or string-pulling tasks (Hirata & Fuwa, 2007; Melis et al 2006ab; 359 Mendres & de Waal 2000) have had more success than those participating in lever-pressing 360 (Chalmeau et al. 1997, Visalberghi et al. 2000). One exception to this is Crawford's (1937) original weighted tray task, which required extensive training. However, Crawford's chimpanzees 361

362 were juveniles and in later experiments (including the current study) the participants were all

adults. Additionally, the chimpanzees in Crawford's study did show an understanding of the
partner's role: one chimpanzee would recruit the other to help him. Since the chimpanzees in the
current study could clearly see the mechanical results of their actions and how their actions
resulted in food delivery it is not surprising they developed an understanding of the task.

367 Another unexpected finding was how highly successful the apes were despite the group 368 setting in which they were operating. The potential for competition and free-loading did not seem 369 to deter them. Previous studies have demonstrated obstacles to cooperation under free choice 370 conditions due to a lack of inter-individual tolerance (Burton 1997; Chalmeau 1994; Chalmeau & 371 Gallo 1996; Chalmeau et al. 1997; Fady 1972; Petit et al 1992). However, in all of these studies 372 the reward for cooperation was a single monopolizable food reward. For most participants in the 373 task, there was no net gain. In the current study, in contrast, each individual received their own 374 reward, resulting in a net gain for all participants. Although this design did not allow us to ask 375 how reward division might influence future partner choice, ensuring a net gain for all participants 376 is the essence of mutualism, which allowed us to examine the details of partner choice.

377 Kinship and rank distance were the best predictors of partner choice: the chimpanzees 378 tended to approach individuals of similar rank to themselves unless the individual at the 379 apparatus was their kin. Interestingly, this did not only apply to low ranking individuals 380 approaching other low ranking individuals; high-ranking individuals also preferred approaching 381 high-ranking individuals. Closeness in rank and kinship probably foster partnerships in which 382 competition is mitigated (Silk 1982; de Waal & Luttrell 1986; de Waal 1986). These partnerships 383 are characterized by higher social tolerance than ones with large discrepancies in rank, which 384 often results in the higher-ranking individual forcefully claiming food. Our results are consistent 385 with previous studies that reported higher levels of cooperation between tolerant individuals (de 386 Waal & Davis 2003; Melis et al. 2006a; Petit et al. 1992). In one previous study of partner choice, 387 the alpha male monopolized the apparatus and rewards, resulting in a lack of interest of the group

to approach while he was there (Chalmeau 1994). In the current study, there was a high level of participation by 10 out of the 11 individuals present, acting in a wide variety of partnerships. The alpha male participated, but without excluding others. His most frequent partners were middle- to high-ranking females, i.e. females fairly close to his own rank. Unfortunately, we had only one male in the group so were unable to measure male-male cooperation and its effect on cooperation with and among females.

Further evidence of the high level of social tolerance between partners is demonstrated by the low rate of agonism observed throughout the study. Agonism was extremely rare, occurring in only about 1% of all trials. Escalated agonism (e.g. slapping, biting, or grabbing) was rarer still, occurring in only 0.1% of trials.

398 The emphasis on tolerant partnerships does means that the chimpanzees were not choosing the 399 most successful partners available. These results, combined with previous work (Burton 1997; 400 Chalmeau 1994; Chalmeau & Gallo 1996; Chalmeau et al. 1997; Fady 1972; Petit et al 1992) 401 seem to suggest that while theoretically the chimpanzees should be choose the most successful 402 individuals to maximize their own gain, there may be social constraints on their ability to display 403 this tendency. Indeed, when social constraints are taken away by limiting partner choice to only 404 two individuals who were socially tolerant, chimpanzees did choose the most successful partners 405 (Melis et al 2006b). From an evolutionary standpoint, social relationships are long-term 406 investments that encompass a variety of interactions (including grooming, agonistic support, sex, 407 play, and food sharing). Cooperation is only one of many different currencies being exchanged in 408 a marketplace. Rather than being "irrational," choosing a tolerant partner may reflect the most 409 economical choice: a safe investment that is likely to lead to equal outcomes for all participants, 410 in the present and in future interactions.

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Figure captions 489

490 Figure 1. The test apparatus and set-up. (a) Each barrier was connected to a steel rod that 491 extended 20 cm into the chimpanzee enclosure. Pulling on the rod caused the barrier to drop 492 down via a spring/pulley mechanism. Once the barrier (or barriers in the triadic condition) was 493 pulled down a second individual used a similar rod (also extending 20 cm into the enclosure) to 494 pull in the whole tray. The only part of the test apparatus that was inside the enclosure were the 495 pull bars, the rest was outside. Note that barrier 2 (on the left) was only present during the triadic 496 sessions. The apparatus was set up exactly the same for dyadic sessions but barrier 2 and the 497 corresponding pull bar were missing. (b) Three chimpanzees participating in the triadic 498 cooperation task.

Figure 2. Success by individual chimpanzee. The total number of successes for each 499 chimpanzee across all of the test sessions. All individuals except for MA achieved at least 80 500 successes, with nine chimpanzees achieving over 100. 501

502 Figure 3. Number of pulls to success during the acquisition and proficiency phases.

503 Extraneous pulling that did not lead to success decreased between the two phases for both dyadic 504 and triadic partners. There was no significant difference between the dyadic and triadic 505 conditions.

