Bonobo (*Pan paniscus*) Behaviors Exhibited in a Prosocial Choice Task

Seth P. Shaw

Ape Initiative, Des Moines, IA, USA 50320

BRIEF. A Prosocial task found flaws in the choice task methodology.

ABSTRACT. A key element of understanding the social behavior of bonobos (*Pan paniscus*) in captive environments involves assessing their propensity for prosocial behavior. Prosocial behavior is a behavior exhibited by an individual that benefits another individual. Bonobos are very social animals, indicating that they likely exhibit prosocial behaviors. Prosocial behavior is typically examined using prosocial food choice tasks, however studies on bonobos have found contradicting results using this methodology. One main issue found in this methodology is the introduction of a location bias. This study aims to test bonobos using a prosocial food choice task while controlling for possible biases formed in the subjects towards a particular choice. Bonobos were paired and the subjects were allowed to complete the prosocial choice tasks. The placement of tray options was switched throughout the study to control for a location bias. The results yielded no significance in the data when analyzing prosocial choices, however subjects were found to have a location bias. This would indicate that the prosocial choice task is not salient enough to bonobos. An approach that makes the identity of one choice as a "sharing" behavior more salient to the subject may need to be tested in this species.

INTRODUCTION.

Prosocial behavior is any behavior performed by one individual to alleviate another's need or improve their welfare [1]. This is a behavior especially present in humans, however it is hypothesized to be exhibited in other species as well [2]. Some theorize that prosocial behavior developed in certain species to improve survivability through sharing excess resources. The main species studied in this regard are chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) due to their evolutionary relatedness to humans. Through studying evolutionary relatives of humans, more can be learned about how prosocial behavior may develop or present itself in primate species. Variations of prosociality have also been tested between what objects are shared.

Many apparatuses have been used to perform a prosocial choice test. At the core of this type of testing, a "prosocial" and "asocial" option are presented to a subject. In order to complete this task, many paradigms have been used. Researchers have tested using apparatuses that require tools to gain fruit [2, 3], using buttons as representations of outcomes to make a choice [4], and physically presenting two tray options [5]. These studies are meant to test the degree to which apes have the propensity for prosocial behavior; however, many studies have had contradicting findings. One study found a location bias in which apes preferred the prosocial choice when using the prosocial choice task. This led them to question the paradigm of this research [5].

Tan et al. developed a basic prosocial choice task with many steps in order to ensure cognitive understanding of the experiment on the bonobos' part. This paradigm, however, may have introduced experimental error. Researchers theorized that a location bias was introduced during the pretests that affected the rest of the experiment.

The current study aimed to solve and control for this location bias by making two main changes. First, trays' locations were switched between different trials in order to observe whether there is a location bias for tray placement. Second, Pretests were eliminated altogether in an effort to have more simplicity and to eliminate the formation of a location bias.

Another aspect of this study examines the way relationships between individuals are calculated. Typically care staff reports are used to determine the general consensus of the type of relationship that exists between two individuals. This study used two methods for this, care staff reports and Logshift data. Logshift data is data collected that documents which individuals shifted cages with each other. The rationale for using logshift data is to assess whether individuals shift with preferred social partners. In this way, we may assess the degree of social partner preference based on the amount of time an individual chooses to spend shifting from one location to another with that individual. These two methods were compared to determine whether these methods are reliable forms of quantifying relationships.

MATERIALS AND METHODS.

Subjects

Seven Bonobos (4M:3F) from the Ape Initiative participated in this study (mean age 20.6 years, Table 1). The subjects had access to food and water throughout the day. They were not deprived of resources such as food or water. Participation was voluntary and subjects could refuse at any point in time.

Experimental Trials

Research was conducted at the Ape Initiative located in Des Moines, Iowa. Experimental trials were conducted first, and no preliminary testing or learning was provided to the participants. Participants were brought into cages opposite each other. One was the "subject" cage, and one was the "recipient" cage. The participants could see each other during the entire session of 10 trials, and were asked to sit closest to the fence that the experimenter was sitting near. A red tray and blue tray were placed in front of the human experimenter by the experimenter, and a green bucket was placed next to the blue tray.

The experiment was conducted in sessions. Subjects and recipients participated in sessions consisting of 10 trials in a row. Each session had a unique dyad combination, although some dyads were reversed. This was done to accommodate bonobos' choice to participate in the study on any given day.

Trays were placed to either the left or right of the experimenter, depending on what side was assigned to which tray. Trays were switched to either the left or right side of the experimenter throughout the trial. Trays were presented on each side an equal number of times. However, the order in which the tray would be placed on either side was random, and the tray was not switched in between every single trial. Whenever the trays switched, the bucket would be moved as well to be placed next to the blue tray.

To start a trial, the experimenter placed two grapes on each tray. Trays were then slid forward and the subject was allowed to make a choice.

