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Chimpanzees Cooperate in a Competitive World

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Abstract

Chimpanzees Cooperate in a Competitive World

By Malini Christine Suchak

Experimental cooperation studies on primates often remove several important challenges to successful joint action. By testing the primates in pairs, partner choice is eliminated and competition and freeloading are sharply reduced. Wild primates, including chimpanzees (*Pan troglodytes*), are able to handle these challenges, whereas the mixed outcome of pairwise testing may have been due to limited ecological validity. The purpose of this study was to examine cooperative behavior in an open group setting by testing how captive chimpanzees coordinate with multiple partners of their own choosing. All members of the group (n=11) had access to the cooperation apparatus in a large outdoor compound. Chimpanzees were tested under two conditions: (1) dyadic cooperation, requiring two individuals and (2) triadic cooperation, requiring three individuals, to pull in a tray baited with food. The chimpanzees learned to solve the task in both conditions and were extremely successful, performing 3,565 cooperative pulls (in 94 one-hour sessions). Efficiency increased over time and the chimpanzees began to pull more when a partner was present, demonstrating that the chimpanzees gained an understanding of the task in both conditions. Chimpanzees preferentially approached the apparatus when individuals of similar rank or kin were present and were more successful when working with kin versus non-kin. Cheating was not particularly widespread with 98.90% of rewards being obtained by the individual who worked for them. A number of responses seemed to discourage freeloading: withdrawing to prevent further opportunities for freeloading, withholding pulling until the cheater left, and in rare cases agonism. This experiment demonstrates that in the midst of a complex social environment, subject to competition and intolerance, chimpanzees can initiate and maintain a high degree of cooperative behavior.

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Chapter 1. Introduction

The art of cooperation consists of investing the right amount in the right partner at the right moment (Noë, 2006)

Faced with the decision to engage in a cooperative interaction rather than pursue an individual strategy, the question is: Whom should I cooperate with? Has that individual been a good partner in the past? How much should I invest in my partner and what do I expect in return? Will I benefit more from cooperating than pursuing this goal individually? All of these questions highlight the complexity of cooperative behavior, and yet for such a seemingly complex phenomenon it is surprisingly ubiquitous across a wide variety of taxa (Dugatkin, 1997; Gadakar, 2006). This paradox has inspired a considerable amount of research examining the emergence and maintenance of cooperative behavior at both the ultimate and proximate levels.

From an evolutionary standpoint, the emergence of cooperation (in which all individuals involved obtain fitness benefits) presents less of a puzzle than altruism (in which one individual incurs a fitness cost to benefit another; Trivers, 1971). Still, since cooperation is thought to involve at least a temporary cost (i.e. the "investment" in the cooperative interaction), which is vulnerable to freeloading, a great deal of attention has been given to two theoretical mechanisms by which cooperation may have evolved. Specifically, kin selection is an ultimate mechanism to explain cooperation between related individuals (Hamilton, 1964) and reciprocal altruism can account for cooperation between unrelated individuals (Trivers, 1971). Theoretically, these ideas have been very influential, yet demonstrating kin selection and reciprocal altruism empirically has proven challenging.

On the proximate level, the emphasis has been on identifying the cognitive mechanisms that make cooperation possible such as communication, contingent reciprocity, and punishment of freeloaders. In nonhuman primates, considerable attention has been given to determining whether individuals have the necessary cognitive abilities to coordinate their actions with one another.

Defining Cooperation

On both an ultimate and proximate level, cooperation is usually defined by the outcome of the interaction: in the former we identify cooperation by its fitness consequences and in the latter by whether or not individuals are successful at achieving a goal (Noë, 2006). But what about individuals who engage in joint action but fail to actually achieve their goal? For example, many species of social carnivores regularly hunt in groups but fail to capture prey on all but a minority of occasions (Lamprecht, 1981). If cooperation were identified solely by the outcome, then by definition failed hunts would not be considered cooperative. For this reason, Boesch & Boesch (1989) argue that the behavior of the individuals acting together, or the form of the interaction (c.f. Noë, 2006), is important in identifying cooperation.

In this study, cooperation will be defined as "the acting together of two or more individuals that brings about, or could potentially bring about an outcome for one, both, or all of them that could not have easily been brought about individually" (adapted from Brosnan & de Waal, 2002).

The definition of cooperation provided here would include a wide variety of behaviors from an equally wide variety of species: such as, birds mobbing a predator, collective foraging of wrasse fish, ants building a trail, lionesses hunting, chimpanzees patrolling the territory of their boundary, and humans engaged in business transactions (Dugatkin, 1997). Clearly, these are very diverse behaviors and likely result from a variety of cognitive mechanisms.

To account for this variation within the general definition of cooperation, Boesch & Boesch (1989) proposed four levels of cooperation, each increasing in cognitive complexity. The first level was similarity, which occurs when individuals are performing similar actions to achieve a goal, but without keeping track of the spatial or temporal relation between each individual's actions. For example, when a honeybee nest is disturbed, defender bees quickly swarm the "predator," acting individually but simultaneously to defend the colony (reviewed by Dugatkin, 1997).

The second level of complexity is synchrony (Boesch & Boesch, 1989). Synchrony differs from similarity in that individuals are coordinating their behavior in time. However, they do not necessarily need to be aware of the spatial relationships between one individual's actions and another. For example, when wrasse fish enter a damselfish nest to eat the eggs, a group of 30 or more fish must all enter the nest at approximately the same time in order to overcome the defense of the damselfish (reviewed by Dugatkin, 1997). They do not need to coordinate their actions in space, simply all entering at the same time is enough to overpower the damselfish and gain access to the eggs.

The third level is coordination (Boesch & Boesch, 1989). Coordination builds upon synchrony, in addition to coordinating action in time, it also requires individuals to be aware of the spatial relationship between their actions and others. A typical example of coordinated behavior can be found in social carnivore hunting. For example, in order for lions to take down a large prey animal, they must both coordinate the timing of their effort and also fan out around the prey to surround it (thus demonstrating spatial coordination; Stander, 1992). An important element of coordination is that although individuals are aware of each other's locations and actions, they are all essentially performing the same actions and not taking on different roles.

The fourth and final level of complexity is collaboration (Boesch & Boesch, 1989). Collaboration is distinguished from all of the other levels by the fact that individuals take on different, but complementary roles to achieve their goal. For example, chimpanzees in the Taï forest appear to perform different roles when hunting colobus monkeys (Boesch, 2002). Drivers force the prey to move in a particular direction, blockers obscure escape routes, chasers attempt to catch up with the prey, and ambushers move ahead of the prey to capture them.

The current study requires, at the very least, coordination, since individuals must be pulling at the same place at approximately the same time. If the chimpanzees are not timing their pulls at least somewhat precisely, it is unlikely they will solve the task with any degree of efficiency. Although both positions require pulling, it is possible that some degree of collaboration could develop since there are effectively two roles: one individual moves the barrier and a second individual pulls in the tray. The emergence of specialization for specific roles would be evidence for collaboration.

In addition to different cognitive mechanisms driving each of these levels of cooperation, there may also be different motivational requirements that drive collaboration (Rekers et al., 2011). The degree to which humans collaborate is far beyond that observed in other species, and since some species (like chimpanzees) have shown similar cognition during cooperative tasks, researchers have suggested that the motivation to act and work together separates human from nonhuman cooperation. This suggestion was supported by the findings that, all things being equal, children but not chimpanzees show a strong preference for collaborating over acting alone (Bullinger et al., 2011; Rekers et al., 2011). It is important to note, however, that in these experiments cooperation was also confounded by competition and the results may really reflect differing responses to competition. The current study extensively explores the role of competition in a cooperative-problem solving task.

Although there may be distinct differences between the cooperation required for the current task and human collaboration, there are also differences between cooperation in this experiment and naturally occurring cooperation in other species such as eusocial insects. These insects do show a high level of complexity in some regards when it comes to cooperation (reviewed by Dugatkin, 1997), including complex communication, multiple roles, and even punishment. However, cooperation in these species seems to be rule-based and somewhat inflexible. For example, although different honeybees take on different roles in the hive, these roles are usually genetically determined and fixed throughout an individual's lifetime. It is this role that also determines whether or not an individual engages in a cooperative act; eusocial insects typically do not have a choice to participate or abstain. As a result, partner choice is either limited or absent.

In contrast, in the current experiment requires the chimpanzees to actively make a number of decisions, including whether or not to engage in the task and which partners to work with. Thus, the chimpanzees have the ability to exhibit some flexibility in their cooperative behavior and the task is designed to elicit such flexibility. When cooperation requires decision-making, there is the possibility to develop strategies or tactics to maximize cooperative returns. Distinguishing a strategy from associative learning, however, may be difficult. For example, in a previous study chimpanzees chose partners with whom they have had the most success with in the past (Melis et al., 2006b). On the surface, this may seem like the chimpanzees developed a strategy to work with the most profitable partners. But, as the most profitable partners were also those with whom they had obtained the most rewards, their choices can be explained by simple associative learning. In sum, although flexibility in cooperative decision-making has the potential to lead to strategic or tactical cooperation, more parsimonious explanations must be ruled out first.

Observational evidence for cooperation in nonhuman primates

Nonhuman primates have attracted considerable research on the topic of cooperation both because of their close evolutionary ties to humans and observations of cooperation in nature (reviewed by de Waal & Suchak, 2010). Perhaps the most ubiquitous example of cooperation in the field is coalition formation (Harcourt & de Waal, 1992). In this phenomenon, which is particularly well studied in Old World Primates, individuals provide agonistic support to their group mates. Often support is given to close relatives or affiliates and there is considerable evidence that individuals tend to support those who support or groom them the most (for two meta-analyses of the relationship between grooming and support in a variety of primate species see Schino, 2007; Schino & Aureli, 2008). In chimpanzees, coalitions can help males attain their status, which, insofar as dominance rank is related to reproductive success, can have significant fitness consequences (Muller & Mitani, 2005).

In addition to coalitions during intra-group conflicts, chimpanzees also cooperate during inter-group encounters. Chimpanzees cooperatively patrol the boundaries of their territories and actively search for chimpanzees of neighboring groups to attack (Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001; Muller & Mitani, 2005). This primarily male activity, although females in the Taï forest do occasionally participate in the patrols, seems to serve the sole function of seeking out and attacking strangers (Muller & Mitani, 2005). Upon encountering a stranger, the male chimpanzees engage in a coordinated attack, cooperating to immobilize the victim and taking turns attacking him. Usually, for male victims these attacks result in death; females may be left alone particularly if they are young and in estrus. Although this behavior surely must carry some cost for the participants, the risk to the attackers in these instances is debatable since there are no reported injuries for attackers (Watts & Mitani, 2001). Furthermore the benefit of this behavior may be increased food resources, territory expansion or acquisition of females, but is not yet fully understood (Mitani, Watts & Amsler, 2010; Muller & Mitani, 2005).

As another form of cooperation in chimpanzees, hunting has received a lot of attention from field researchers. At every long-term field site chimpanzees hunt red colobus monkeys (and occasionally other prey) in groups (Boesch et al., 2006). As success increases with increasing number of individuals in the hunting party (up to six individuals), it has been suggested that chimpanzees hunt cooperatively because it is too difficult to capture prey individually (Mitani & Watts, 1999; Boesch & Boesch-Achermann, 2000). However, the degree to which chimpanzees are truly cooperating (e.g., engaging in joint action) rather than simultaneously but individually pursuing prey is under debate (Boesch, 2002). At Gombe Stream, for example, the chimpanzees all seem to individually pursue the prey without taking into account the actions of the other hunters (Stanford, 1998). In contrast, at Ngogo the chimpanzees seem to coordinate their movements in time and space with other individuals (Mitani & Watts 1999) and at the Tai Forest, the chimpanzees appear to be taking in different but complementary roles during hunting (e.g. one chimpanzee "chases" the monkey towards another chimpanzee waiting to "ambush" the prey; Boesch, 2002; Boesch & Boesch, 1989). It is unclear whether these differences are population differences or result from differing observers and methodologies.

Experimental evidence for nonhuman primate cooperation

Early studies of cooperation in chimpanzees and capuchin monkeys required the subjects to perform coordinated actions, such as simultaneously pressing levers to release food ("simultaneous action tasks," Chalmeau, 1994; Chalmeau et al., 1997; Visalberghi et al., 2000). For both species tolerance between partners played a major role in their level of success: when there were large discrepancies in dominance between partners, the presence of the dominant individual at the apparatus inhibited the lower ranking individual from interacting with it. Several other studies have also indicated a role for tolerance or close social relationships in facilitating cooperative behavior (Melis et al., 2006a, Brosnan et al., 2006, de Waal & Davis, 2003).

When the subjects in simultaneous action tasks did achieve some success, it was unclear whether their success was due to actually working together with the partner or coincidental success (Chalmeau, 1994; Chalmeau et al., 1997; Visalberghi et al., 2000). For example, the capuchin monkeys were just as likely to press the lever when their partner was absent as they were when their partner was present at the apparatus (Visalberghi et al., 2000). This suggests that success was due to coincidental action, rather than coordination of behavior; in other words the subjects were “acting apart together” (Noë, 2006). These results are similar to what has been observed at Gombe, where chimpanzees simultaneously, but independently pursue prey (Stanford, 1998). These results led some researchers to conclude that nonhuman primates are incapable of “true” cooperation (Visalberghi et al., 2000).

However, when capuchin monkeys were required to pull food closer to themselves (similar to Crawford’s, 1937, classical bar-pulling paradigm), they achieved a high rate of success, which was attributed to the task being more intuitive than the simultaneous action tasks described above (Mendres & de Waal 2000). In the bar-pulling task communication between both partners seemed to play an important role. When an opaque barrier was placed between them, the capuchins failed to succeed. Furthermore, when only one individual was rewarded, the capuchins seemed to demonstrate an understanding of when their partner’s help was needed: the subject that received the food shared more with their partner when they needed their help than when they were able to complete the task by themselves (de Waal & Berger, 2000). Similarly, when two cotton-top tamarins had to simultaneously pull bars to release food, they were more likely to pull when their partner was present versus absent (Cronin et al., 2005). Although attention to partner presence alone does not necessarily demonstrate that the tamarins were communicating to coordinate their behavior, the experiment at least demonstrated an understanding of their partner needing to be at the apparatus in order to succeed.