506 Figure 4. Comparison of pulling rates per minute during the acquisition and proficiency

phases for dyadic cooperation. Partner "ready" indicates that a partner was both present at the 507 apparatus in a position to be able to pull on the tray. The pattern was similar for triadic pulling 508 509 rates.

- 510 **Table captions**
- Table 1. Subjects. Subjects are listed in rank order, with age and any maternal kinship relations 511
- provided. Rank was determined using pant grunts, a unidirectional submissive signal. 512

- Table 2. Results of the best fit GLMM during the proficiency phase. Fixed effects in bold had
 a significant influence on whether or not an individual approached. In both dyadic and triadic
- 515 sessions, individuals were more likely to approach others close in rank to themselves, unless the
- 516 potential partner was kin.
- 517

Figure 1

Figure 1. The test apparatus and set-up. (a) Each barrier was connected to a steel rod that extended 20 cm into the chimpanzee enclosure. Pulling on the rod caused the barrier to drop down via a spring/pulley mechanism. Once the barrier (or barriers in the triadic condition) was pulled down a second individual used a similar rod (also extending 20 cm into the enclosure) to pull in the whole tray. The only part of the test apparatus that was inside the enclosure were the pull bars, the rest was outside. Note that barrier 2 (on the left) was only present during the triadic sessions. The apparatus was set up exactly the same for dyadic sessions but barrier 2 and the corresponding pull bar were missing. (b) Three chimpanzees participating in the triadic cooperation task.







Figure 2

Figure 2. Success by individual chimpanzee. The total number of successes for each chimpanzee across all of the test sessions. All individuals except for MA achieved at least 80 successes, with nine chimpanzees achieving over 100.

Figure 2



Figure 3

Figure 3. Number of pulls to success during the acquisition and proficiency phases.

Extraneous pulling that did not lead to success decreased between the two phases for both dyadic and triadic partners. There was no significant difference between the dyadic and triadic conditions.



Figure 4

Figure 4. Comparison of pulling rates per minute during the acquisition and proficiency phases for dyadic cooperation. Partner "ready" indicates that a partner was both present at the apparatus in a position to be able to pull on the tray. The pattern was similar for triadic pulling rates.



Table 1(on next page)

Table 1

Table 1. Subjects. Subjects are listed in rank order, with age and any maternal kinship relations provided. Rank was determined using pant grunts, a unidirectional submissive signal.

| Chimpanzee | Sex | Age | Rank | Kin |
|------------|-----|-----|------|----------------|
| SK | М | 24 | 1 | DN |
| GG | F | 31 | 2 | BO, RI, KT, TA |
| RN | F | 24 | 3 | |
| BO | F | 47 | 4 | GG, RI, KT, TA |
| MA | F | 47 | 5 | MS |
| KT | F | 22 | 6 | BO, GG, RI, |
| | | | | TA |
| AJ | F | 31 | 7 | |
| RI | F | 24 | 8 | BO, GG, KT, |
| | | | | TA |
| DN | F | 21 | 9 | SK |
| TA | F | 16 | 10 | BO, GG, KT, |
| | | | | RI |
| MS | F | 18 | 11 | MA |

Table 2(on next page)

Table 2

Table 2. Results of the best fit GLMM during the proficiency phase. Fixed effects in bold had a significant influence on whether or not an individual approached. In both dyadic and triadic sessions, individuals were more likely to approach others close in rank to themselves, unless the potential partner was kin.

Table 1

| Variable | ß | SE | Ζ | р | |
|---------------------------|----------|------|-------|---------|--|
| Dyadic Proficiency | | | | | |
| Fixed Effects | | | | | |
| Intercept | -1.98 | 0.46 | -4.30 | < 0.001 | |
| Kin | -1.38 | 0.67 | -2.07 | 0.04 | |
| Affiliation | 0.12 | 0.10 | 1.22 | 0.22 | |
| Rank Distance | -0.32 | 0.08 | -3.86 | <0.001 | |
| Kin*rank distance | 0.52 | 0.13 | 3.80 | <0.001 | |
| Affiliation*rank distance | -0.03 | 0.03 | -1.12 | 0.26 | |
| Random effects | | | | | |
| Individual present | variance | 0.26 | | | |
| Individual Approaching | variance | 0.23 | | | |
| Session | variance | 0.00 | | | |
| | | | | | |
| Triadic Proficiency | | | | | |
| Fixed Effects | | | | | |
| Intercept | -1.79 | 0.35 | -5.11 | <0.001 | |
| Kin | -0.47 | 0.45 | -1.05 | 0.30 | |
| Affiliation | -0.02 | 0.05 | 26 | 0.80 | |
| Rank Distance | -0.02 | 0.04 | -0.58 | 0.56 | |
| Kin*rank distance | 0.22 | 0.08 | 2.67 | 0.007 | |
| Affiliation*rank distance | 0.02 | 0.01 | 1.26 | 0.21 | |
| Random effects | | | | | |
| Individual present | variance | 0.21 | | | |
| Individual Approaching | variance | 0.19 | | | |
| Session | variance | 0.08 | | | |

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