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Chimpanzees (*Pan troglodytes*) Tolerate Some Degree Of Inequity While Cooperating But Refuse To Donate Effort For Nothing

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Abstract

In cooperative hunting, a carcass cannot be divided equally, and hunts may be unsuccessful. We studied how chimpanzees respond to these two variables, working for unequal rewards and no rewards, which have been rarely included in experimental cooperative tasks. We presented chimpanzees with a task requiring three chimpanzees to work together and varied the reward structure in two separate experiments. In experiment 1, two individuals received more rewards than the third, making the outcome unequal. We wanted to know if cooperation would continue or break down, and what mechanisms might maintain performance. Experiment 2 used equal rewards, but this time one or more locations were left unbaited on a proportion of trials. Thus, there was the chance of individuals working to receive nothing. In experiment 1, the chimpanzees worked at a high rate, tolerating the unequal outcomes, with rank appearing to determine who got access to the higher value locations. However, equal outcomes (used as a control) enhanced cooperative performance, most likely through motivational processes rather than the absence of inequity aversion. In experiment 2, performance dropped off dramatically when the chimpanzees were not rewarded on every trial. Their strategy was irrational as donating effort would have led to more rewards in the long run for each individual. Our results lead to a hierarchy of performances by condition with equity > inequity > donating effort. Chimpanzees therefore tolerate mild inequity, but cannot tolerate receiving nothing when others are rewarded.

Graphical Abstract

Keywords

cooperation; inequity; effort; motivation; chimpanzees

INTRODUCTION

Cooperation is widespread in animals (Dugatkin, 1997), yet questions remain about the origins of human cooperation. The flexibility, scale, and complexity of human cooperation require certain cognitive mechanisms, and researchers have wondered whether or not these mechanisms are shared with other species (Albiach-Serrano, 2015; Hall & Brosnan, 2017; Tomasello & Call, 1997). Early successful studies of cooperation typically used highly structured designs (reviewed by Albiach-Serrano, 2015; Noë, 2006), but in the wild there are many sources of unpredictability. We studied two variables, receiving fewer rewards than others and receiving no rewards, which exist in the wild but have been rarely modeled in captive studies of cooperation by nonhumans.

In the wild, nonhuman animals must ensure that their cooperative efforts are rewarded. In the case of cooperative hunting, the reward often comes in the form of large, divisible carcasses, which are shared. A carcass cannot be divided equally, so some individuals will get more, or possibly better parts (Boesch & Boesch, 1989), than others. There is also a risk of receiving nothing, either because a hunt is unsuccessful or because others do not share. Despite these issues, cooperation is common (Dugatkin, 1997). Therefore, cooperative hunters must tolerate some amount of inequity, but this may be balanced by the need for *intolerance* of excessive inequity, which includes receiving nothing. Brosnan and de Waal (2014) described this interwoven relationship between sensitivity to outcomes and cooperation. Individuals who receive too little or nothing at all would lose fitness, and continuing to cooperate in the future would be a losing strategy (Brosnan & de Waal, 2014). These variables lead to decisions about when to participate based on the other actors and the likelihood of success, whether to freeloader on the efforts of others, and the tension between cooperating to gain resources and competing over them once acquired. To study some of these questions, we presented a captive group of chimpanzees (*Pan troglodytes*) with a cooperative task and asked how unequal outcomes and being unrewarded would impact performance. Both would be expected to negatively impact cooperation, yet both are unavoidable in the wild. Therefore, we examined the mechanisms for tolerating these outcomes as well as potential limits of doing so.

One way to minimize inequity, the risk of exploitation, and the risk of failure is through partner choice. Hyenas (*Crocuta crocuta*, Drea & Carter, 2009), chimpanzees (Melis, Hare, & Tomasello, 2006a), and coral trout (*Plectropomus leopardus*, Vail, Manica, & Bshary, 2014) appear to choose partners to maximize success and minimize failure. However, these studies are limited by requiring only two individuals to work together (cooperation in the wild often involves multiple individuals), and by the experimenters selecting and providing (or simulating, as in Vail et al., 2014) the potential partners to choose from. Therefore, the choices do not reflect who the individuals would prefer to work with from all of the options.

Suchak, Eppley, Campbell, & de Waal, (2014) and Suchak et al., (2016) studied partner choice by providing a single apparatus to an entire social group of captive chimpanzees. The apparatus included a triadic phase, which required 3 individuals to perform one of two slightly different actions for rewards to be delivered to each. With 11 chimpanzees and 3 locations in Suchak et al., (2014) there were 165 distinct triadic combinations of partners who could work at the apparatus at any one time. With 15 chimpanzees in Suchak et al., (2016), the number of potential combinations was even greater. Thus, the possibilities for partner selection were much higher than what previous studies allowed. Cooperative hunting by chimpanzees can include over 6 individuals performing different roles (Boesch & Boesch, 1989), so expanding beyond two individuals is useful to explore cognitive mechanisms of cooperation with a more complex task and when more individuals are involved. Lastly, the open design of this experiment allowed for the risk of exploitation, which could be expressed as attempts to steal rewards. Thus, with this design Suchak et al., (2014) and Suchak et al., (2016) incorporated issues of group size, role, partner choice, and competition, all of which exist for cooperation in the wild.

The apparatus involved a two-step solution: two chimpanzees had to pull bars to lower barriers, then a third chimpanzee had to pull a bar to bring a tray with food forward (more details in our Methods). Their success showed that chimpanzees could coordinate two spatially and temporarily distinct actions, or roles (Suchak et al., 2014). The high rate of efficiency, without any explicit training, showed that chimpanzees could understand and coordinate their actions with not only one, but two other individuals (Suchak et al., 2014). These two results support the idea that chimpanzees have the cognitive capacity to simultaneously track multiple individuals performing different actions, as would be required for collaboration as described by Boesch & Boesch (1989). The analysis of partner choice showed that chimpanzees preferred to work with kin and nonkin who were close in rank (Suchak et al., 2014). These preferences are similar to those of hyenas (Drea & Carter, 2009), kea (*Nestor notabilis*, Schwing, Jocteur, Wein, Noë, & Massen, 2016), wolves (*Canis lupus*, Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017), and ravens (*Corvus corax*, Massen, Ritter, & Bugnyar, 2015) but see Asakawa-Haas, Schiestl, Bugnyar, & Massen, (2016) for different results in ravens.