Thus, there is behavioral evidence that capuchin monkeys, and cotton-top tamarins actively communicate with their partners during a cooperative task. Recently, a modification of the pulling paradigm developed for chimpanzees directly assessed whether they knew when they needed another individual to help them, using a pulling apparatus baited with food (Hirata & Fuwa, 2007; Melis et al., 2006b). This apparatus consisted of a long board (outside of the chimpanzees reach) with loops on all of the corners. A rope was threaded through the loops with the ends extending into the enclosure. During “cooperative” tests, the two ends of the rope were far enough apart that one individual could not reach both ends (Melis et al., 2006b). If they tried to solve the task themselves by pulling on only one end, the rope would release and the tray could not be pulled in. In order to successfully solve this task both individuals had to pull on the ends of the rope at the same time. These “cooperative” tests were compared with “solo” tests, during which the two ends of the rope were close together so that one individual could pull both ends at the same time.

To directly assess whether chimpanzees understood the role of the partner, the authors allowed the chimpanzees to decide whether or not they needed a partner’s help (Melis et al., 2006b). Initially one chimpanzee was let into the experimental booth and a second was locked in an adjoining room. The first subject had the ability to release the lock and allow the second subject to enter if they chose. Subjects chose to let the second subject in significantly more often during the “cooperative” tests when help was needed than during the “solo” tests. These studies provide the first convincing evidence of chimpanzees understanding the need for and role of a partner in a cooperative task. Similar results have been demonstrated in other mammals tested using the same apparatus (elephants: Plotnik et al, 2011; hyenas: Drea & Carter, 2009) but interestingly, both bird species tested did not show an understanding of the need for a partner (parrots: Péron et al, 2011; rooks: Seed et al, 2008). Although the birds were able to achieve some success at the task, they did not wait for a partner to approach the apparatus before pulling, which suggests that they may not have been fully aware of the role of the partner.

After establishing that chimpanzees could indeed coordinate their behavior with a partner to achieve a goal, Melis and colleagues (2006a,b; 2008; 2009) began to ask basic questions about tendencies that modulate cooperation. For example, when given the option to pick between two potential partners, chimpanzees chose the partner they had had the most past success with (Melis et al., 2006b). Note that although the chimpanzees showed clear preferences for the more proficient partner, the underlying mechanism could be extremely simple: if they succeed more with one partner versus another, they get more rewards with one partner than the other, which can lead to associative learning. There was also a weak effect of reciprocity; chimpanzees were more likely to help those who had helped them in the past (over those who had chosen to help someone else; Melis et al. 2008). Finally, a follow-up study determined that not only were chimpanzees aware of the role of their partner, they were also paying attention to their own payoff relative to their partner’s (Melis et al., 2009). In this study the chimpanzees had a choice between two differently-baited apparatuses—one that provided equal rewards to both individuals and one with unequal rewards. Although the dominant individual tended to initially pick the unequal tray (advantaging themselves) the subordinate individual would wait by the equal tray until the dominant gave up and came over to help them. This suggests that the chimpanzees were also monitoring the outcomes of their interactions.

Inequitable outcomes tend to have a negative impact on cooperation (reviewed by de Waal & Suchak, 2010). In capuchin monkeys, for example, pairs that spontaneously divided food equitably were more likely to succeed at a cooperative task (Brosnan et al., 2006; de Waal & Davis, 2003). This is not surprising given that prosocial tendencies disappear when the outcome is inequitable unless there is an opportunity for future reciprocity (de Waal et al., 2008; Suchak & de Waal, 2012).

Competition for rewards and freeloading can also induce inequitable outcomes, which interfere with cooperation. For example, when rewards are clumped, one individual tends to monopolize them and cooperation generally breaks down (de Waal & Davis, 2003; Melis et al., 2006a). Laboratory studies that try to alleviate competitive pressures by, for example, delivering dispersed rewards directly to the individual who worked for them or pairing the chimpanzees with individuals with whom they have a very tolerant relationship have found a great deal of success (Hirata & Fuwa, 2007; Melis et al., 2006b). In essence, these studies were designed to minimize the chance of inequitable outcomes.

In contrast, in studies where there was a great deal of competition for rewards produced by cooperative actions, to the point where the individuals working at the task often did not get any benefit due to freeloading, most of the chimpanzees ceased to participate in the task (Schneider et al., 2012). The failure of chimpanzees to show prosocial behavior in many studies (e.g. Silk et al., 2005; Jensen et al., 2006; Vonk et al., 2008) has been attributed, at least in part, to the chimpanzees being preoccupied with obtaining their own rewards, which researchers have suggested stems from high intra-group competition for food (Melis et al., 2011). These results, combined with evidence that chimpanzees perform better on tests when paired with a human competitor versus a human cooperator have led some research to suggest that chimpanzees are competitive rather than cooperative (Hare, 2001; Hare & Tomasello, 2004). It has even been suggested that competitive paradigms to test social cognition in chimpanzees have more ecological validity than cooperative paradigms (Hare, 2001).

However, given the high degree of cooperation in the wild, it should be expected that chimpanzees have the ability to regulate their competitive tendencies in favor of a more profitable cooperative outcome. Failure to do so in previous experimental studies may be due more to limits of the typical laboratory setting, rather than limits of the chimpanzees' ability to inhibit competition in favor of cooperation. To date, no study has systematically examined the effects of spontaneous tendencies to freeload and naturally occurring competition on cooperation in an open-group setting.

There may be several ways for chimpanzees to regulate these tendencies in their social groups, where repeated interactions and a free choice of partners are possible. First, repeated interactions allow individuals to attempt to modulate the behavior of their partner in the future. Known as partner control mechanisms, these include things like reciprocity and punishment, which tend to increase the likelihood of future cooperation and decrease the probability of future defection (Noë, 2006). Chimpanzees do engage in both reciprocity (de Waal, 1997) and punishment (Jensen et al., 2007) but the effect of these behaviors in reinforcing cooperative behavior is yet unknown.

The alternative to partner control strategies is partner choice, in which the ability to choose and switch partners drives cooperative relationships (Noë, 2006). Having a choice of partners, for example, allows an individual who has experience with multiple partners to assess who the best partner is and choose to work with that individual. It also allows for options: instead of having to respond negatively towards lack of cooperation, one can simply find a more cooperative partner. This creates an incentive to behave cooperatively if an individual wants or needs to maintain cooperative relationships.

In all likelihood, a combination of partner choice and control mechanisms contributes to the development and maintenance of cooperative relationships in a group. However, partner choice in experimental studies has been extremely limited. A notable exception has been Melis and colleagues (2006b, 2008) studies where the chimpanzees did have a choice between two different partners. These studies suggest that chimpanzees have the ability to distinguish between more beneficial and less beneficial partners. This raises the question of how much past success influences partner choice when the chimpanzees can freely choose and switch partners, and how this interacts with tolerance and affiliation, other factors which have been demonstrated to affect cooperative tendencies (Chalmeau, 1994; Melis et al., 2006a).

Exploring these questions in an open-group setting allows us to examine how chimpanzees cooperate in a competitive environment, and what role partner choice and partner control mechanisms play in maintaining cooperation. This setting, in fact, creates multiple types of competition: first, for access to the task and second, for access to food rewards. If chimpanzees are truly unable to inhibit competition, in an open-group setting it should be impossible for them to develop and sustain cooperative relationships. If they spontaneously develop partner control and partner choice mechanisms for inducing cooperation, we expect them to achieve high levels of cooperation.

Outline of the current paper

In the following chapters, I will address these critical questions surrounding partner choice and partner control through an experimental task done in the group setting in chimpanzees. In chapter 2, I will discuss the development and maintenance of a cooperative task in a group of chimpanzees. This task required either dyads or triads to cooperate, presenting the first evidence that three chimpanzees are capable of coordinating their behavior. I will also examine mechanisms of partner choice from both a form (who do the chimpanzees choose to work with?) and outcome (who are the most successful partners?) perspective. In this context I will also discuss the role competition for access to the task played in partner choice and overall individual success. In chapter 3, I will address a different aspect of competition, freeloading. Specifically, I will examine the prevalence of freeloading, responses of the individuals who were targeted by freeloaders and how the chimpanzees prevented rampant freeloading to achieve widespread success. Finally, in chapter 4, I will synthesize what we now know about chimpanzee cooperation from across the studies and provide some areas for future research.

Chapter 2: Chimpanzees successfully cooperate in duos and trios despite potential competition: Partner choice

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Abstract

Experimental cooperation studies on primates often remove several important challenges to successful joint action. By testing the primates in pairs, partner choice is eliminated and open competition and freeloading are sharply reduced. We know that primates in the wild, especially chimpanzees (*Pan troglodytes*), are able to handle these challenges, whereas the mixed outcome of pairwise testing may have been due to their limited ecological validity. The purpose of this study was to examine cooperative behavior in an open group setting by testing how captive chimpanzees coordinate with multiple partners of their own choosing. All members of the group (n=11) had access to the cooperation apparatus in a large outdoor compound. Chimpanzees were tested under two conditions: (1) dyadic cooperation, requiring two individuals and (2) triadic cooperation, requiring three individuals, to pull in a tray baited with food. Without prior training, chimpanzees learned to solve the task in both conditions. Success increased over time and the amount of pulling when a partner was not present decreased, demonstrating that the chimpanzees gained an understanding of the task in both conditions. Chimpanzees preferentially approached the apparatus when individuals of similar rank or kin were present and were more successful when working with kin versus non-kin. This experiment demonstrates that in the midst of a complex social environment, subject to competition and intolerance, chimpanzees can initiate and maintain a high degree of cooperative behavior.

Key Words: Cooperation, Chimpanzee, *Pan troglodytes*, Partner Choice

Introduction

Cooperation, joint action by two or more individuals to achieve a goal, is often regarded as less puzzling than altruistic behavior, in which one individual benefits another at a cost to himself or herself. While that may be true in the evolutionary sense, on a proximate level, cooperation often consists of a series of potentially complex decisions involving a choice of partners (Noë, 2006).

Nonhuman primates have attracted considerable research on the topic of cooperation both because of their close evolutionary ties to humans and observations of cooperation in nature including coalition formation, food sharing and cooperative hunting (de Waal & Suchak, 2010; Mitani, 2006). However, in the wild it has been difficult to determine if the chimpanzees are actually cooperating by coordinating their behavior in space and time or by simultaneously but individually pursuing a common goal, thus giving the appearance of cooperation (Noë, 2006; Stanford, 1998).

Given the ambiguity of the field data, laboratory studies of cooperation have largely focused on elucidating the proximate mechanisms underlying cooperative behavior. Indeed, some scientists have questioned whether nonhumans are cognitively capable of achieving cooperation at all. Early work suggested that the ability of chimpanzees to coordinate was limited. Although they could work together to pull in a tray, they only did so after considerable training (Crawford, 1937). In other studies, the majority of the chimpanzees did not seem to understand the role of or need for a partner; they were just as likely to pull on the apparatus when a partner was present versus absent (Chalmeau, 1994). These results, combined with other failures in other nonhuman primates such as capuchin monkeys, led some researchers to conclude that nonhuman primates were not capable of true coordination and any success achieved was a result of coincidental co-action rather than true coordination (Chalmeau et al., 1997; Visalberghi et al., 2000).

However, more recent studies borrowing a more intuitive paradigm from an early study by Crawford (1937) have found that both capuchin monkeys (Mendres & de Waal 2000) and chimpanzees (Hirata & Fuwa, 2007; Melis et al., 2006a,b) not only can succeed at the task, but also recognize when they need a partner versus when they can solve the task alone. These new studies also demonstrated that chimpanzees were paying attention to the outcomes for both themselves and their partners and differentiated between potential partners on the basis of tolerance and past success (Melis et al., 2006a,b; 2008).

Despite improvements in methodologies that have established that chimpanzees and some species of monkeys are able to coordinate their behavior with a partner, many questions remain regarding the mechanisms that might enable naturally occurring cooperation. One key discrepancy between captive experiments and wild observations of cooperation is that all experiments on nonhuman primate cooperation have been limited to two individuals working together. In nature, however, chimpanzees act in much larger groups. In Kibale National Park in Uganda, for example, chimpanzees hunt in groups of up to six individuals and an increasing number of hunters leads to increased benefits (Mitani & Watts, 1999). Understanding the ability of chimpanzees to act jointly with more than one other individual simultaneously is an important step in understanding the abilities and limits of chimpanzee cooperation.

The strict control present in typical laboratory studies has also limited our abilities to ask questions about how cooperation is achieved in a competitive arena, in which the choice of partners is not imposed by the experimenter but made by the subjects themselves and in which many others are present who may steal the rewards or otherwise thwart achievement of the goal. Chimpanzees are often thought to lack the capacities to regulate competitive tendencies, which would suggest that in order to evolve human-level cooperation from that found in apes, early humans had to become less aggressive/competitive and more tolerant/friendly with one another (Hare & Tomasello, 2004; Moll & Tomasello, 2007) In light of these views, it is important to test if chimpanzees are able to achieve and maintain cooperation in an environment in which competition is not only possible but highly likely given the presence of more dominant and aggressive individuals who may usurp the rewards or access to the task. To answer this important question, the current study was conducted in the outdoor enclosure with all of the group members present. Thus, all chimpanzees had the ability to potentially access the apparatus and the choice to participate in the task, interfere with the attempts of others, or do something else entirely such as grooming, solitary foraging or sleeping.

The primary aim of this study is therefore to examine the ability of chimpanzees to overcome competition in a cooperation task with free partner choice. Previous work has demonstrated that when experimenters pair up tolerant individuals they are more successful at the task and that preexisting relationships between individuals play an important role in establishing cooperation (Melis et al., 2006a; Melis et al, 2008). If tolerance is the primary constraint on partner choice, then chimpanzees should work with those with whom they are most socially close outside of the experimental setting or their kin. An alternative hypothesis is that they will preferentially choose those with whom they have had the most past success as they did in Melis et al (2006b).

Who the chimpanzees choose as their cooperative partners is an important step in elucidating the mechanisms of how cooperation develops. However, in nature cooperation often requires working with more than one other individual. Indeed, the most common party size in chimpanzees when hunting is six individuals (Mitani & Watts, 1999). Increasing the number of individuals increases the difficulty of coordination and may provide more information about the capability of chimpanzees to engage in joint action. The second aim of this study is to test the ability of chimpanzees to coordinate their behavior with two other individuals. If they are coordinating their actions with other individuals through communication, then they should be able to succeed when a third individual is involved. If they are coincidentally succeeding by acting individually, then success should decrease with three individuals and there should be no difference in attempts to succeed when the correct number of partners is present versus absent.

Methods

Subjects and Housing

Subjects were 11 chimpanzees (1 male, 10 females) living in a large social group at the Field Station of the Yerkes National Primate Research Center (YNPRC) of Emory University. Out of the 90 total dyadic relationships, there were 22 maternal kinship relationships, all among females; the remaining 68 dyadic relationships were all non-kin. The group's 711m^2 outdoor compound contained a large climbing structure and several enrichment items (barrels, tires, etc.) and was adjacent to five indoor interconnected runs containing sleeping platforms and swings. Testing occurred in the outdoor compound with the entire group present and so did not require separating the subjects from their group (Figure 1). During testing, subjects had access to the indoor sleeping quarters. Chimpanzees are fed two daily meals consisting of fruits, vegetables and grains at approximately 8h30 and 15h00 and have access to water ad libitum. All food used in this study was supplemental to the chimpanzees daily intake and at no time was food or water restricted. All procedures were approved by Emory University's Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the study.

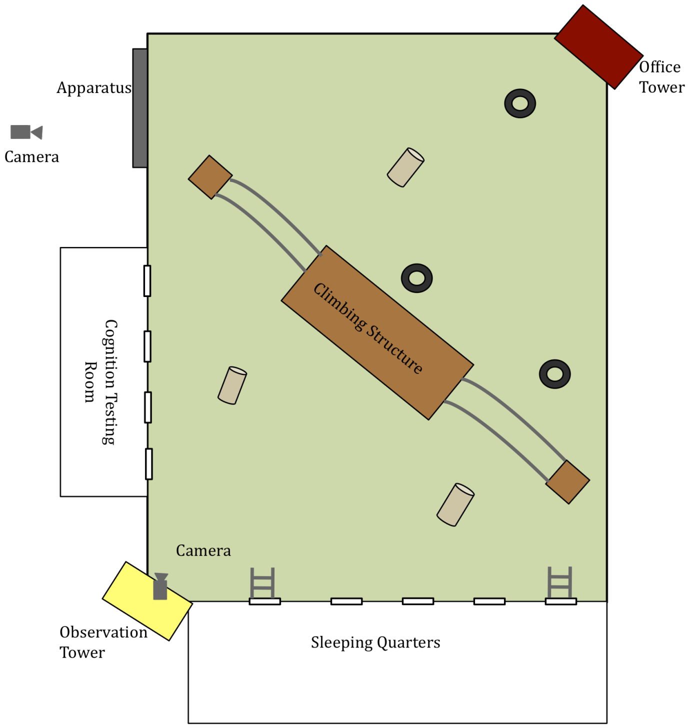

Figure 1. The test set-up. All sessions took place in the outdoor enclosure with the chimpanzees having free access to the test apparatus. The majority of the apparatus was located outside of the chimpanzees' reach, with just the pull bars extending into the enclosure.

Apparatus

The apparatus required that one (or more) chimpanzee(s) remove a barrier in order for another chimpanzee to simultaneously pull in a tray baited with food (Figure 2). Initially one barrier was blocking the tray and thus required two individuals to coordinate their behavior to obtain food (dyadic cooperation). The barrier was connected to a steel rod that extended 20 cm into the chimpanzee compound. Pulling on the rod caused the barrier to drop down via a spring/pulley mechanism. Once the barrier was pulled down a second individual used a similar rod (also extending 20cm into the compound) to pull in the tray. Once the tray was pulled in all the way (approximately 30 cm) food rewards dropped into a funnel, which delivered the rewards to the chimpanzees sitting at the apparatus. Food rewards were one grape, two raisins, a small slice of sweet potato or small slice of banana per trial and were randomly varied from trial to trial. Following the establishment of dyadic cooperation, a second barrier was added such that three individuals had to coordinate their behavior to solve the task (two to pull down barriers and a third to pull in the tray; triadic cooperation; Figure 2). The rods to pull down the barriers and pull in the tray were sufficiently far apart (~1.6m) so that one individual could not participate in both roles.

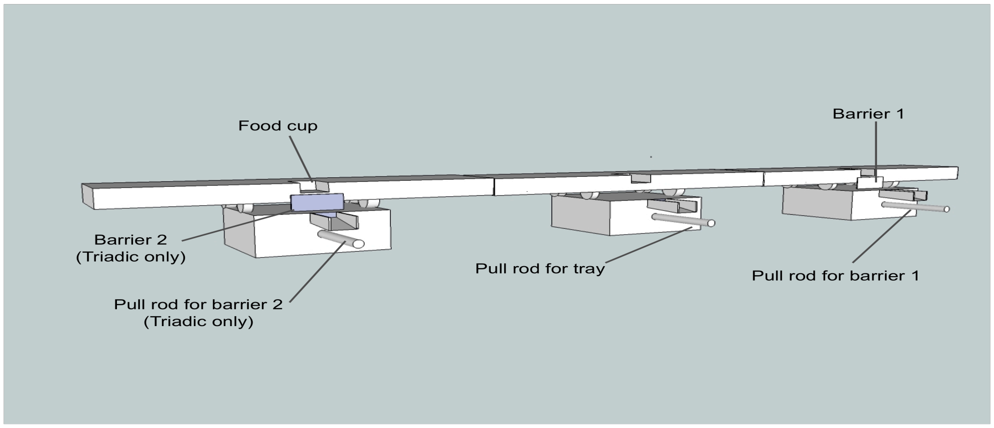

Figure 2. The test apparatus. The only part of the test apparatus that was inside the enclosure were the pull bars, the rest was outside. Note that barrier 2 (on the left) was only present during the triadic sessions. The apparatus was set up exactly the same for dyadic sessions but barrier 2 and the corresponding pull bar were missing.

Procedures

Test Sessions. A trial began when the tray was baited with food. Following successful trials, the experimenter waited for the chimpanzees to release the rods (and barriers) and then reset the tray back in the starting position and re-baited the tray. If the chimpanzees did not solve the task within 5 minutes, the trial was considered a failure, the food removed, and a one-minute time out commenced prior to re-baiting. Each session lasted 1 hour and consisted of as many trials as could be accomplished in that time period. Since dominant individuals could monopolize the apparatus early in the session, a longer session allowed more individuals to interact with the apparatus. Only one session was run per day.

Test Phases.

Phase 1a: Dyadic cooperation acquisition. 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, we waited for the majority of the chimpanzees to establish consistent success before moving onto the next phase.

Phase 1b: Triadic cooperation acquisition. Following the 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.

Behavioral Coding

Each trial was videotaped from two angles (a side and front view) using HD digital video cameras. Additionally, one experimenter had a digital voice recorder to record a narrative of any social interactions that occurred during testing. Success or failure of each trial, which chimpanzees solved the task, and which chimpanzees received rewards were recorded in-person and later confirmed from video. Latency to success and the number of pulls before success were also recorded from video. Social behaviors that occurred in the context of the experiment were also coded from the video and audio recordings and included: aggressive behavior, affiliative behavior in proximity to the apparatus (grooming, greeting, sitting in close proximity), recruitment and other requesting behavior, and displacements at the apparatus. In addition to data collected as part of the experiment, affiliation data collected as part of routine observations was used to form a sociometric matrix and provide a quantitative measure of affiliation for each dyad. Inter-rater reliability was excellent for latency (r=0.99), pulling (r = 0.85) and displacement behavior (kappa=0.88).

Analyses

Acquisition of the task. To test whether the chimpanzees learned about the need for and role of the partner, we compared behavior during the acquisition phases (phases 1 a and b) to the proficiency phase (phase 2). Within-subjects mixed measures ANOVAs were run to compare differences between phases and partner conditions (dyadic and triadic) for latency, efficiency, and pulling. Latency and efficiency (number of pulls to success) were both measured from the time the succeeding pair or triad arrived at the apparatus until the time of success, when they obtained the food. We compared the pulling rate (pulls per minute) of each individual when the correct number of partners was at the bar "ready" to pull versus when there were not enough partners present. This is a very strict criterion as chimpanzees who momentarily stepped away from the apparatus or were approaching but not yet within reach of the bar were not considered to be "present." In the dyadic condition we compared the pulling rate when a partner was present versus absent and in the triadic condition we compared the pulling rate when all three partners were in place versus fewer than three partners in place. In addition to looking at pulling rates by the number of partners, we also looked to see if pulling rates changed between the acquisition and proficiency phases. All acquisition analyses were run using SPSS 20.0.

Partner Choice. We were interested in which chimpanzees chose to approach the apparatus when other chimpanzees were available as potential partners. When a chimpanzee was present at the apparatus, they had 9 potential partners that could approach. If an individual approached, they were scored as a 1; individuals who did not approach were scored as 0. This was done by session, so if a chimpanzee was never at the apparatus during a given session, they were excluded from the analysis for that session (since they had to be at the apparatus in order for someone to approach to work with them). All triads were broken down into their corresponding dyads for the purpose of analysis.

To determine which factors influenced another chimpanzee's willingness to approach to work with another individual, we ran a generalized linear mixed model (GLMM), with approach as a binomial dependent variable. Kinship, long-term affiliation, rank distance between the two individuals, recent success (from the current phase) and relative past success (the percentage of that individuals success from the previous phases with each other individual) were included in various combinations as fixed terms. Models were constructed examining each fixed effect independently as well as interactions between the effects. None of the fixed effects were correlated with each other. We also ran a full model which contained all of the fixed effects and a null model that contained only the random effects for all phases. As relative past success could not be determined for the dyadic acquisition phase (since there were no previous phases) it was included in the analysis for triadic acquisition and proficiency only (phases 1b and 2), resulting in 10 models being compared for phase 1a and 14 models for phases 1b and 2. Phase 2 dyadic and triadic were analyzed separately. Identity of the chimpanzee already present at the apparatus, identity of the chimpanzee that approached, and session were included as random effect to control for repeated sampling 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.

Although one chimpanzee had to approach another at the apparatus in order to succeed, there was not a direct relationship between approach and success in that one approach could lead to multiple successes or none at all. We also tested whether these same factors—kinship, affiliation and rank distance played a role in the amount of success each pair had. To do this, we ran a linear mixed model (LMM) with number of successes by each dyad as a continuous dependent variable. Kinship, long-term affiliation, and rank distance and the interaction between these factors were included as fixed terms. Models were constructed examining each fixed effect independently as well as interactions between the effects, which resulted in a total of 6 models tested for each phase. Dyadic and triadic were again tested separately. None of the fixed effects were correlated with each other. Dyad and session were included as random effects to control for interdependence between dyads and repeated sampling. We again used an ANOVA to determine which model had the most explanatory power by comparing the AIC for all of the possible models. Once the best model was identified, a Markov chain Monte Carlo simulation of 10,000 interactions was used to obtain significance values. All partner choice analyses were run using R, with the lme4 package.

Results

Acquisition of the task

For both dyadic and triadic tests, the chimpanzees spontaneously solved the task within the first 2 hours of exposure. In total, 10 out of the 11 chimpanzees solved the task at least once during both the dyadic and triadic tests for a total of 2,462 dyadic successes and 1,103 triadic successes. Although 10 out of the 11 chimpanzees solved the dyadic task during the acquisition phase, only eight out of 11 solved the task during the triadic acquisition phase. Two of the remaining three chimpanzees did solve the triadic task during the proficiency phase. The same chimpanzee, Mai, did not solve the task in either the learning phase or the proficiency phase and in fact ceased pulling by the proficiency phase. Since her overall pulling rates were more than two standard deviations below the average, she was eliminated from the analysis. By the end of the acquisition phase, the average chimpanzee had succeeded 139 times at the dyadic task and 99 times at the triadic task. This increased to an average success of 447 times at the dyadic task and 301 times at the triadic task by the end of the proficiency phase. Figure 3 shows the average cumulative success over time.