Lastly, the preference in partners by chimpanzees added significance because it was one mechanism, along with protest and third-party punishment, used to limit competition and ensure a high degree of cooperation (Suchak et al., 2016). Likewise, both hyenas (Drea & Carter, 2009) and ravens (Massen et al., 2015) used partner choice to minimize competition. Ravens employed the additional mechanism of withholding effort (Massen et al., 2015),

which is similar to what was observed in chimpanzees (Suchak et al., 2016). These results are consistent with the idea that mechanisms to limit unequal outcomes are essential to the evolution of cooperation (Brosnan & de Waal, 2014).

In the current study, we chose to examine unequal reward distributions and the chance of receiving nothing more directly by manipulating payouts in a cooperative task. We used the same apparatus as Suchak et al., (2014) and Suchak et al., (2016) that required 3 chimpanzees to work together to obtain rewards. In experiment 1 we studied inequity by providing an unequal reward distribution with two chimpanzees receiving more rewards than the third. As stated above, an unequal distribution is the certain outcome of chimpanzees dividing a carcass after a successful hunt. As chimpanzees continue to hunt together, there appears to be some tolerance of unequal rewards. Tolerating unequal outcomes is juxtaposed with research showing that many nonhuman animals, chimpanzees included, have shown aversion to inequity (Brosnan & de Waal, 2014). Evidence for inequity aversion across studies and species has been mixed (see Brosnan & de Waal, 2014 for a comprehensive review), nonetheless primates, dogs (*Canis familiaris*), crows (*Corvus corone corone*), and ravens have all shown sensitivity to unequal outcomes under at least some testing conditions (Brosnan & de Waal, 2014). Most notable for the current study, Brosnan, Schiff, & de Waal, (2005) found variable responses to inequity in chimpanzees, with tolerance under some conditions (principally when individuals had a strong relationship) and intolerance under others in a task that did not involve cooperation. Testing a different group of chimpanzees, social relationships did not influence response to inequity, but personality did (Brosnan et al., 2015).

A few studies have combined cooperation with an unequal reward distribution. Chimpanzees (Chalmeau, 1994) and capuchin monkeys (*Sapajus/Cebus apella*, Chalmeau, Visalberghi, & Gallo, 1997) could not sustain cooperation when one non-divisible reward was dropped onto the floor between two individuals. Tested differently, capuchin monkeys cooperated to receive a single reward, but unlike Chalmeau et al., (1997) the reward was unambiguously delivered to one individual of a divided pair, who then facilitated sharing (de Waal & Berger, 2000). When a pair of capuchins was free to take either position at an apparatus, cooperation persisted when rewards were unequal with some evidence for turn-taking at the larger amount (Brosnan, Freeman, & de Waal, 2006). Chimpanzees have shown variable performance when cooperating for a monopolizable, but shareable, reward. Mother-offspring pairs of chimpanzees could not sustain cooperation under these conditions (Melis, Hare, & Tomasello, 2006b), but different pairings performed better (Hare, Melis, Woods, Hastings, & Wrangham, 2007). A similar level of performance was achieved by chimpanzees working for unequal rewards in a design that permitted a choice between equitable and inequitable distributions (Melis, Hare, & Tomasello, 2009). All of these studies except for Chalmeau (1994) and Chalmeau et al. (1997) chose pairs of test subjects and temporarily isolated them from their group for testing. The response to unequal outcomes during cooperation, including behavioral mechanisms of tolerance or intolerance, may be different when individuals are among the entire group. That is where cooperation takes place in the wild, after all.

In experiment 2 we studied the chance that an individual may not be rewarded by leaving some locations unbaited on a percentage of the trials. In the wild, attempts to cooperate are not always successful. A hunt may fail, and even a successful hunt could carry the risk of food not being shared. Although captive chimpanzees seem able to tolerate mild inequity when cooperating in pairs (Hare et al., 2007; Melis et al., 2009), they may be less willing to accept no reward at all (Jensen, Call, & Tomasello, 2007; Kaiser, Jensen, Call, & Tomasello, 2012). Rejecting zero offers but accepting all non-zero offers (even inequitable ones) is typically interpreted as rational maximization. However, chimpanzees accept even zero offers 40-55% of the time and donate effort in some situations (Crawford, 1937; Melis et al., 2011; Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2009), which may be an economically rational response to promote cooperation for long-term gains. To assess chimpanzees' tolerance to receiving no reward in a cooperative setting, we baited the food cups only on a predetermined proportion of trials. Thus, sometimes one or more individuals would need to work for nothing on a given trial for the trio to succeed. This allowed us to test how often the chimpanzees would choose to work under varying rates of reward.

Our studies aimed to examine how chimpanzees cope with unequal rewards and working for nothing when among their entire social group to decide whether to cooperate or not. With these two experiments we hoped to learn more about the behavioral mechanisms and decision-making chimpanzees employ to limit exploited effort, as Brosnan & de Waal (2014) described as necessary for cooperation to evolve.

Experiment 1: Unequal rewards

To study the relationship between cooperation and inequity in a group of chimpanzees, we used the same apparatus and testing environment as Suchak et al. (2014) and Suchak et al. (2016). This apparatus required 3 chimpanzees to work together to access the rewards, but two locations were baited with 3 grapes each while one location was baited with 1 grape. Discrimination between 3 vs. 1 grape and a preference for the larger amount is well within the established numeric abilities of chimpanzees (Beran, Parrish, & Evans, 2015). Our questions were, 1) would cooperation continue when rewards were unequal, or would individuals opt out to the point that activity ceased? And, 2) if cooperation continued, what behavioral mechanisms allow for the acceptance of an unequal reward distribution?

METHODS

Subjects: We studied a single group of 15 adult chimpanzees (*Pan troglodytes*, 12 females, 3 males) previously tested by Suchak et al. (2016) at the Field Station of the Yerkes National Primate Research Center (Lawrenceville, Georgia, USA). The chimpanzees had an outdoor enclosure (711 m²) with a 3-story climbing structure, enrichment items, and two indoor areas for sleeping and cognitive testing. The chimpanzees had indoor and outdoor access throughout the day and two main feedings of fresh fruits and vegetables (approximately 8h30 and 15h00), with primate chow and water always available. The rewards used in this experiment were supplemental to the daily diet, and at no time were the chimpanzees food or water deprived. The experiment took place outside with the apparatus presented to the entire group of chimpanzees at once. During testing the chimpanzees had *ad libitum* access to the indoors, primate chow, and water. All participation was voluntary, including both starting

and stopping to work, and the chimpanzees were never forced, coerced, or compelled to participate. Both experiment 1 and experiment 2 abided by the ASP Principles of Ethical Treatment of Non-Human Primates. The following procedures were approved by Emory University's Institutional Animal Care and Use Committee (IACUC), protocol #YER-2000180-53114GA.