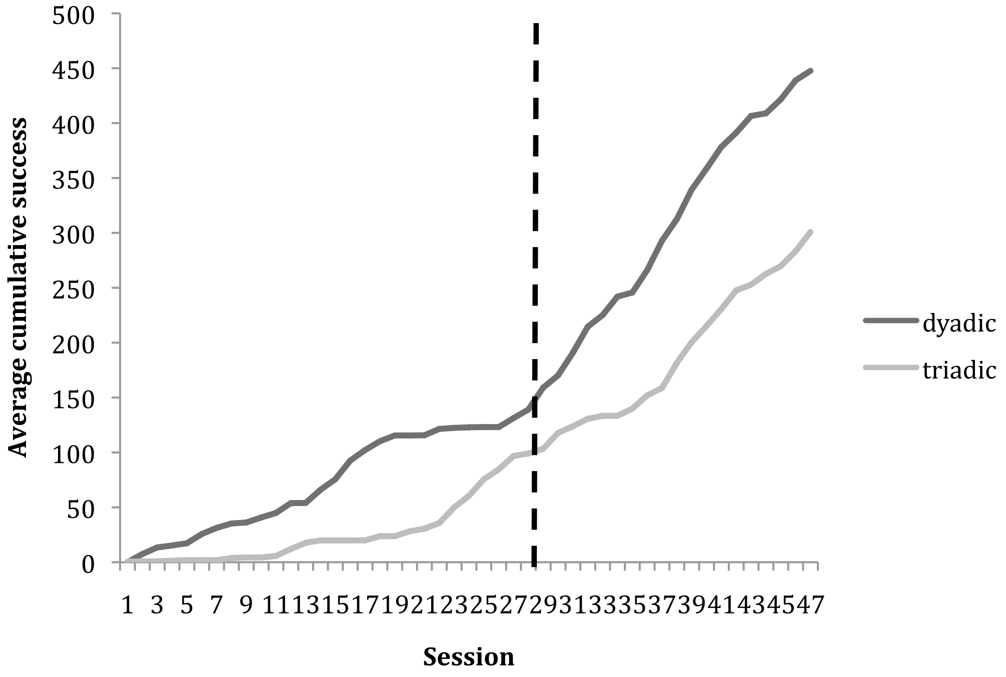

Figure 3. The average cumulative success of the chimpanzees over time. The dashed line represents the arbitrary marker between the acquisition phase and the proficiency phase. Note that the first 28 dyadic sessions were followed by 28 triadic sessions, but the final 38 sessions (to the right of the dashed line) were alternating between dyadic and triadic cooperation (19 of each dyadic and triadic).

Several analyses tested proficiency and understanding of the cooperative aspects of the task between the acquisition phase and the proficiency phase. Latency to success was significantly lower per individual subject in the proficiency phase than in the acquisition phase (Mixed Measures ANOVA: $F_{1,7} = 21.29$, $p = 0.002$). There was no significant effect of dyadic versus triadic tests on latency ($F_{1,7} = 0.11$, $p = 0.75$) however there was a significant test phase by number of partners (dyadic versus triadic) interaction such that the decrease in latency was much larger from the acquisition phase to the proficiency phase for the dyadic condition than the triadic condition. It is important to note, however, that these phases for dyads (phases 1a and 2) were separated in time by the triadic acquisition phase (phase 1b), whereas the proficiency phase for triads immediately followed the triadic acquisition phase.

A second analysis was conducted to examine efficiency at the task, or number of pulls it took to achieve success. There was again a significant effect of phase in that the chimpanzees succeeded with significantly fewer pulls during phase 2 (Mixed Measures ANOVA: $F_{1,7} = 16.83$, $p = 0.005$) and also a significant partner condition by phase interaction ($F_{1,7} = 10.37$, $p = 0.015$; Figure 4). Again, there was a larger decrease in the dyadic partner condition than in the triadic. A perfect efficiency would be one pull per success for each individual, during the proficiency phase there was an average of 1.58 pulls during the dyadic condition and 2.25 pulls for the triadic condition.

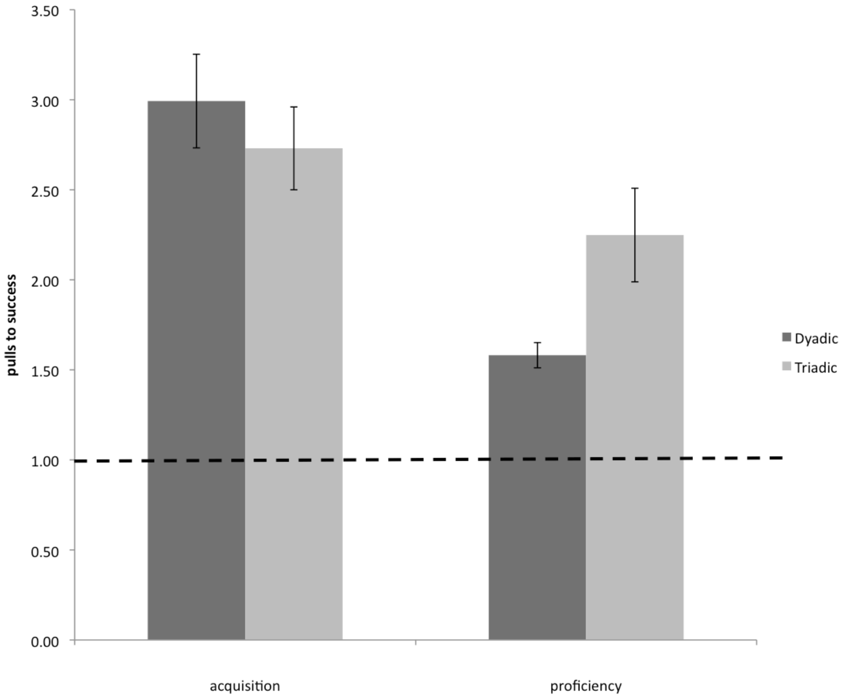

Figure 4. Efficiency at the task. Bars represent each individual's average number of pulls (±SEM) to success during the acquisition versus the proficiency phase. Dashed line indicates perfect efficiency; the task required a minimum of one pull to succeed.

Finally, to assess whether the chimpanzees developed an understanding of the need for a partner, we compared pulling rates when the correct number of individuals were present and able to pull to when not enough chimpanzees were present. In the dyadic test sessions there was a significant effect of partner presence; they pulled more when a partner was at the other bar then when no partner was present (Mixed Measures ANOVA: $F_{1,9}=39.53$, $p <0.001$; Figure 5). There was also a significant phase by partner presence interaction: the ratio of pulls when a partner was present as compared to pulls when a partner was absent was greater in the proficiency phase than in the acquisition phase ($F_{1,9}=14.11$, $p=0.005$). Finally, there was an overall effect of phase, such that individuals had higher overall pulling rates in the proficiency phase than in the acquisition phase ($F_{1,9} = 9.76$, $p = 0.01$).

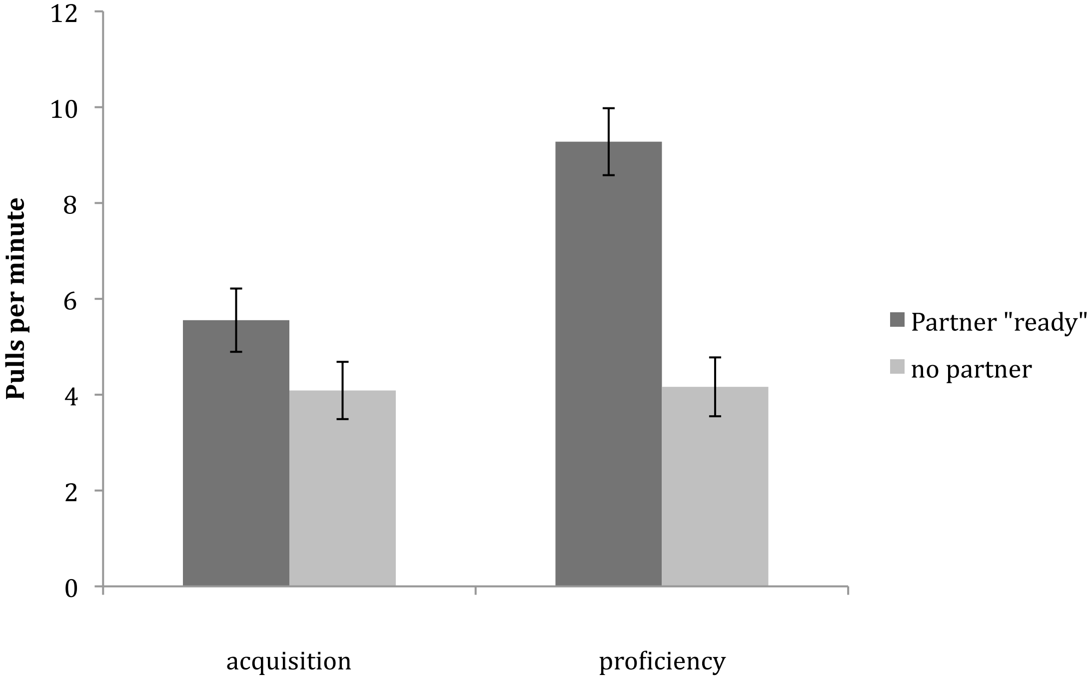

Figure 5. Comparison of pulling rates during the acquisition and proficiency phases for dyadic cooperation. Partner "ready" indicates that a partner was both present at the apparatus in a position to be able to pull on the tray.

In the triadic test sessions, the pattern was much the same. 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 ($F_{1,8}$=15.97 p=0.004; Figure 6). Similar to the dyadic test sessions, there was a significant phase by partner presence interaction: the ratio of pulls when the correct number of partners were present as compared to pulls when no partner or only one partner was present, was greater in the proficiency phase than in the acquisition phase ($F_{1,8}$=5.32, p=0.05). Unlike dyadic tests, however, there was no main effect of phase; the chimpanzees did not pull more overall during the proficiency phase as compared to the acquisition phase ($F_{1,8}$=1.47, p=0.26). When triadic pulling was broken down into three levels: two partners present, one partner present and no partners present, there was again a significant effect of the number of partners present ($F_{1.12,10.99}$ = 11.62, p = 0.006, Greenhouse-Geisser corrected due to lack of sphericity), 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).

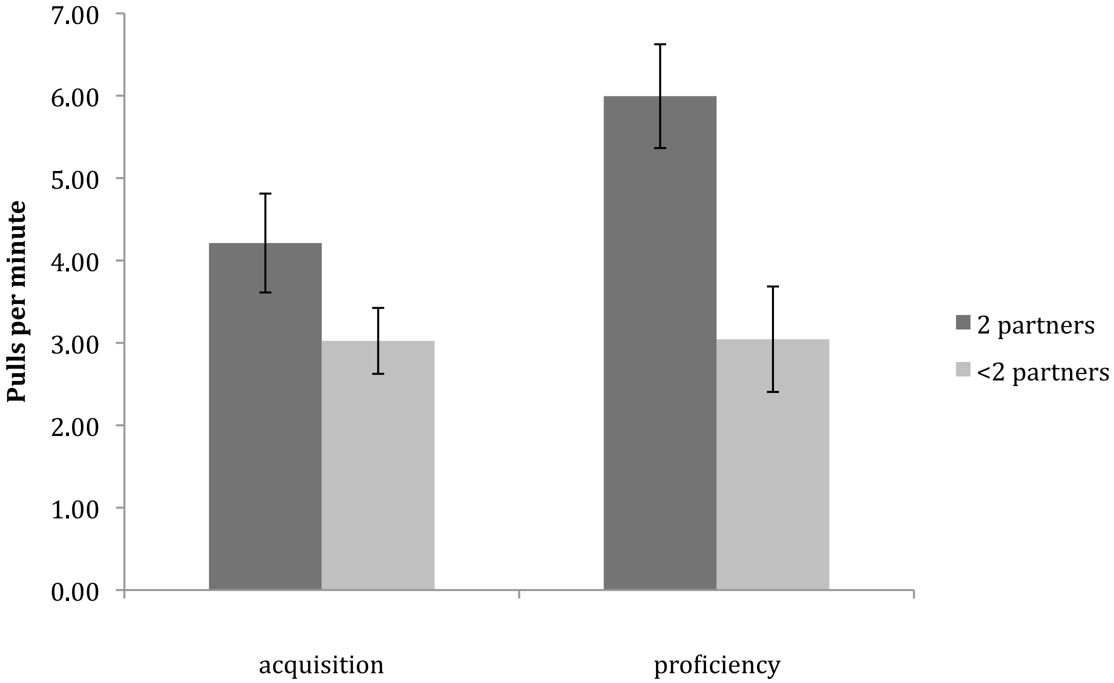

Figure 6. **Comparison of pulling rates during the acquisition and proficiency phases for triadic cooperation**. Note that the comparison was between the correct number of partners present (2 partners) and the incorrect number of partners (one or zero partners).

Partner choice

There were a total of 45 possible unique dyads (90 directional dyads) and 120 possible triads in the group (accounting for all possible combinations of chimpanzees who solved the task). During the acquisition phase, 24 different dyads and 32 unique triads successfully solved the task. During the proficiency phase, 29 dyads and 32 triads solved the task. These included both stable partnerships as well as new partnerships that occurred only during the proficiency phase. There were also pairs or triads that worked together during the acquisition phase, but did not work together during the proficiency phase.

We examined factors that might influence whether or not one individual approaches another already present at the apparatus. Across all phases, there was a significant influence of the random effects (intercept; dyadic acquisition: $Z = -9.07$, $p < 0.001$; triadic acquisition: $Z = -5.48$, $p < 0.001$; dyadic proficiency: $Z = -4.30$, $p < 0.001$; triadic proficiency: $Z = -5.11$, $p < 0.001$; see Table 1 for a list of the random effects). 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 the identity of the chimpanzees, rather than the session number (Table 1).

Once individual identity was controlled for, there was a significant influence of the fixed effects for all phases except triadic acquisition. During dyadic acquisition, the model with the best explanatory power only included affiliation (AIC = 850.11, $\chi^2 = 5.11$, df = 0, $p < 0.001$; Table 1). Affiliation with the individual already present at the apparatus significantly increased the likelihood of another chimpanzee approaching ($Z = 2.63$, $p = 0.009$). In the triadic acquisition phase, none of the fixed effects had significant explanatory power once the random effects were controlled for, making the null model (which includes random effects only) was the best fit model (AIC = 1526).

Variable	**ß**	**SE**	***Z***	***p***
Dyadic Acquisition (1a)				
Fixed Effects				
Intercept	**-2.92**	**0.32**	**-9.08**	**<0.001**
Affiliation	**0.09**	**0.03**	**2.63**	**0.009**
Random effects				
Individual already there	variance	0.26		
Individual approaching	variance	0.13		
Session	variance	0.04		
Triadic Acquisition (1b)				
Fixed Effects				
Intercept	**-1.99**	**0.36**	**-5.55**	**<0.001**
Random effects				
Individual already there	variance	0.21		
Individual approaching	variance	0.26		
Session	variance	0.09		

Table 1. Results of the best fit GLMM during the acquisition phase. Fixed effects in bold had a significant influence on whether or not an individual approached. In the triadic acquisition phase, no fixed effects were significant once the random effects were controlled for.

Once the chimpanzees had attained proficiency (phase 2), different factors seemed to be influencing their willingness to approach. The same model had the best fit for both dyadic and triadic sessions and included kinship, affiliation and the interaction between these factors and rank distance (dyadic: AIC = 601.44, $\chi^2 = 9.68$, df = 0, $p < 0.001$; triadic: AIC = 1199.22, $\chi^2 = 4.12$, df = 0, $p < 0.001$; Table 2). Specifically, the interaction between kinship and rank distance was highly significant (dyadic sessions: $Z = 3.80$, $p < 0.001$; and triadic sessions: $Z = 2.667$, $p = 0.007$). The chimpanzees were less likely to approach the greater their rank distance was from the individual already present, unless they were related to that individual. Additionally, for the dyadic sessions, there was a main effect of kinship (Z = -2.07, p = 0.04) and rank distance (Z = -3.86, p < 0.001) but not for triadic sessions (kinship: Z = -1.05, p = 0.30; rank distance: Z = -.58, p = 0. 56). Affiliation and the interaction between affiliation and rank distance were not significant in either the dyadic or triadic sessions.

Variable	**ß**	**SE**	***Z***	***p***
Dyadic Proficiency (2)				
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 already there	variance	0.26		
Individual Approaching	variance	0.23		
Session	variance	0.00		
Triadic Proficiency (2)				
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 already there	variance	0.21		
Individual Approaching	variance	0.19		
Session	variance	0.08		

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.

Approaches tended to be reciprocal—that is, the more individual A approached B at the apparatus, the more likely B was to approach A. In the dyadic acquisition phase this was not significant (Spearman's rank order correlation between approaches in one and the other dyadic direction rho = 0.17, n = 90 dyads, $p = 0.06$) but in the triadic acquisition phases the effect became significant (rho = 0.57, n = 90, $p < 0.001$) as it did in the proficiency phases (dyadic: rho = 0.42, n = 90, $p < 0.001$; triadic: rho = 0.56, n = 90, $p < 0.001$). Thus, there was a clear effect of time—during the first 28 sessions (dyadic acquisition phase) reciprocity between approaches was not significant, but beginning in the triadic acquisition phase the relationship was significant. Note that the p-values reported are exact two-tailed p-values obtained from 10,000 permutations, to compensate for interdependence between dyads.

When examining which pairs were the most successful at the task there were large inter-individual differences (dyadic acquisition: $t = 2.52$, $p = 0.01$; triadic acquisition: $t = 3.48$, $p < 0.001$; phase 2 dyadic: $t = 1.99$, $p = 0.04$; phase 2 triadic: $t = 3.14$, $p = 0.002$). For the first phase, the dyadic and triadic acquisition phases, no other factor had explanatory power above the random effects, making the null model the best fit model (Table 3).

Variable	**ß**	**SE**	***t***	***p***
Dyadic Acquisition (1a)				
Fixed Effects				
Intercept	**0.55**	**0.22**	**2.52**	**0.01**
Random effects				
Dyad	variance	0.16		
Session	variance	0.06		
Triadic Acquisition (1b)				
Fixed Effects				
Intercept	**0.86**	**0.25**	**3.48**	**<0.001**
Random effects				
Dyad	variance	0.13		
Session	variance	0.19		

Table 3. Results of the best fit LMM during the acquisition phase In both the dyadic and triadic acquisition phase, none of the fixed effects significantly influenced the amount of success each dyad had. Bold indicates significance.

In contrast, in the third phase the fixed effects did have significant explanatory power over and above individual variability. The best model included only kinship (dyadic: AIC = 5920; triadic: AIC = 5597). When the individual differences in chimpanzee behavior were controlled for, kin pairs were more likely to succeed than non-kin pairs (dyadic: $t = 3.40$, $p < 0.001$; triadic: $t = 2.81$, $p = 0.005$; Table 4).

Variable	**ß**	**SE**	***t***	***p***
Dyadic Proficiency				
Fixed Effects				
Intercept	**1.09**	**0.55**	**1.99**	**0.05**
Kin	**3.94**	**1.16**	**3.40**	**<0.001**
Random effects				
Dyad	variance	0.40		
Session	variance	0.00		
Triadic Proficiency				
Fixed Effects				
Intercept	**1.88**	**0.60**	**3.14**	**0.002**
Kin	**3.14**	**1.12**	**2.81**	**0.005**
Random effects				
Dyad	variance	0.42		
Session	variance	0.28		

Table 4. Results of the best fit LMM during the proficiency phase. Fixed effects in bold had a significant influence on the amount of success of each dyad. In both the dyadic and triadic acquisition phase, kin were significantly more successful than non-kin.

Description of recruitment events

Another way the chimpanzees initiated cooperation was by recruiting a specific partner to come work with them. These were relatively rare events and difficult to quantify. For example, during the second dyadic test session, Tara had been sitting at the apparatus by herself for several minutes. She approached Socko, who was sitting nearby but not at the apparatus, gave him a kiss, and then re-approached the apparatus, while repeatedly looking back over her shoulder at Socko. Within 15 seconds, Socko approached and the two of them began to work together. On other occasions, multiple individuals would approach from the indoor sleeping quarters simultaneously making their way across the compound to the apparatus. It is impossible to know what, if any, communication prompted that behavior, but instances of individuals approaching together may be indicative of partner choice. Finally, on one occasion when Tara and Borie had been working together, Katie displaced Tara who protested but retreated to a nearby climbing structure. Borie only completed one more trial before leaving, which left Katie without a partner. Katie went up to Tara, reconciled and then the two of them approached together. Interestingly, Tara headed for Katie's preferred position (the barrier), and Katie went to the tray; these were the only successes that Katie had at the tray.

Constraints on Partner Choice

Although the chimpanzees could freely approach the apparatus and participate in the task, there were two factors beyond kinship, affiliation, and past success that may have limited partner choice. First, there were only two or three positions available to work. This created the potential for competition to access the apparatus. If all the positions were occupied an individual either needed to wait for someone to leave or displace someone. Displacements were relatively uncommon, occurring only 282 times over the course of the entire experiment (an average of three per one-hour test session). Chimpanzees tended to displace those lower in rank than themselves, and this tendency was greater the greater the rank distance between the two individuals (rho = 0.31, n = 90 dyads, exact $p < 0.001$). The advantage high-ranking individuals had in competing over access to the task is also reflected in the fact that they tended be there earlier in the session than lower-ranking individuals, although this effect was limited to the proficiency phase (dyadic acquisition: rho = 0.04, exact $p = 0.25$; triadic acquisition: rho = 0.05, $p = 0.14$; dyadic proficiency: rho = 0.2, $p = 0.001$; triadic proficiency: rho = 0.09, $p = 0.07$). The weaker effect in the triadic versus dyadic proficiency phase may be due to the fact that there was less competition for access and more chimpanzees required to solve the task, allowing some lower ranking individuals earlier access. Although high-ranking individuals may have had an easier time gaining access to the apparatus, this did not result in more successes for them (Spearmans' rank correlation between individual rank and number of successes; rho = 0.07, n = 10 individuals, p = 0.44).

The second constraint on partner choice was that although every individual solved the task in both the barrier and the tray position, most of the chimpanzees spontaneously developed preferences for a particular position. In the dyadic task, three chimpanzees had significantly more success at the barrier position than the tray position, two chimpanzees had no preference and five chimpanzees had significantly more success at the tray position than the barrier position (Figure 7a). In the triadic condition, there was a bit more skew towards barrier preference, likely due to the fact that there were two barrier positions available and only one tray position (Figure 7b). Preferences for particular positions were so strong that nearly half of all displacements (46.78%) occurred despite the fact that there was another position available. Of these displacements, 94% (124 out of 132 occurrences) were when the displacer's preferred position was occupied. In other words, the chimpanzees were choosing to displace individuals at their preferred positions, rather than performing the task at their less preferred position. Interestingly, these preferences did not translate into specialization. Chimpanzees were neither more efficient (dyadic: Z = 0.14, N = 8, p = 0.89; triadic: Z = 0.94, N = 5, p = 0.35) nor were they quicker to solve the task (dyadic: Z = 0.68, N = 8, p = 0.50; triadic: Z = 0.14, N = 5, p = 0.89) when they were at their preferred position.

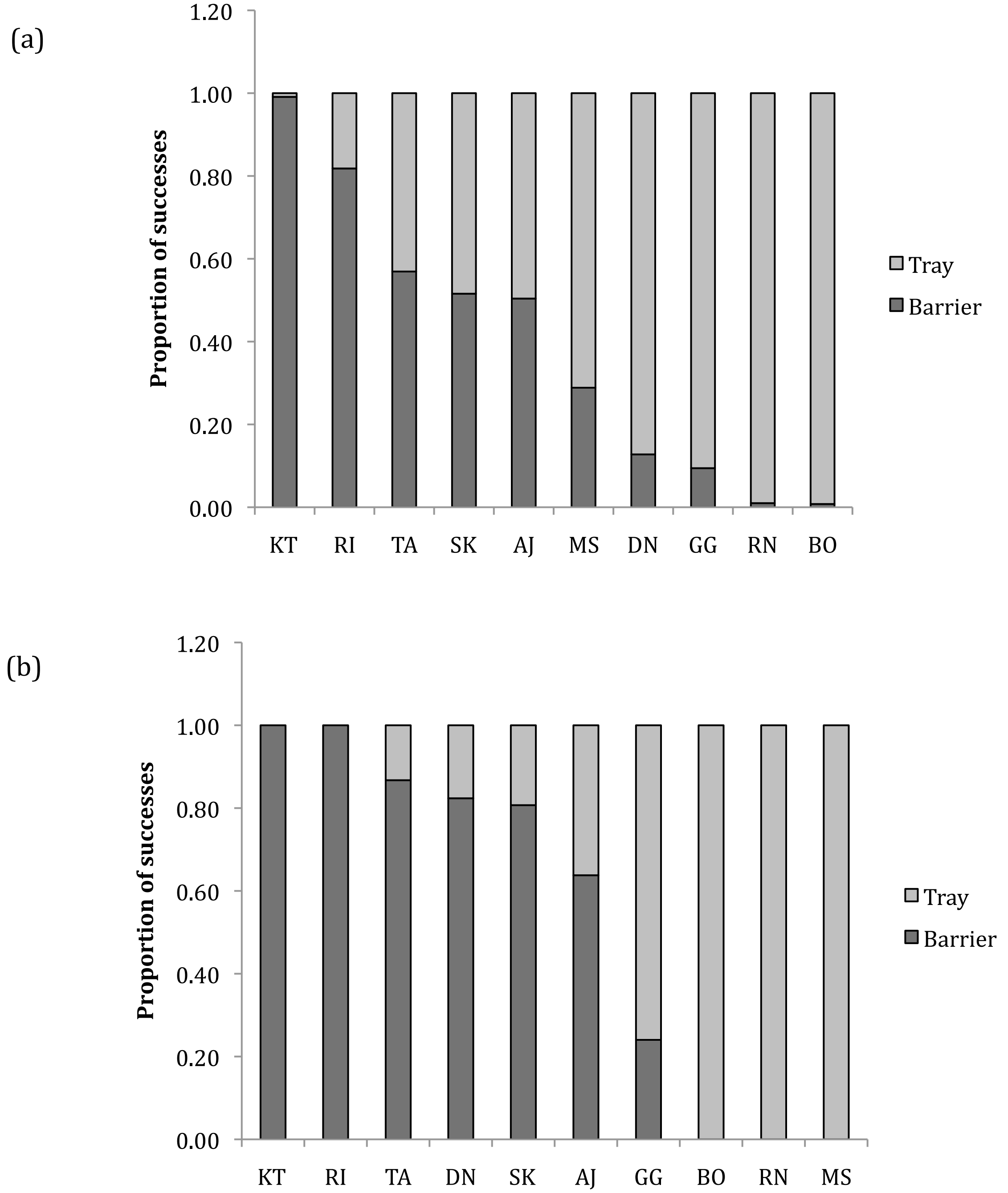

Figure 7. Individual preferences for the different positions during (a) dyadic and (b) triadic sessions. All individuals except SK & AJ in the dyadic and AJ in the triadic condition show a significant preference (binomial test by individual, $p<0.05$).

Discussion

Without any training, the chimpanzees spontaneously solved the task and were extremely successful in both the dyadic and triadic conditions. The high success rate, with a total of 3,565 completed cooperative acts, provides a strong argument against the view that the ability to overcome competition in favor of joint action evolved only in the human lineage. These chimpanzees operated in an open environment in which others could easily interfere with or prevent cooperation, yet they managed to cooperate anyway.

As expected, we observed a significant increase in understanding of the task over time. By the proficiency phase the chimpanzees were more efficient at the task, solving it faster and with fewer pulls. At that point they were also pulling much more often when a partner was ready to pull versus when a partner was not ready or absent. This is in contrast to previous studies where the chimpanzees have required extensive training (Crawford, 1937), or have been previously individually familiarized with the apparatus before cooperative testing (Melis et al., 2006a). In the only previous study without any training at all, 5 out of the 6 chimpanzees did not show an understanding of the task and were just as likely to pull when a partner was present versus absent (Chalmeau, 1994).