Materials: The apparatus consisted of a long tray (~3.3 m), three food cups, and three pull bars, as described previously (Figure 1; Suchak et al., 2014; Suchak et al., 2016). The tray was positioned outside of the chimpanzees' enclosure with the bars extending into the enclosure where they could be grasped by the chimpanzees. The bars were positioned far enough apart that one chimpanzee could not grab two at once. The bars allowed the chimpanzees to pull the tray toward them until the food cups tipped forward and released the rewards. Two of the bars worked differently from the third. At the locations on either end, the bar attached to a barrier raised in front of the tray. Pulling a bar lowered the barrier so that the tray could pass over. At the middle location, the bar was attached to the tray. Pulling this bar brought the tray toward the chimpanzees, but only if both barriers were lowered. Thus, success required two successive steps: first, the chimpanzees at either end had to lower the barriers, and second, a chimpanzee in the middle had to pull the tray in, delivering rewards to all three individuals. If either step was not completed in full, the rewards could not be obtained. The bars for the barriers were spring loaded, such that releasing the bar returned the bar and barrier to its original position. This prevented the task from being solved by only one or two chimpanzees working sequentially to remove barriers and then pull in the tray. At all times, three chimpanzees were required to work together to obtain the rewards (see supplemental materials published with Suchak et al., 2014 for a video of the apparatus).

Procedure: We ran a total of 30 sessions with only one session per day and 2-3 sessions per week. A session began when we baited the tray and lasted for 60 minutes, re-baiting continuously, with the exception of 3 sessions that needed to be stopped early. In sessions 6 (36 min 25 s) and 14 (47 min 12 s) we ran out of rewards, and we stopped session 21 (42 min 9 s) due to persistent fighting that began between some bystanders. During the one-hour sessions the chimpanzees were free to work or not as they chose. After each success we reset the tray and immediately re-baited it. If the chimpanzees did not obtain the rewards within 5 minutes of baiting, a time-out was implemented in which we removed the rewards and waited 1 minute before re-baiting the tray. The total number of successes in a session was determined by the chimpanzees; they could solve the task as many times as they were able within the 60 minutes.

The 30 sessions were divided into 3 phases. The first phase consisted of 10 sessions in which one location (the one at the far left of the apparatus in Figure 1, labeled location A) was baited with 1 grape, while the other two were baited with 3 grapes. The second phase consisted of 10 sessions with the same ratio of rewards, except that the 1-grape location was switched to the opposite end (location C in Figure 1). The third phase consisted of 10 sessions in which each location was baited with 3 rewards (see Table 1 for an outline of the

phases). Thus, there were 20 sessions with an unequal reward distribution followed by 10 control sessions with an equal reward distribution.

The location of the lower-value reward was switched half way through the inequity sessions to control for side biases and to ensure that the chimpanzees were sensitive to the reward distribution. We chose the two barrier locations to alternate the reward value since they had the same mechanism, and previous testing showed that some chimpanzees developed a significant bias for one mechanism over the other (Suchak et al., 2014). Any bias for removing the barriers or tray, which required slightly different actions and strategies to be successful, would not be affected by alternating between the two barriers. By switching the higher/lower value rewards between the two barriers, chimpanzees who used these locations could switch to follow the higher value location, if they understood and were motivated to do so. Had we switched the higher/lower value rewards between a barrier and the tray and chimpanzees had formed biases, they may have been unable to move with the greater number of grapes even if they wanted to. Thus, we would not have been able to see evidence of understanding of the reward outcomes and behavioral responses to the unequal reward distribution.

Two further choices impacted the design of the study. Firstly, with limited time to collect data, we decided not to start with control sessions of all locations baited with 1 grape. Doing so would have limited the number of inequity sessions we could have run, which is the new part of this experiment. With two prior publications on the chimpanzees' cooperative responses when a single reward was at each location (Suchak et al., 2014; Suchak et al., 2016), more such sessions would not have been informative. Rather, we decided to run more inequity sessions and make statistical comparisons to the previously collected data to analyze changes in performance.

Secondly, we deliberately decided not to randomize the reward distribution every trial. We opted not to do this because the chimpanzees would need to be able to see what food was in each cup perfectly from any position. The apparatus was long (~3.3 m), which put the two chimpanzees on the ends quite far from each other. In between the chimpanzees and the apparatus was heavy mesh, reinforcement bars, and two steel I-beams. While the chimpanzees could see the food cup directly in front of them, the structure of the enclosure impeded lateral visibility, especially from one end to the other. Thus, we did not have confidence that on any given trial, the chimpanzees could know exactly how many rewards were at each location, and adjust their position accordingly. Rather, we assumed that the chimpanzees would need to experience the rewards at each location to build an understanding of the distribution.

Lastly, we also decided not to intersperse higher value and lower value sessions to prevent frustration effects. After session 10 we switched the location of the higher value reward, but it was still present. If we went from sessions where the chimpanzees were certain to receive more rewards (e.g., 3 grapes) to sessions where they were certain to receive fewer (e.g., 1 grape), performance could drop due to lower motivation, loss of associative value (Domjan, 2005), or frustration effects. We would not be able to distinguish between these possibilities. In the worst-case scenario, frustration effects could lead the chimpanzees to completely stop

participating, such that they might not even learn when rewards subsequently increased again. Thus, we decided to only move upward in reward quantity. Our previous studies offered 1 reward at each location (Suchak et al., 2014; Suchak et al., 2016), then we moved to 20 sessions in which two locations received 3 rewards, and lastly 10 sessions in which all locations received 3 rewards. This design resulted in equity sessions before and after inequity, the maximum number of inequity sessions to be run, and never reducing the number of rewards.

Data Collection: All sessions were recorded by two HD video cameras, one positioned facing the apparatus from outside the enclosure, and one capturing a side view from an observation tower. In addition, a running commentary was kept on a digital voice recorder by the experimenters baiting the tray noting who was present at the apparatus, who worked at each location during a success, and observations of agonism, including displacements, thefts of rewards, and attempted thefts. All three sources of information were combined into one video in iMovie 10.x (Apple, Inc.). Successes were transcribed from the audio description by SMB, and MWC coded agonism from the videos. Data were analyzed using SPSS 24 (IBM, Inc.).

Behavioral Definitions

- **Location possession:** An individual sitting in front of one of the bars within arms-reach. If more than one individual was within arms-reach, the one who actually pulled the bar was considered to have “possession.” Possession was never shared; the individual in possession needed to withdraw (voluntarily or by displacement) for the bar to change possession.
- **Bystanders:** Any chimpanzee not in possession of a bar within 5 m of the apparatus.
- **Location choice:** At which location did an individual establish possession when more than one of differing values was available? If only one location was open, the approach was not scored as demonstrating a preference since no alternative existed. If only 2 high value locations were open, the approach was not scored as demonstrating a preference for high value because no alternative existed. Choice did include leaving possession of one location to establish possession at another, when the reward values differed, as this can be seen as a preference for the new location value rather than the previous one.
- **Displacement:** Displacements involved a bystander attempting to take possession of a bar. This could take the form of subtle behaviors like putting one’s hand on the bar and trying to position oneself between the possessor and the bar. It could also involve agonism, such as bluff displays, dirt and object throwing, pulling at the possessor, and mild hitting, with increasing intensity possible. Attempted and successful displacements were analyzed together.
- **Theft:** A chimpanzee tried to intercept one or more rewards from a possessor. Attempted and successful thefts were analyzed together. Theft could be performed by a bystander or by one location possessor toward another.

Data on Rank: We used the Elo-rating system to assess relative dominance ranks (Albers & de Vries, 2001; Neumann et al., 2011). Elo ranks were obtained from the sequence of *ad libitum* pant-grunt (de Waal, 1982) data collected since the group was formed one year prior to the study. Due to the rarity and unpredictable occurrence of pant-grunts, data were recorded opportunistically by lab members whenever pant-grunts were heard. This yielded a final sample of 413 pant-grunts by 3 observers. Initial rank points were identical for all chimpanzees and updated after each pant-grunt. If chimpanzee A pant-grunted to chimpanzee B, then chimpanzee B gained points and chimpanzee A lost points. The number of points gained and lost depended on the expected direction of the pant-grunt, which was based on the current rating of the two chimpanzees. The chimpanzee with more points was expected to be more likely to receive a pant-grunt. Expected pant-grunts resulted in smaller changes in rank points, whereas unexpected pant-grunts led to bigger changes in rank points (as detailed in Albers & de Vries, 2001; Neumann et al., 2011).

Analysis: We had a hierarchical series of questions we wanted to answer with our data. Our first question was simply, would cooperation continue when rewards were unequal? We answered this by comparing the present performance to past performance (independent *t*-test with data from Suchak et al., 2014). Since cooperation continued in the presence of inequity, we then proceeded to test potential behavioral mechanisms for tolerating unequal outcomes. We tested whether the chimpanzees were sensitive to the reward distribution. If they did not know or care about the differing reward amounts, cooperation could continue without any further behavioral complexity. We answered this question by testing whether the chimpanzees preferred the high value locations to the low value location (binomials). We next probed whether there were differences in performance between the equal and unequal sessions (ANOVA). Given that performance increased during the equal reward phase, we examined motivation and competition (multiple nonparametric tests of medians) as two alternative hypotheses.

RESULTS

Did cooperation continue when rewards were unequal?: Eleven of the 15 chimpanzees attempted to solve the task at some point in the study, though not all were successful. In the 20 inequity sessions, the chimpanzees had 711 successes, at a rate of 35.55 per session. This response rate is comparable to the previous rate when rewards were equal (740 successes in 19 sessions, or 38.95 per session during the last triadic phase of Suchak et al., 2014, independent *t*-test: $t_{37} = 0.482$, $p = 0.632$). Since cooperation continued, we proceeded to study how the behavior was maintained.

Were the chimpanzees sensitive to the reward distribution?: One mechanism for maintaining cooperation could have been that the chimpanzees did not know or care about receiving more grapes at some locations. If the chimpanzees were sensitive to the reward outcomes, however, we predicted that they would choose to occupy the higher value barrier location over the lower value barrier location when the choice was available (unoccupied by another chimpanzee). We compared only the barrier locations because they worked exactly the same, so they presented a clear choice in where an individual wanted to work. When there was a choice between open positions, the chimpanzees chose to occupy the high value

location significantly more often than the low value location in phase 1 (binomial, $N = 95$, $p < 0.001$). Of the 8 chimpanzees who participated in this phase, 6 chose the high more often than the low, 1 chose the low more often than the high, and 1 was tied. A Wilcoxon signed-ranks test showed a strong trend for the choices of the high value location (median = 4.5) to be greater than the choices of the low value location (median = 2.5, $z = 1.873$, $p = 0.061$). In phase 2, the chimpanzees similarly chose to occupy the high value location significantly more often than the low value location (binomial, $N = 66$, $p < 0.001$). Of the 10 chimpanzees who participated in this phase, 6 chose the high more often than the low, 2 chose the low more often than the high, and 2 were tied. A Wilcoxon signed-ranks test showed a similar strong trend for the choices of the high value location (median = 2) to be greater than the choices of the low value location (median = 1, $z = 1.843$, $p = 0.065$). In phase 3 of the study when the rewards were equal across the two locations, the chimpanzees showed no preference between the two barriers (binomial, $N = 39$, $p = 0.500$). Of the 8 chimpanzees who participated in this phase, 3 chose location A more than C, 3 chose location C more than A, and 2 were tied (see Figure 1 for location labels). A Wilcoxon signed-ranks test showed no significant preference for location A (median = 0.5) vs. location C (median = 1, $z = 0.315$, $p = 0.752$).