Even more notable is that the chimpanzees were highly successful in the triadic condition. Even though they solved fewer trials during triadic as compared to dyadic sessions, they still solved the task over 1,000 times when it required three individuals. Since the latency to success was not significantly different between the dyadic and triadic conditions, the lower number of successes was probably due to it taking us longer to reset and re-bait the tray for three subjects instead of two. Since the chimpanzees had as many trials as they could solve during the one-hour test sessions, the baiting issue meant they had fewer trials during triadic sessions. Similarly, although they were slightly less efficient in the triadic sessions, they still showed the expected differences in pulling that reflect a developing understanding of the task over the two phases. To our knowledge, this is the first demonstration that three chimpanzees can deliberately coordinate their behavior.

Other studies have used visual communication (through looking) as evidence for understanding of the task (Noë, 2006). For example, when visual communication was interrupted, capuchin monkeys failed to succeed at a pulling task (Mendres & de Waal, 2000). Although looking behavior might have helped elucidate the level of understanding and coordination in the current task, we were unable to measure gaze direction or looking. In addition to the difficulty of telling where a chimpanzee is looking because they do not have white sclera, the open setup of the current task also made it impossible to know what exactly the chimpanzees were looking at. For example, a chimpanzee at the first barrier looking to her left, could be looking at either of her partners. But, since the majority of the compound (and likely other group members) was also in that direction it was impossible to know for sure what they were looking at. In a more limited, controlled setting, it might be possible to determine where or who the chimpanzees were looking at during a cooperative task.

The open nature of the task in the group setting also presented the chimpanzees with a unique set of circumstances: unlike most previous studies they had free partner choice, but this also introduced competition and potential intolerance. The only previous study of this nature found that the alpha male monopolized the apparatus and the food rewards, which led to the rest of the group refusing 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 possible individuals, acting in a wide variety of partnerships. There was no clear, single individual that seemed to deter others from approaching.

Rank also played a role in the present study, particularly in the proficiency phase. The chimpanzees were less likely to approach an individual that ranked far above them, unless the partner was kin. This does not mean, however, that high-ranking individuals monopolized the apparatus and were more successful. There was no correlation between dominance rank and the amount of success by an individual. Rather, it seems that the chimpanzees were preferentially approaching individuals who were close in rank to themselves. Closeness in rank and kinship are probably qualities that lead to tolerant partnerships. This is consistent with previous research that found tolerance was a primary constraint on cooperation (Melis et al., 2006a) and work in capuchins that demonstrated that kin pairs were better able to mitigate the effects of competition in a cooperative task (de Waal & Davis, 2003).

We also observed preferences for particular roles or positions. This reflects the complexity of relationships in the social group; they are multi-dimensional and influenced by past interactions. The influence of repeated interactions was seen in this experiment in that individuals seemed to develop mutual preferences for partners. That is, the more individual A approached individual B, the more likely individual B was to approach A. This effect developed over time; in the first sessions they did not show these preferences. This is in contrast to a previous study, which found only a weak effect of past partner choice, which led the authors to conclude that interactions in the cooperative experiment could not override pre-existing social relationships from outside the test environment (Melis et al., 2008). A key difference between this previous study and the current experiment is that Melis and colleagues (2008) limited partner choice to two individuals: one who had chosen to help the subject in the past and one who had not. The current experiment allowed for much wider variety of choices and placed the decision in the context of the pre-existing social relationships of the subjects. Without allowing for free partner choice, we may not be able to see the full range of influences on cooperative decision-making and, more importantly, we may not develop an understanding of how these influences interact with each other.

That the chimpanzees chose their partners non-randomly, as indicated by the GLMM analysis, and also found a great deal of success in the task suggests that partner choice may play an important role in the development an maintenance of cooperation. These results are in contrast to previous studies where cooperation was only achieved in limited environments and often with considerable training. The chimpanzees in this study demonstrated that, given the opportunity to freely interact in a cooperative context, they are capable of initiating and maintaining cooperation in the midst of a complex, competitive environment.

Chapter 3. Why freeloading does not pay in chimpanzees

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Abstract

Although freeloading is potentially a major threat to sustaining cooperative relationships in a group of individuals, cooperation remains widespread throughout the animal kingdom. In the current experiment, we ran a cooperation experiment in the open group of 11 adult captive chimpanzees. We did not attempt to induce cooperation or freeloading and instead let the chimpanzees choose if and when to participate in the cooperative task or to freeload on others. Despite ample opportunities for dominance assertion, intolerance and cheating, the chimpanzees were extremely successful at the task, performing 3,565 cooperative pulls in a total of 94 one-hour sessions. Cheating was not particularly widespread with 98.90% of rewards being obtained by the individual who worked for them. When thefts did occur, the primary response of the worker was to leave, preventing the cheater from engaging in further thefts. Although agonism was rare, partial interventions were significantly more often directed against the cheater than the target of the theft. These responses, combined with the high level of benefits to be obtained through cooperation as compared to cheating may have discouraged freeloading.

Introduction

Freeloaders pose a challenge for the development and maintenance of cooperative societies. For the individual, it has the potential of being a more profitable strategy than cooperation, thus giving rise to a social dilemma, or Collective Action Problem (i.e. CAP; Nunn, 2000).

There is ample evidence for freeloading across a variety of species. Typically this arises when not all individuals contribute equally to communal efforts: for example, a male chimpanzee might opt out of participating in a risky boundary patrol yet benefit from the group effort by other males (Mitani, 2006). Similarly, in both lions and feral dogs, some individuals refrain from defending their territories against intruders (Bonanni, Valsecchi, & Natoli, 2010; Heinsohn & Packer, 1995). And yet, in all of these cases, the entire group benefits from the action of these individuals.

Cleaner fish may cheat by taking a bite out of their client fish and consuming mucus, rather than parasites (Bshary & Grutter, 2002). Even nitrogen-fixing bacteria may “cheat” their host plants by not fixing as much nitrogen as they could, while still reaping the nutritional benefits of being associated with a host plant (Kiers, Rosseau, West & Denison, 2003). Given the benefits of freeloading, and its undermining effect on cooperation, it is puzzling how prevalent cooperation still is in a wide variety of taxa. There are a number of ways in which cheating might be regulated in a social group. First, the victim of the theft might retaliate or punish the thief. For example, client fish who have been bitten by cleaner fish will aggressively chase them away (Bshary & Grutter, 2002). Retaliation need not be limited to an aggressive response. In an experimental study of chimpanzees that allowed one individual to knock another individual’s food out of their reach, the chimpanzees did this more often when the second individual had previously stolen food from them (Jensen, Call, & Tomasello, 2007). In both of these cases, however, it is unknown if these responses helped deter future cheating.

In humans, punishment clearly deters future freeloading and facilitates future cooperation. In a public goods game where individuals repeatedly interacted with the same partners, responses quickly rose to almost 100% cooperation when a punishment mechanism was instituted: freeloading virtually disappeared (Fehr & Gächter, 2000). In the absence of punishment, contributions converged to full freeloading. This suggests that punishment or retaliation is necessary in this context for humans to sustain cooperative behavior. Human societies also have social norms and sanctions against those who violate social norms, which are thought to be essential to prevent freeloading (Fehr & Fischbacher, 2004). In economic games, for example, people engage in third-party punishment, where they pay a cost to punish an individual who has violated a cooperative norm, even though their own payoffs have not been affected by the violation. While this strategy serves to increase cooperation in humans in artificial economic experiments (Fehr & Fischbacher, 2004; Fehr & Gächter, 2000), its applicability to real-world interactions has been questioned (Melis & Semmann, 2010). It remains unclear, however, how much of a role such punishment plays in other species. Indeed it has been claimed that such punishment is uniquely human (Fehr & Gächter, 2000). In the same experimental task examining chimpanzee punishment described above, the apes responded negatively (retaliated) when their own rewards were stolen, but did not take the opportunity to remove food from the thief when someone else's rewards were stolen

(Reidl, Jensen, Call & Tomasello, 2012). Although we know chimpanzees engage in triadic interactions, they did not engage in third party punishment under these conditions.

An alternative way to deter freeloading might be the avoidance of cheaters. Partner choice allows individuals to preferentially benefit fair partners and avoid those who take advantage (Noë & Hammerstein, 1995). For example, pairs of capuchin monkeys who were more equitable in their division of food were more likely to solve a cooperative task (de Waal & Davis, 2003). This example illustrates, however, that when only one partner is available, the only alternative to cooperating with an unfair partner is to not interact at all and thus no one benefits.

In natural environments, however, there is often more than one partner available and there may be other individuals around who do not participate in the cooperative task yet benefit from it. In this case, the most profitable strategy may be to cease benefiting the freeloader and resume your efforts only in the presence of fair partners (Noë & Hamerstein, 1995). There is ample evidence that nonhumans distinguish between cooperators and non-cooperators, and so should be able to identify the best partners (reviewed by Cheney, 2011). In interspecific cleaner/client fish mutualisms, when cleaner fish cheat, clients switch to other cleaners if they have the option to do so (Bshary & Shäffer, 2002).

In multi-party interactions in naturalistic social groups, the relationship between individuals usually extends beyond the short-term cooperation scenario. So, although switching to a more beneficial partner might be the most profitable short-term strategy, in the long-term, the freeloader might provide some sort of reciprocal benefit, or the long-term relationship or benefit that could be obtained by continuing, might out-weigh the short-term loss (Cheney, 2011; Noë & Hammerstein, 1995). In a multi-faceted, complex environment, punishment or avoidance of freeloaders may not be best option, nor is it strictly necessary to enforce cooperation. If the benefits of cooperation are high enough, there is less incentive to cheat than to cooperate, and a collective action problem may be avoided altogether, with cooperation emerging as the primary strategy (Melis & Semmann, 2010).

Although there are several ways to enforce cooperation in a social group, and chimpanzees in the wild show a high degree of cooperative behavior (Mitani, Merriweather & Zhang, 2000), in experimental settings cooperation has been particularly vulnerable to intolerance, competition, and cheating. In an early study, conducted in a small group of chimpanzees, one dominant male monopolized all of the rewards and the majority of "cooperation" that occurred was when he coerced an infant female into helping him (Chalmeau, 1994). In later, more controlled studies, only dyads who had a high degree of tolerance in the group were able to succeed at a pulling task, even when rewards were dispersed and there was a low degree of competition (Melis et al., 2006a). Finally, in a recent study in which one or two chimpanzees produced benefits for a group of up to six individuals, experimenters found that chimpanzees were less willing to produce benefits when (1) group size was larger than three individuals, (2) cooperation was necessary to produce the benefits, and (3) the individual pulling was of low rank (Schneider et al., 2012). In general, chimpanzees are often characterized as more competitive than cooperative (Hare & Tomasello, 2004).

The purpose of the present study was to examine spontaneous responses to freeloading during a cooperative task in an open-group setting in larger group of chimpanzees (n=11). All group members had access to the cooperative pulling apparatus and thus could choose their own partners and beneficiaries. Although a reward was delivered as directly as possible to each participant in the task, the open set-up also allowed for the possibilities of freeloaders, since chimpanzees who did not solve the task could potentially take food from those who did. Unlike previous studies that set out to examine responses to freeloading, opportunities to freeload were not induced or controlled by the experimenters but rather came about spontaneously from the chimpanzees. We evaluated two possible hypotheses: (1) Chimpanzees are too competitive: If intolerance and competition inhibit cooperation, then while cooperating in a group setting where an individual is competing with 10 others, chimpanzees will be unable to achieve or sustain cooperation in the face of cheating; and (2) Chimpanzees overcome competition: If chimpanzees develop mechanisms to deter cheating, such as partner choice and/or discouragement, we expect them to achieve a high level of cooperation.

Methods

Subjects and Housing

Subjects were 11 chimpanzees (1 male, 10 females) living in a large social group at the Field Station of the Yerkes National Primate Research Center (YNPRC) of Emory University. The group's 711 m^2 outdoor compound contained a large climbing structure and several enrichment items (barrels, tires, etc.) and was adjacent to five indoor interconnected runs containing sleeping platforms and swings. Testing occurred in the outdoor compound with the entire group present and so did not require separating the subjects from their group. During testing, subjects had access to the indoor sleeping quarters. The chimpanzees were fed two daily meals of fruits, vegetables and grains at approximately 8h30 and 15h00 and had access to water *ad libitum*. All food used in this study was supplemental to the chimpanzees daily intake and at no time was food or water restricted. All procedures were approved by Emory University's Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the study.

Apparatus

Dyadic cooperation: The apparatus required one chimpanzee to remove a barrier in order for another chimpanzee to simultaneously pull in a tray baited with food. One barrier was blocking the tray and thus two individuals were required to coordinate their behavior to obtain food. The barrier was connected to a steel rod that extended 20 cm into the chimpanzee compound. Pulling on the rod caused the barrier to drop down via a spring/pulley mechanism. Once the barrier was pulled down a second individual used a similar rod (also extending 20 cm into the compound) to pull in the tray. Once the tray was pulled in all the way (approximately 30 cm) food rewards dropped into a funnel, which delivered the rewards to the chimpanzees sitting at the apparatus. Food rewards were one grape, two raisins, a small slice of sweet potato or a small slice of banana per trial and were randomly varied from trial to trial.

Triadic cooperation: Following the establishment of dyadic cooperation, a second barrier was added such that three individuals had to coordinate their behavior to solve the task (two to pull down barriers and a third to pull in the tray). The rods to pull down the barriers and pull in the tray were sufficiently far apart (~1.6 m) so that one individual could not perform both actions.

Procedures

Test Sessions. A trial began when the tray was baited with food. Following successful trials, the experimenter waited for the chimpanzees to release the rods (and barriers) and then reset the tray back in the starting position and re-baited the tray. If the chimpanzees did not solve the task within 5 minutes, the trial was considered a failure, the food removed, and a one-minute time out commenced prior to re-baiting. Each session lasted 1 hour and consisted of as many trials as could be accomplished in that time period. Since dominant individuals could monopolize the apparatus early in the session, a longer session allowed more individuals to interact with the apparatus. We ran 94 test sessions (47 of each dyadic and triadic cooperation) but only one session was run per day.