We also predicted that if the chimpanzees were motivated by the larger number of grapes, there would be more competition over these locations. We started by looking at whether the individual at the high value barrier outranked the one at the low value barrier. One individual was removed from this analysis (only) because he only ever succeeded at one barrier location. This one individual never experienced the difference between the two barriers, and thus his choice reflected a side bias and not a preference for the number of grapes. To support this conclusion, the individual was a very high ranking male, so he could easily have accessed any location he wanted. He succeeded at the high value barrier location in phase 1, which became the low value barrier location in phase 2, yet he maintained working at the same location. Since he never experienced that within each phase the different locations offered different rewards, we did not feel that it was appropriate to count his successes as a preference for that reward amount. His location appeared to be the product of a rigid habit or side-bias rather than a flexible choice. With this individual removed, the chimpanzee at the high value barrier was significantly more likely to outrank the individual at the low value barrier in phase 1 (binomial, $N = 178$, $p < 0.001$) and phase 2 (binomial, $N = 300$, $p < 0.001$). When looking at displacements, high-ranking chimpanzees were more likely to displace at the high value barrier than the low value one (Mann-Whitney U, $N = 177$, $z = 5.974$, $p < 0.001$).

Did equity sessions differ from the inequity?: In the 10 equity sessions, the chimpanzees achieved 678 successes. This rate of 67.8 per session is significantly greater than the 35.55 achieved during inequity (independent t-test: $t_{28} = 4.221$, $p < 0.001$) and the 38.95 per session during the triadic phase of Suchak et al. 2014 (independent t-test: $t_{27} = 3.546$, $p < 0.001$). To statistically test the difference in success between the different phases of Experiment 1, we grouped sessions into 5-session bins to smooth out day-to-day noise in the performance of the chimpanzees. There was a significant cubic trend for the rate of success to increase across the bins (One-way ANOVA, $F_{5,24} = 11.758$, $p < 0.001$; Cubic polynomial

trend $f_{1,24} = 7.160$, R^2 cubic = 0.959, $p = 0.013$; Figure 2). The increase across the first 10 inequity sessions can be attributed to learning the reward distributions, but learning cannot account for the plateau for the next 10 inequity sessions and then increase during the final 10 equity sessions. Therefore, much of the remainder of the analysis is a comparison between the 10 equity sessions and the previous 10 inequity sessions.

Does increased motivation to work for rewards explain the increase in performance during equity?:

One way to increase successes over a 60 minute session is to start earlier. The latency to first success decreased over all 30 sessions (Kruskal-Wallis, $\chi^2_5 = 12.345$, $p = 0.030$), but the entire effect was driven by high latencies in the first bin (median = 428 s). When comparing the 10 equity sessions (median = 19.5 s) to the previous 10 inequity sessions (median = 16 s) only, the latencies are statistically similar (Mann-Whitney U: $N = 20$, $z = 0.076$, $p = 0.940$). Another way to increase successes would be to decrease the time between successful trials, so we predicted that the inter-trial latency might be lower in the 10 equity sessions than the previous 10 inequity sessions. There is a significant difference, but it is in the opposite direction than predicted, with the equity sessions having a significantly longer inter-trial latency (median = 42.25 s) than the inequity sessions (median = 37.25 s, Mann-Whitney U: $N = 20$, $z = 2.349$, $p = 0.019$).

A third possibility to increase the number of successes would be to work longer, as measured by the time of the last success. The median time of the last successful trial was significantly later for the 10 equity sessions (59.07 min) than the previous 10 inequity sessions (43.48 min, Mann-Whitney U: $N = 20$, $z = 2.256$, $p = 0.024$, Figure 3). If the chimpanzees were less motivated by the 1-grape reward than the 3, and this motivation explains the inequity sessions ending earlier than the equity, then we predicted that the chimpanzee at the 1-grape location should leave before the others, bringing the successes to an end. In 12 of the 20 inequity sessions the chimpanzees stopped working before the end of the session. Of these 12, the 1-grape location was the first to be vacated 9 times, which is a strong trend (binomial, $N = 12$, $p = 0.073$).

Does decreased competition explain the increase in performance during equity?:

Separately from motivation to work, competition could factor into the number of successes received in a session. Our prediction here was that during inequity sessions there would be greater competition for access to the high value locations, and this competition would interfere with cooperation. We calculated the same index comparing rates of cooperation to competition as in Suchak et al. (2016): we took the total successes, subtracted the total agonistic acts (i.e., thefts and displacements), and divided by the sum of both. The index can range from +1 (complete cooperation with no competition) to -1 (complete competition with no cooperation). This index was similar in the 10 equity sessions (median = 0.54) as the 10 inequity sessions (median = 0.51, Mann Whitney U: $N = 20$, $z = 0.340$, $p = 0.734$, Figure 4).

DISCUSSION: The chimpanzees maintained cooperation when rewards were unequal, but performance improved when rewards were equal. This improvement cannot be explained by learning. Learning functions are linear or quadratic (Domjan, 2005; Ferster & Skinner, 1957), and this function is cubic (Figure 2). The cubic function implies that some behavioral

difference in the equity sessions allowed the chimpanzees to achieve more successes. Competition remained the same, so changes in competition cannot account for the increase in productivity. We did not see an unwillingness to work at the low value location, as would be predicted by inequity aversion. The best explanation involves motivation. An even reward distribution with the higher amount appears to have led to more even motivations across the 3 actors. The result was chimpanzees willing to work longer at the apparatus, therefore achieving more successes.

Experiment 2: Working for no reward

In this experiment we varied how often each location was baited in a given session. The proportion was the same for each session but was calculated independently for each location. Thus, trials could have 0, 1, 2, or all 3 locations baited, based on chance. Our question was, would the work rate of the chimpanzees correspond to the reward frequency associated with each session? Deviations above the rate of reward would demonstrate a willingness to donate effort (i.e., pulling more often than one will be rewarded for), whereas deviations below the rate of reward would demonstrate sensitivity and aversion to receiving nothing for one's efforts.

METHODS—The subjects, apparatus, and data collection were the same as experiment 1.

Procedure: The procedure was the same except for the distribution of rewards. We studied 6 different frequencies of rewards. The frequency was the same at each of the 3 locations of the apparatus in a session. Locations could be baited on 0%, 20%, 40%, 60%, 80%, or 100% of trials within a session. We ran 5 consecutive sessions for each frequency for 30 total sessions. The order of the different frequencies was determined randomly, resulting in the testing sequence shown in Table 2. Whether a location was baited on a given trial was determined independently of the others based on the percentage for the session. On any given trial, there could be 0, 1, 2, or 3 locations baited, but over the whole session each location experienced the same percentage of baited trials. No location was better than any other (i.e. rewarded more often). We included the 0% condition, in which all locations were unbaited in all trials, as a control condition to account for the possibility that chimpanzees might work for no rewards at all (e.g., out of habit, boredom, or just because experimenters were present). Rewards consisted of a slice of banana (approximately 1 cm thick).

Unlike experiment 1, we randomized the conditions in experiment 2. Because we did not vary the quantity of rewards between greater and lesser amounts, we were not as concerned about frustration effects in experiment 2 as in experiment 1. In experiment 2, what varied was whether an individual was rewarded for its effort or not, which was plain for each individual to see. They could simply choose not to pull on trials in which their location was unrewarded if they preferred. Frustration effects, loss of associative value, and the like are more concerning when effort previously rewarded at one level is suddenly rewarded at a lower level (e.g., like getting paid less to do the same work). In addition, we tried to mark the difference between the experiments for the chimpanzees by changing the type of reward from grapes in experiment 1 to highly valued (to these chimpanzees) banana slices in experiment 2. While we were less concerned about frustration effects in experiment 2, they

could have still contributed to any drop in performance when moving from higher percentages to lower percentages. This is an inherent limitation to a randomized design, and like experiment 1, it can only be addressed by future studies employing different designs.

Behavioral Definitions

- Approach: An individual coming to the apparatus and taking possession of one of the bars. A new approach was counted if individuals had left (see below).
- Leave: An individual stepping away from the apparatus for at least 5 minutes or stepping away more than 5 meters from the apparatus for any amount of time. Simply switching bars was not considered a leave and thus also did not count as a new approach.
- Bout length: The number of consecutive trials for which the same triad (i.e., the same three individuals) was present at the apparatus and either did successfully cooperate (success bouts) or did not (unsuccessful bouts). Individuals did not have to remain in the same positions.

Analysis: As we expected a large number of unsuccessful (i.e., timed-out) trials in some parts of experiment 2, we added a measure of efficiency calculated as the number of successes divided by the number of trials. The primary result of interest was if and under which conditions the chimpanzees would attempt to solve the task. Each location contained the same quantity of rewards and frequency of reward overall. Thus, we did not pursue analyses of location choice since all locations had the same overall rate of payout within a given condition.

RESULTS

How did reward frequency affect successes and efficiency?: There were 362 successes by 8 individuals. The chimpanzees were more successful at the task as the percentage of rewarded trials increased (Figure 5). Using the 100% condition as a gauge of maximum effort, the chimpanzees received fewer rewards in the 20%, 40%, 60%, and 80% conditions than if they had simply worked indiscriminately on every trial (Table 3).

A MANOVA using Pillai's Trace statistic revealed a significant effect of reward frequency on the number of successes and efficiency, $\Lambda = 1.08$, $F_{10, 48} = 5.58$, $p < 0.001$, $\eta^2 = 0.54$ (Figures 5 and 6). We followed up with a discriminant analysis, which revealed two discriminant functions. The first variate explained 71.7% of the variance, canonical $R^2 = 0.65$, whereas the second explained 28.3%, canonical $R^2 = 0.42$. In combination these discriminant functions significantly differentiated between levels of reward frequency, $\Lambda = 0.20$, $\chi^2_{10} = 40.1$, $p < 0.001$, and the second function discriminated between levels of reward frequency after removing the first function, $\Lambda = .58$, $\chi^2_4 = 13.80$, $p = 0.008$. The correlations between outcome variables and the discriminant functions revealed that both number of successes and efficiency loaded highly on the first function ($r = 0.77$ and $r = 0.997$, respectively), whereas only number of successes loaded on the second function ($r = 0.64$; efficiency: $r = -0.08$). The discriminant function plot (Figure 7) shows that the first function discriminated sessions with low reward rates (0% through 60%) from those with

high reward rates (80% and 100%). The second function differentiated sessions in which successful cooperation was either very unlikely or very likely to happen (0%, 20%, and 100%) from those with more uncertain outcomes (40%, 60%, and 80%).

There was a significant effect of reward frequency on the length of triads' success bouts, Kruskal-Wallis test: $H_3 = 18.09$, $p < 0.001$. Post-hoc comparisons using homogenous subsets revealed that success bouts were significantly longer in the 100% condition than in the 40%, 60%, and 80% conditions, $p < 0.05$ (Figure 8; note that there were no successes in the 0% and the 20% conditions). Reward frequency did not influence the length of triads' unsuccessful bouts, $H_5 = 3.58$, $p = 0.611$.

How did reward frequency affect choices to stay or leave?: A one-way ANOVA revealed a significant effect of reward frequency on the number of approaches, $F_{5, 24} = 6.07$, $p = 0.001$, $\eta^2 = 0.56$. A trend analysis indicated that the data were well fit by a quadratic model, $F_{1, 24} = 20.13$, $p < 0.001$, $\eta^2 = 0.37$, indicating that as reward rate increased, the number of approaches rose initially as well but decreased as the reward rate reached 100% (Figure 9). The number of approaches was significantly lower in sessions in which successful cooperation was either very likely or very unlikely (0%, 20%, and 100% reward rate) than in sessions with more uncertain outcomes (40% through 80%, Ryan-Einot-Gabriel-Welch procedure (REGWQ): $p < 0.005$).

A one-way ANOVA revealed a significant effect of reward frequency on the number of leaves, $F_{5, 24} = 2.95$, $p = 0.033$, $\eta^2 = 0.38$. However, post-hoc tests found no significant differences in the number of leaves between sessions with different reward rates after correcting for multiple comparisons (REGWQ: $p > .05$). Overall there was very little competition (48 displacements across all 30 sessions). Chimpanzees largely chose to approach unoccupied locations and remain until voluntarily leaving, rather than compete for access to locations.