Behavioral Coding

Each trial was videotaped from two angles (a side and front view) using HD digital video cameras. Additionally, one experimenter had a digital voice recorder to record a narrative of any social interactions that occurred during testing. Which chimpanzees solved the task successfully, and which received rewards were recorded in-person and later confirmed from video.

Definition of *cheating event*: We recorded attempted cheating when an individual tried to take food from a spot at which he or she did not pull. This included behaviors such as displacing another individual before this individual obtained the food, putting their hand or mouth at the end of the food funnel, scrounging for dropped food, chasing the puller away, or intimidating (e.g. pilo erection, bluff charge) or physically attacking the puller (e.g. hitting). Any attempt that resulted in the initiator obtaining the food was marked as a success. Both failed attempts and successful stealing were considered *cheating events*.

Behavioral responses to cheating events: We recorded the behavior of the initiator (the thief), the target, and any bystanders involved in the event. Behaviors are defined in Table 1 and included: withdrawing, protest, withholding pulling, agonism and no response (in which all chimpanzees maintained their positions and made no overt responses prior to the baiting of the next trial). Note that some, but not all of these responses are mutually exclusive. For example, a target cannot both withdraw and withhold pulling during a single cheating event, but could protest and withholding pulling or protest and withdraw. A co-worker unfamiliar to the purpose of the study coded a subset of the videos. Interrater reliability was excellent for all behavioral measures (Cohen's Kappa for attempts versus successes: κ= 1.0, for non-agonistic responses: κ= 1.0, agonism κ= 0.80, bystander behavior κ= 0.88).

Behavior	**Definition**
Withdraw	Following any cheating event, but prior to the beginning of the next trial, the target and/or the initiator moves more than one arm's distance away from the apparatus.
Withholding pulling	After the next trial is baited, the target does not pull until the initiator leaves.
Protest	The target or the initiator exhibits a silent bared teeth expression, pout, whimper or scream directed at the other individual involved in the cheating event, without showing any of the agonistic patterns described below.

Agonism	Any agonistic behavior directed from the target to the initiator or vice versa. Included non-contact (bluff, threats, swaying) and contact (hitting, biting, grabbing) agonism. Scored according to van Hooff (1974) and van Hoof & de Waal (1981).
No response	Neither the target nor initiator withdraw, the next trial proceeds as normal, with the target pulling.
Bystander Intervention	An individual who is neither the target nor the initiator got involved in the cheating event. Can be impartial (policing), or on behalf of either individual, and agonistic or non-agonistic.

Table 1. Behavioral outcomes of a cheating event.

Analyses

As cheating events were not normally distributed across all subjects, only non-parametric statistics were used. Unless otherwise specified, statistics were run on the individual (either initiator or target), comparing each individual's behavior across conditions. For statistics run on initiator-target dyads (e.g., rank difference, kinship, and affiliation), there was interdependence between dyads so the data were subjected to 10,000 permutations to obtain an exact p-value. Agonism was too rare to analyze individually, so the analyses represent pooled, group-level data. All analyses were run using SPSS 20.0 and R.

Results

Prevalence of Cheating

Over the 94 test sessions, the chimpanzees solved the task 3,656 times, accumulating a collective 8,233 rewards. There were 175 attempts to cheat (2.12% of rewards), 91 of which were successful (1.10%). So, nearly 99% of all rewards were obtained by the chimpanzees that worked for them.

Every chimpanzee attempted to cheat at least twice (mean per individual, M±SD: 15.90±16.03) and succeeded at least twice (M±SD: 8.27±8.42). Chimpanzees were more likely to attempt and successfully cheat the higher the initiator's rank relative to the target (correlation of the rank difference between an initiator and target with the number of cheating attempts: Spearman rho = 0.25, N = 110 dyads, $p = 0.004$; with cheating successes: rho = 0.39, N = 110, $p = 0.001$). Kin were more likely to attempt to cheat each other, but no more successful at actually obtaining food than with non-kin (kin initiator-target dyads versus non-kin initiator-target dyads: Mann-Whitney U = 1191, N = 110, $p = 0.006$; successes: U = 1080.5, N = 110, $p = 0.19$). There was no effect of long-term affiliation (attempts: rho = 0.03, N = 110, $p = 0.39$; successes: rho = 0.03, N = 110, $p = 0.39$) on dyads involved in cheating events. Note that all p-values for dyadic analyses are exact (2-tailed) p-values calculated using 10,000 permutations to compensate for interdependence between dyads.

Cheating was not the best way to obtain rewards, however. The number of rewards each chimpanzee obtained from cheating was significantly below the number of rewards received as a result of working on the task (Wilcoxon Signed-Ranks Test: Z = -

2.85, N = 11 individuals, p = 0.004; Figure 1). Since cooperating to solve the task was a much more profitable strategy in terms of reward acquisition, we tested whether chimpanzees were more likely to cheat when they did not have a position at the apparatus, that is, when they did not have the opportunity to obtain rewards by working. Individual chimpanzees were more likely to cheat when they did not have a position at the apparatus but were rather sitting nearby not working at the task (Wilcoxon Signed-Ranks Test comparing the number of cheating events from initiator when working versus sitting nearby: Z = 2.94, N = 11, p = 0.003; Figure 2).

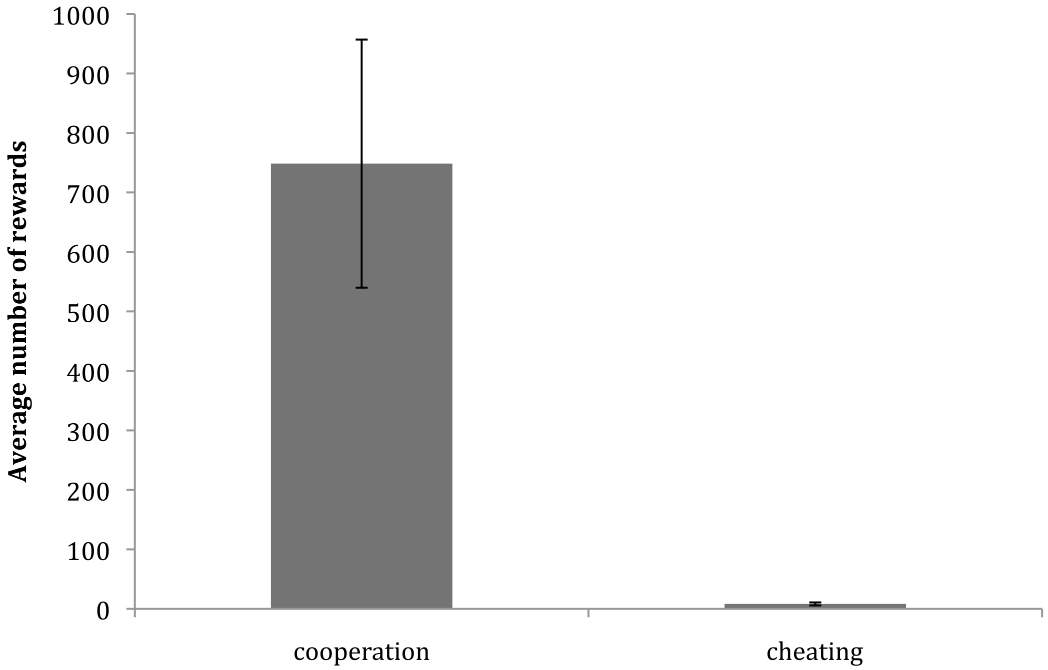

Figure 1. The average number of rewards each individual obtained through cheating versus as a result of work on the apparatus. Error bars represent SEM.

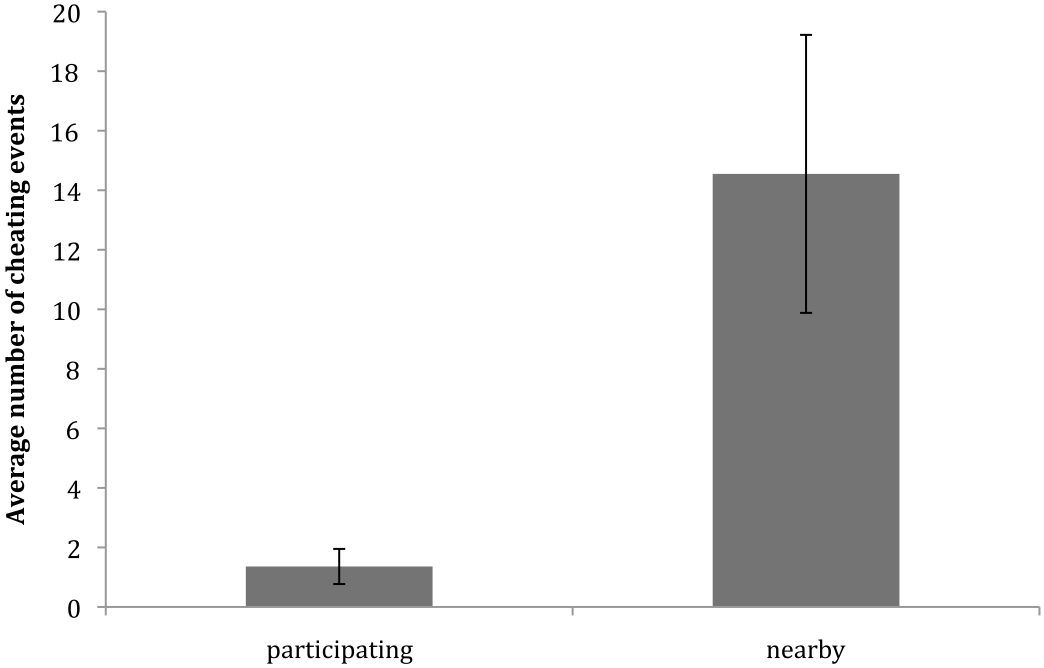

Figure 2. Average number of cheating events initiated by individuals when working on the task versus when nearby but not working on the actual apparatus. Graph represents the average of all individuals in the group, error bars represent SEM.

Responses to Cheating

We recorded several possible behavioral responses to cheating: withdrawal by the target or initiator, protest by the target or initiator, withholding pulling by the target, agonism, or no response from either, in which all chimpanzees maintained their positions and made no overt responses prior to the baiting of the next trial (see Figure 3). In 28.0% of cheating events, there was no response from either chimpanzee and the next trial proceeded as usual. Targets withdrew following 44.0% of cheating events and initiators withdrew following 22.15% of cheating events. We also recorded when the target did not withdraw, but rather maintained their position without pulling until the initiator moved away. This occurred in approximately 15% of cheating events. Interestingly, there was no significant difference in the likelihood of any particular response following failed attempts versus successful cheating events (target withdraw: Wilcoxon Signed-Ranks Test: $Z = 1.86$, $N = 7$, $p = 0.06$; initiator withdraw: $Z = 1.12$, $N = 9$, $p = 0.23$; withholding of pulling: $Z = -0.67$, $N = 7$, $p = 0.50$). Thus, the chimpanzees exhibited the same type of reaction regardless of whether the initiator was actually successful at stealing the food.

Two targets protested (by whimpering, pouting or fear grimacing) a total of 8 times, 3 in response to attempted cheating and 5 following successful cheating. Interestingly, initiators also occasionally protested, although the majority of these (6 out of 7) were following unsuccessful attempts to cheat. The single case of protesting following successfully stealing food was a silent-bared teeth expression in response to a target's protest (silent bared-teeth and whimper). Agonism was rare (occurring in only 9.1% of cheating events) and was significantly more likely to be initiated by the initiator rather than the target of cheating (binomial, $p = 0.02$). Most agonism was relatively low intensity (non-contact aggression) with only 3 interactions escalating to sustained contact aggression.

Third parties intervened 14 times (8.0% of cheating events), mostly in response to agonism between the initiator and the target (12 out of 14 instances), with the remaining two times occurring in response to protests. Four of these interventions were impartial (policing). As the most escalated events had multiple bystanders intervene, there were also 10 partial interventions. Nine out of 10 partial interventions were in favor of the target chimpanzees as opposed to the one trying to cheat (binomial test: $p = 0.005$) and ranged from threatening or chasing off the cheating initiator to mild contact aggression (e.g. hitting the initiator). There were four cases of consolation (where a third party provided affiliative contact), all of which directed towards the target of cheating. In sum, although bystander responses to stealing events were rare, they were significantly biased to favor the target.

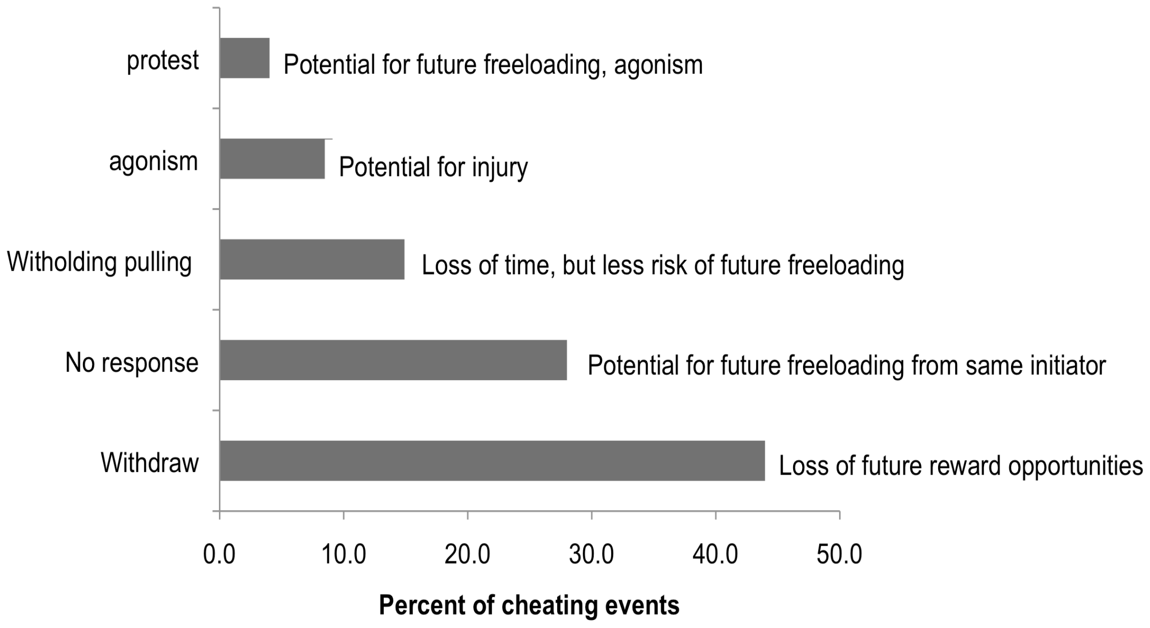

Figure 3. Summary of target responses to cheating events. Text indicates the costs, or potential costs *to the target* of each response. Note that agonism was mutually a target and initiator response and most agonism was started by the initiator. For every response except "no response" there was also a cost to the initiator, usually the loss of future rewards from freeloading.

Discussion

The open-group setting of this experiment invited competition over rewards, yet we observed in fact very little cheating in the form of stealing of rewards. Even though several previous studies have suggested that competition over food can inhibit cooperation (Melis et al., 2006a; Schneider et al., 2012), the chimpanzees in the current study developed mechanisms to deter freeloading and sustain high levels of cooperation.

Thus, our data support the hypothesis that chimpanzees can overcome competition in this context.

Surprisingly, the primary response of the targets of cheating was to leave the apparatus. Additionally, they did not differentiate their responding based on whether or not the other individual actually got the food—they were just as likely to leave after an unsuccessful attempt. By withdrawing, the chimpanzees demonstrate an unwillingness to continue to benefit the cheater, which is costly, but they also forfeited the ability to obtain rewards themselves (Figure 3). Withholding of pulling was an alternative tactic that allowed the chimpanzees to maintain possession of their position at the apparatus (thus ensuring future potential for rewards) but at the same time not fall victim to further cheating. Withholding pulling occurred at a much lower rate; although there was a long-term benefit to waiting, there was a high short-term cost in terms of time and patience. Finally, unlike in previous studies where chimpanzees retaliated against individuals who stole food from them (Jensen, et al., 2007), in the current study, agonism directed from the target towards the initiator was rare. Since the experimental setup did not provide an outlet for retaliation, it was likely far more risky than in previous studies, involving agonism with the whole group present and able to intervene. The cost of potential punishment may therefore drive the likelihood of engaging in such behavior.

So why didn't the chimpanzees cheat more? Given the relatively poor success rate (only 52% of cheating attempts were successful across the entire group) of cheating and the high success rate of working, it may simply not have been worth the risk for most chimpanzees. There was one chimpanzee who was an exception, however. Mai, one of the two oldest females in the group, never once cooperatively solved the task but instead relied on a strategy of exclusive freeloading. However, as with the rest of the chimpanzees, she had a very low success rate in cheating, succeeding only 17 times (out of 50 attempts, 34.0% success) for a total of 17 rewards over the course of the entire experiment. When compared to the rest of the group, where each individual averaged 823.3 rewards from cooperating during the experiment, it is easy to see why exclusive freeloading was not a good strategy. Furthermore, although bystander interventions were rare, the significantly higher amount of support for the target of cheating, rather than the cheater him or herself demonstrates that there could be significant cost to cheating, particularly when the initiator was aggressive towards to the target. For example, in the most severe case of agonism, a cheater grabbed the target and began repeatedly hitting her and attempting to pin her to the ground. Four chimpanzees intervened in that fight: one female simply tried to get in between the two individuals, the other three bystanders, including the alpha male, directed agonism against the initiator. This included threats, bluffing and hitting. The fight was finally broken up with the alpha male charging through and hitting the cheater on the head. Such interactions are suggestive of a social norm against cheating.

One way in which species may naturally avoid CAPs is by creating cooperative outcomes that are so beneficial that freeloading is more costly than cooperating (Nunn, 2000). The behavior that we observed contrasts with the many reports of high levels of competition, low levels of tolerance, and harassment-induced food transfers among chimpanzees (Hare & Tomasello, 2004; Melis, Hare, 2007; Stevens, 2004) in that we recorded over three thousand successful cooperative acts in an open setting that allowed for competition and dominance assertion. That the chimpanzees achieved such high levels of cooperation in the face of potential competition, demonstrates their ability to inhibit or actively regulate these tendencies in favor of higher payoffs. By examining these tendencies in an open-group setting, we demonstrate that allowing the chimpanzees to choose and switch partners, leave in the presence of less than optimal pay-offs, and intervene in conflicts engendered by cheating, plays a fundamental role in the self-regulation of freeloading among chimpanzees.

Chapter 4. General Discussion

To our knowledge, this is the first experiment in the group setting showing that chimpanzees can develop and sustain cooperation in the midst of a complex and competitive social environment. Without any training, 10 out of 11 chimpanzees were extremely successful, achieving a total of 3565 successful cooperative pulls in 94 hours of testing. While this high level of success was unlikely to be achieved coincidentally, behavioral measures such as shorter latency to success, better efficiency (number of pulls to success), and a higher ratio over time of pulling when enough individuals were present to solve the task versus when there weren't enough, are all suggestive of the chimpanzees developing an understanding of the task. These results are in stark contrast to the only previous open-group setting study, in which only one out of six individuals showed any sign of understanding and overall success rates were very low (Chalmeau, 1994).

Half of the test sessions required the chimpanzees to work in triads. Although field data suggests that up to six individuals may be working together when chimpanzees hunt (Mitani, 2006), it is unclear if chimpanzees hunters are actively coordinating their behavior with one another or simultaneously, individually pursuing prey, thus giving a mere appearance of cooperation (Stanford, 1998). Although our study does not necessarily shed light on wild chimpanzee behavior, it does at least tell us that chimpanzees are certainly capable of coordinating their behavior with more than one individual at a time.

When revisiting the levels of cooperation outline in the introduction, it seems quite clear that the chimpanzees in this task achieved a high degree of coordination (Boesch & Boesch, 1989). However, whether or not they were collaborating remains unclear. Although they formed strong preferences for positions, as reflected by highly skewed successes at one position versus another, it is unclear whether this reflects specialization. They were not more efficient at their preferred position versus their non-preferred position, nor were they quicker to solve the task when at their preferred position. As the two roles were quite similar (both pulling) and their overall performance showed that they were pulling more often when the other individual was present, but not achieving perfect efficiency, it is most parsimonious to conclude that the chimpanzees were coordinating, rather than collaborating. Thus they were performing similar actions simultaneously and monitoring their partner's spatial proximity to the apparatus, but not necessarily performing different roles.

Although the chimpanzees did not definitively show collaboration, as we might expect humans to do in a similar situation, the cognition required to solve the task was likely more complex than what we see in many other species. The key difference seems to be the element of decision-making and flexibility in behavior observed during the current task. Selective partner choice, as exhibited by the chimpanzees in this experiment likely reflects a desire to create the most tolerant and therefore most profitable partnerships. This is a key difference from other examples of cooperation, where participation is genetically determined (eusocial insects) or partnerships are solely determined based on kin preferences (reviewed by Dugatkin, 1997). The current study is one of the first to show such flexibility in cooperative decision-making, which likely came about as a result of the open, naturalistic setup of the task.

Why were the chimpanzees so successful at this task? Previous negative results can generally be attributed to one of two possibilities. First, tasks that require simultaneous action with arbitrary consequences (e.g. simultaneous pressing levers or pulling handles which release food) may be poorly understood by the subjects. Tray pulling tasks seem to be more intuitive; and variations on this paradigm have met with a lot of success in carefully controlled laboratory experiments (Mendres & de Waal, 2000; Melis et al., 2006a; Hirata & Fuwa, 2007). This is the first time such a paradigm has been used in the social group setting (as opposed to in a dyadic test) and also the first time that the subjects did not get any pre-training on the task. That the chimpanzees achieved such a high level of success and showed behavioral measures of understanding that developed over time, speaks to the importance and intuitiveness of this experimental design.

The second reason why nonhumans fail at many cooperation tasks is due to competition and/or intolerance between partners. Many dyadic tasks have found that pairs who are tolerant of each other around food and have reduced competition over the food rewards such that subjects get equal shares are the most successful at the task (Melis et al., 2006a; Brosnan et al., 2006; de Waal & Davis, 2003). In some cases, intolerance is so severe that subjects fail to solve the task even when competition is minimized as much as possible (Melis et al., 2006a).

The inability of chimpanzees to overcome these competitive tendencies in laboratory studies has given them a reputation as a competitive, rather than cooperative species and has led to the idea that humans' highly collaborative tendencies are what sets humans apart from nonhuman primates (Hare & Tomasello, 2004; Moll & Tomasello, 2007). However, chimpanzees regularly engage in wide range of cooperative behaviors in the wild, ranging from group hunting to boundary patrols to coalition formation (reviewed in Chapter 1). If wild chimpanzees can overcome these competitive tendencies to cooperate, this raises the question of how chimpanzees might mitigate competition.

In the current study the chimpanzees experienced two types of competition: (1) competition for access to the task and (2) competition over food rewards. Competition for the task primarily took the form of displacements, which were more common when the displacer had a large advantage in rank over the individual they were trying to displace. In addition to purely attempting to gain access to the task, there was an added level of competition for preferred position (tray or barrier) such that half of all displacements actually occurred when there was a position available, but it was not that individuals' preferred position.

Competition over food rewards has historically led to widespread failures of chimpanzees in cooperative tasks (Chalmeau, 1994; Melis et al., 2006b), also in comparison to their more pacific congeners, the bonobos (Hare et al., 2007). In the current experiment competition over food was not engendered by clumped rewards that were easy for one individual to monopolize, but rather by individuals who did not participate in the task lurking near the apparatus to steal food. Given the overall number of food rewards delivered as part of this experiment, cheating of this nature was not widespread, occurring in just 2% of trials.

The high degree of success in the face of not one but two levels of competition suggests that the chimpanzees in this task must have developed mechanisms to mitigate competitive tendencies in favor of cooperative ones. We suggest that there are several mechanisms by which they were able to accomplish this.

First, they preferentially chose to work with tolerant partners. Unlike previous studies which have defined tolerance by one measure (food sharing outside of the experimental context; Melis et al., 2006a, Hare et al., 2007), tolerance between two individuals in a cooperative task can develop in many ways. Systematic exploration of what characterizes tolerance and how this relates to cooperative abilities is an important area for future research. Two factors, in particular, seemed to lead to more tolerant partnerships in this task: close rank distance between partners and kinship. Since large rank distances between partners were associated with both types of competition: displacements and cheating, it is not surprising that over time they started preferentially approaching individuals close to themselves in rank. Similarly, previous studies have found that kin are less competitive with each other, more likely to divide food equitably, and less likely to be sensitive to inequity (capuchins: de Waal & Davis, 2003; Brosnan et al., 2006; chimpanzees: Brosnan et al., 2005). All of these qualities enable kin pairs to better work together at cooperative tasks.

In the current social group, though we had many more female kin that might be expected in a more naturalistic group (where females migrate away from their natal groups at maturity). Furthermore, the group was highly stable, having been formed more than 20 years ago and only having one male. Given the role of tolerance in achieving cooperation, it is reasonable to ask whether the composition of the social group played a role in their overall level of tolerance. There might very well be population differences based on group stability, age and sex distribution, group size, or rearing history.

It is possible that a less stable or more competitive social group would lead to a breakdown of cooperation in this type of task. However, this would provide a true test of the power of partner choice. If the chimpanzees had a free choice of partners, and sought out the most tolerant partners in their group, we should still expect to see successful pairs at the task. One might predict that there would be fewer compatible pairs or less widespread participation than in the social group tested in this experiment (where 10 out of the 11 chimpanzees solved the task a minimum of 100 times). To answer this question requires extending this type of experiment to multiple chimpanzee groups, and correlating the results with measures of stability and tolerance of the social group outside of the experimental setting.

A second mechanism the chimpanzees developed to mitigate competition was the spontaneous deterrence of freeloading. For the initiator, freeloading had high potential costs (agonistic interventions against the freeloader) and low benefits (far fewer rewards than cooperating). The target also developed behaviors to deter freeloading such as withdrawing and withholding of pulling, which prevents future freeloading from that particular initiator with that target. Giving the chimpanzees the option to leave and avoid particular individuals is a key aspect of partner choice and may have played an important role in sustaining cooperation in this experiment.

In the current task, self-regulation of freeloading seemed to emerge from both the initiator's side and the target's. However, chimpanzees engage in cooperative behaviors where the risk/benefit payout is quite different than in the current study. For example, when chimpanzees hunt in groups, one individual is responsible for capturing the monkey and gets first share of the food. At all but one field site (Taï Forest: Boesch & Boesch, 1989), there is no evidence that chimpanzees who participated the hunt get more food than bystanders who did not help capture the prey (Mitani & Watts, 2001; Stanford, 1996; Gilby, 2006). In this context, freeloading is probably a much more profitable strategy than it was in the current experiment.

A task where the chimpanzees cooperate for a single, large, shareable reward would allow us to test whether chimpanzees use the strategies they developed in the current task, develop alternative methods, or succumb to the problem of freeloading when freeloading has a greater benefit than cooperating. One potential alternative method would be to develop a reciprocity system, where cooperation on the task and food sharing and reciprocated in different "currencies" (for example by affiliation or coalition formation). Reciprocity of social benefits is widely hypothesized to explain food sharing following cooperative hunting in wild chimpanzees (Mitani, 2006; but see Gilby et al., 2006).

The current study demonstrated that chimpanzees have the ability to overcome multiple sources of competition to achieve high levels of cooperation in an experimental task. Free partner choice seems to play a critical role in mitigating competition. To our knowledge, this study is the first of its kind to successfully achieve cooperation in such a complex and competitive social environment and provides many avenues for future research.

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