DISCUSSION—The chimpanzees adjusted their efforts based on the reward outcomes. The approaches and leaves to the apparatus show that the chimpanzees assessed the reward situation before choosing to expend effort on the task. This ensured that they would receive rewards and not put effort into cooperation that would not yield benefits. Indeed, the chimpanzees did not succeed at all when there were no rewards to be gained, suggesting that cooperation was not due to habit, boredom, or experimenter presence. Interestingly, the chimpanzees did not receive the maximum number of rewards possible. Had the chimpanzees pulled at the same rate as they did in the 100% condition, regardless of the presence of a reward, they would have received more rewards in every condition (Table 3). This does not necessitate that the effort would have been profitable energetically (for example, pulling on 55 trials to receive 11 rewards in the 20% condition). That analysis would require a measurement of the caloric expense in pulling, which was outside the scope of this experiment. Nonetheless, the chimpanzees forewent rewards by being unwilling to donate effort, which indicates that chimpanzees are focused on their immediate potential outcome when choosing to cooperate or not.

GENERAL DISCUSSION

Cooperation in which there is a choice of partners requires sensitivity to payouts in order to avoid exploitation (Brosnan & de Waal, 2014). In experiment 1, chimpanzees tolerated a mild amount of inequity (a 3:1 ratio) and were as successful at the task as when every individual received 1 reward in a previous study (Suchak et al., 2014). This was expected given that wild cooperative hunting by chimpanzees could not result in carcasses being divided completely evenly, so tolerance for a degree of inequity must exist. However, when all individuals received 3 rewards, the rate of success increased significantly, most likely by ensuring that all individuals had similar levels of motivation. This increased performance is unlikely to be due to order effects or learning effects since those do not take the form of cubic trends (figure 2; Domjan, 2005; Ferster & Skinner, 1957). We also did not see evidence of disadvantageous inequity aversion, through refusals or increased agonism detracting from cooperation. Rather, all of the increase in performance appears to be attributable to motivation for greater rewards. This result highlights a potential benefit to cooperators who share equitably with others: greater rewards generates greater motivation, which generates a greater chance of success in the future. Previous studies described how exploited individuals opted out of participating in the future (Massen et al., 2015; Suchak et al., 2016), limiting the long-term gains for exploiters. Maximizing the motivation of partners may be another selection pressure that would favor an even distribution of resources during cooperation.

Though not described by Brosnan & de Waal (2014), maximized motivation could even support the evolution of advantageous inequity aversion and a sense of fairness. Cooperators who share equitably with others would provide their partners with the maximum motivation possible to cooperate in the future. The long-term gains that heightened motivation would produce on cooperative success could outweigh the short-term gains of exploiting others. Selection for resource possessors to distribute resources equally would necessitate sensitivity to receiving more than others, hence advantageous inequity aversion (see Brosnan & de Waal 2014 for a review of advantageous inequity aversion). However, it is worth pointing out that like Hopper, Lambeth, Schapiro, & Brosnan, (2013), most tests of advantageous inequity aversion have focused on reward comparisons or economic games (Brosnan & de Waal, 2014); they have not utilized cooperative tasks. It is not clear whether the effort involved in mutualistic cooperation with other individuals influences the expression of advantageous inequity aversion. The role of motivational enhancer also applies to human economic endeavors, as it implies that the success of group activities (e.g., a corporation) will be dependent upon the productivity of the least motivated member of a team (Beaumont & Harris, 2003; Ding, Akhtar, & Ge, 2009; Siegel & Hambrick, 2005). Essentially, the least motivated individual provides a ceiling of productivity: other individuals who are compensated more and are motivated more will not raise the collective gains because of the lower motivation level of the lesser compensated individual. Hence, when the effort is the same, it does not pay to pay some individuals less than others, even when possible, because the reduced motivation of these individuals will limit the productivity of the entire group (Beaumont & Harris, 2003; Ding et al., 2009; Siegel & Hambrick, 2005).

Whereas the chimpanzees tolerated a mildly uneven reward distribution, they could not tolerate an absolute difference in which they worked for nothing. In experiment 2, the number of successes did not scale proportionally with the linear change in rewards (Figure 6). Using the number of successes in the 100% condition as the benchmark for maximum effort, the chimpanzees could have received more rewards in all of the other conditions (except 0%) had they pulled at this maximum rate (Table 3). Thus, the chimpanzees achieved fewer rewards than they could have because they were unwilling to donate pulls. The discrepancy between possible rewards and actual rewards received shows that the chimpanzees were not merely responding as if the task was on a variable-ratio (VR) schedule of reinforcement. VR schedules produce strong rates of response as subjects are conditioned *not* to expect a reward on every attempt (Domjan, 2005). In experiment 2, what was effectively a VR schedule produced a weaker response than continuous reinforcement. We see two possible explanations for this. Firstly, the subjects could see whether a reward was in front of them or not, so they knew the outcome of their effort in advance. In typical reinforcement training, the subject is not informed ahead of time whether the response will be rewarded. This difference in design could explain why our effective VR schedule did not produce a typical VR response. Alternatively, this task was cooperative, and reinforcement training has long been a solitary task (Ferster & Skinner, 1957). It is possible that attending to the cooperative nature of the task, the rewards of others, and the risk of exploited efforts changes response patterns. This explanation raises an interesting side issue that all of what we know about schedules of reinforcement comes from individuals working alone (Ferster & Skinner, 1957), and thus may only apply to individuals working alone. Cooperation may change the rules about schedules of reinforcement.

The underperformance of the chimpanzees when not rewarded on every trial is also economically irrational, since economics stresses ultimate total gains over immediate ones. Continued pulling would have resulted in the most possible (even if intermittent) rewards, whereas ceasing to pull resulted in no rewards at all. In the most extreme condition (20%), the chimpanzees could have obtained 11 rewards by pulling at the same rate as the 100% condition; instead, the chimpanzees received 0 rewards (Table 3). The difference is even greater in the 80% condition (Table 3). The chimpanzees did not attempt to switch positions and follow the rewards; rather they maintained possession of a location until withdrawing. Therefore, we did not have a situation where low ranking chimpanzees were always in front of the 0 locations, and by not pulling they were exercising some kind of protest or negotiation (which was not an option in this study). Rather, all of the chimpanzees would have received far more rewards had they donated pulls at the apparatus. Donating cooperative effort is within the abilities of chimpanzees (Crawford, 1937; Melis et al., 2011; Warneken & Tomasello, 2006; Yamamoto et al., 2009), but it may be restricted to very closely bonded individuals or other specific circumstances, such as exchanges. Our study involved 3 chimpanzees working together, thus each individual would have a different relationship with each of its partners. That may have introduced enough complexity to limit effort donation. Instead, the chimpanzees in experiment 2 would only expend effort when they had a reward in front of them, and perhaps the opportunity to trade effort across trials was more abstract than providing an object for a groupmate (Crawford, 1937; Melis et al., 2011; Warneken & Tomasello, 2006; Yamamoto et al., 2009). Only working for an

immediate reward prevented the chimpanzees from receiving more rewards, perhaps because they did not gain the needed experience to build something like a partial reinforcement effect. By only acting when they were guaranteed to receive a reward, the end result over a session was that the chimpanzees did not maximize their rewards, and thus they did not act like rational maximizers. One might argue that only working for an immediate reward is rational in the short-term, but the problem with this argument is that the only thing that truly matters in economics (profit) and evolution (fitness) is the long-term or lifetime gains. From the latter perspective, the chimpanzees did not realize maximum long-term gains, thus making their decisions irrational by definition. In typical cooperative endeavours, including cooperative hunting, the chimpanzees' decisions make sense as negotiation is a factor, so withholding effort is a way to prevent exploitation and ensure future rewards, maximizing long-term gains. In artificial tasks like this one and many of the economic games played with humans, both species show a strong aversion to exploitation that leads to irrational economic decisions.

In studying aspects of more complex cooperation, we examined how chimpanzees respond to moderate inequity and varying levels of risk. Chimpanzees could accommodate some individuals receiving more than others but not receiving nothing at all. Interestingly, productivity was maximized when rewards were equal. From our results we can build a hierarchy of the chimpanzees' performances via their cooperative output: the highest level of performance stemmed from all individuals receiving the same, greater amount of food; next was performance when some individuals received more than others, but with everyone rewarded; and the lowest performance came when individuals had to donate short-term effort to realize long-term gains. The situation that appears to be the hardest for chimpanzees to tolerate is an exchange of effort, meaning working for no reward now, with reciprocity leading to future rewards. Thus, we expect cooperative hunting to be maintained in chimpanzees by contributors being rewarded on each and every hunt (as opposed to across successive hunts), as has been observed (Boesch, 1994), even if the amounts are not and cannot be completely equal. Chimpanzees were highly sensitive to working for nothing, even to their long-term detriment. This result implies that chimpanzees are unlikely to maintain cooperation by a mechanism of sometimes one individual getting all of the food, sometimes another, with a long-term net benefit for all, as is the case for cooperative hunting by fish (Bshary, Hohner, Ait-el-Djoudi, & Fricke, 2006). Rather, our results imply that chimpanzees expect to be rewarded if the hunt is successful, otherwise they would not participate. In the wild, this could lead to selection pressure on the "haves" to share to ensure future cooperation and on the "have-nots" to withhold future effort if they are unrewarded.

Future studies could expand on both the inequity and donating effort topics. During inequity, we only offered one ratio of the same rewards (grapes), so we do not know if chimpanzees would have rejected 1) more extreme ratios (although they did not in Melis et al., 2009) or 2) qualitatively different rewards (e.g., a grape vs. something lower in quality, like a vegetable). For donating effort, we showed the chimpanzees what the outcome would be, but in reality this cannot be known ahead of time. It would be interesting to conceal the outcome until after cooperative effort was expended, with the outcome varying in a risky fashion. In addition, there are ways to combine both inequity and risk into the same design, rather than the separate designs we employed. Based on our results and life in the wild, we would

expect chimpanzees to be more sensitive to the chance of receiving nothing than inequity, but all things have their limits.

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Figure 1.

The apparatus required two individuals to remove the barriers at locations A and C by pulling the rods before another individual could pull in the whole tray at location B. When the tray moved all the way in rewards were dispensed to each individual from the food cups.

Figure 2.

Successes per hour over the course of experiment 1. The 30 sessions were grouped into 5 session bins for analysis. The inequity sessions were the first 4 bins, or sessions 1-20. The last 2 bins (sessions 21-30) were the equity sessions in which all locations were baited with the same number of grapes. Performance followed a significant cubic trend over the course of the experiment. Error bars represent 95% confidence intervals.

Figure 3.

Time of last success (in minutes) in the phase 2 inequity sessions vs. phase 3 equity sessions. Box plots show the median (solid horizontal line), inter-quartile range (IQR; hinges), values within 1.5×IQR (whiskers), and outliers (solid circles).

Figure 4.

Cooperation index in the phase 2 inequity sessions vs. the phase 3 equity sessions. Box plots show the median (solid horizontal line), inter-quartile range (IQR; hinges), values within $1.5 \times \text{IQR}$ (whiskers), and outliers (solid circles).

Figure 5. Mean successes and trials for each condition, in order of testing. Error bars represent 95% confidence intervals.

Figure 6.

Mean efficiency for each reward rate. Errors bars represent 95% confidence intervals.

Figure 7. Canonical discriminant function at the group centroids by reward rate. Note that the group centroids for the 0% and 20% conditions overlap.

Figure 8. Mean bout length by reward rate for continuous successes and non-successes. Errors bars represent 95% confidence intervals.

Figure 9. Mean number of approaches and leaves by reward rate. Error bars represent 95% confidence intervals.

Table 1

The reward scheme for experiment 1 by session.

	Sessions	Location A	Location B	Location C
Phase 1 rewards:	1-10	1	3	3
Phase 2 rewards:	11-20	3	3	1
Phase 3 rewards:	21-30	3	3	3

Table 2

The rates of reward for experiment 2 by session.

Session	Reward rate
1-5	40%
6-10	80%
11-15	0%
16-20	60%
21-25	20%
26-30	100%

Table 3

The chimpanzees solved the task 279 times in the five 100% sessions, an average of 55.8 rewards per individual per session. The 'potentially obtainable' column is calculated by multiplying the reward rate by the chimpanzees' actual performance in the 100% condition. Example: if 55.8 is the theoretical maximum rewards an individual could obtain on average across sessions, multiplying this number by the 80% rate equals a potentially obtainable amount of 44.6 rewards. The table shows that chimpanzees could have obtained far more rewards in the 80%, 60%, 40%, and 20% conditions if they had simply pulled the bars at the same rate as they did in the 100% condition.

Rate	Total successful trials	Actually obtained average rewards per individual per session	Potentially obtainable average rewards per individual per session
100%	279	55.8	NA
80%	57	10.3	44.6
60%	18	2.9	33.5
40%	8	1.3	22.3
20%	0	0	11.2
0%	0	0	0