Table 1. Participant Information

Subject			Recipient						
Name	Sex	Age	Name	Sex	Age	Logshift (4 groups)	Logshift P/U	Carestaff (4 group)	Carestaff (Preferred/ Unpreferred)
Maisha	M	21	Clara	F	11	c	Preferred	c	Preferred
Maisha	M	21	Kanzi	M	40	d	Preferred	d	Preferred
Kanzi	M	40	Maisha	M	11	d	Preferred	c	Preferred
Elikya	F	24	Kanzi	M	40	b	Unpreferred	c	Unpreferred
Teco	M	11	Elikya	F	24	b	Unpreferred	b	Unpreferred
Teco	M	11	Nyota	M	23	d	Preferred	d	Preferred
Elikya	F	24	Nyota	M	23	a	Unpreferred	c	Preferred
Nyota	M	23	Elikya	F	24	b	Unpreferred	d	Preferred
Clara	F	11	Mali	F	14	d	Preferred	d	Preferred
Elikya	F	24	Mali	F	14	b	Unpreferred	b	Preferred
Mali	F	14	Clara	F	11	c	Preferred	d	Preferred
Mali	F	14	Maisha	M	21	b	Unpreferred	b	Preferred
Nyota	M	23	Maisha	M	21	a	Unpreferred	c	Preferred
Kanzi	M	40	Mali	F	14	b	Unpreferred	b	Unpreferred
Nyota	M	23	Teco	M	11	d	Preferred	a	Unpreferred
Clara	F	11	Teco	M	11	a	Unpreferred	c	Preferred
Maisha	M	21	Teco	M	11	a	Unpreferred	b	Preferred

*When classifying relationships into four groups, the categories were "a", "b", "c", and "d". These indicated a relationship strength of least preferred, slightly preferred, moderately preferred, and most preferred. Percent values were categorized as a (0-10%), b (11-20%), c (21-30%), and d (>30%).

If the subject did not make a choice within a minute, trays would be pulled back and grapes would be discarded. The experimenter would then repeat this process. The subject would only be allowed to make one choice. A choice would be indicated by a subject pointing or poking their finger, a piece of straw, or their lips out of the mesh clearly to one side.

If the red tray was chosen, this would indicate a prosocial choice. One grape would be removed from the tray and given to the recipient bonobo or placed in its cage. The second grape would be given to the subject. Both trays would be pulled back and the remaining grapes on the blue tray would be discarded.

If the blue tray was chosen, this would indicate an asocial choice. One grape would be removed from the tray and placed in the green bucket. The bucket would then be tilted to show the subject bonobo. The second grape on the blue tray would then be given to the subject. Both trays would then be pulled back and the grapes on the red tray would be discarded.

Control Trials

The control trials were run in a similar way to the experimental trials with sessions consisting of 10 trials. One session was run for each subject. The differences between control trials and experimental trials was that no recipient was present in control trials.

In addition, rather than the green bucket being to one side close to the blue tray, it was placed in the middle of both trays. Both trays had the same outcome, meaning that there was no difference between either choice. The trays still switched locations according to a randomized pattern throughout the session.

When the subject chose either tray, one grape would be taken from the chosen tray and placed in the bucket. The bucket was tilted to show the subject its contents. The second grape on the chosen tray was then given to the subject. The trays were then slid back to the experimenter and the remaining grapes were discarded.

Logshift Data

Logshift groups were quantified by counting the percent of total shifts an individual made with each conspecific. Percents tended to range from 0-40%, so this range was used to determine relationship strength

Number of prosocial choices by Control and Experimental
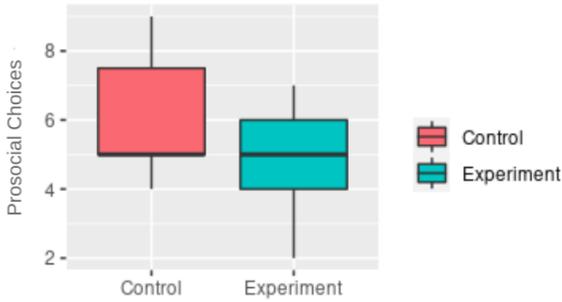
Figure 1. Number of prosocial choices grouped by control and experimental groups. The control data is pictured on the left in red. The Experimental data is pictured on the right in blue. No significance was found (p>0.05).

Number of right side choices by Control and Experimental
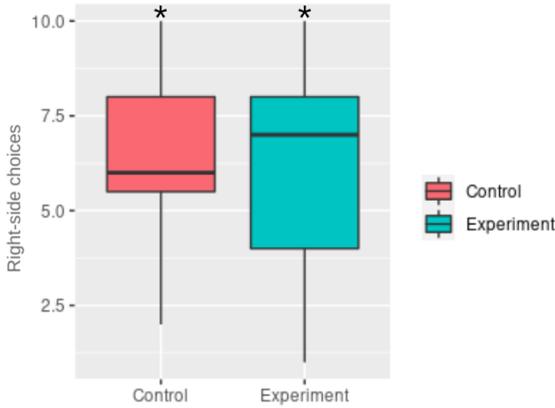
Figure 2. Number of "right tray" choices grouped by control and experimental. The control data is pictured on the left in red. The Experimental data is pictured on the right in blue. Significance was found when comparing data to chance (p<0.05).

and the preference of partnerships. If the percent value for two individuals was at or under 20%, the relationship was classified as unpreferred. If the percent value was over 20% it was classified as a preferred relationship. See table 1 for how the four relationship groups were calculated.
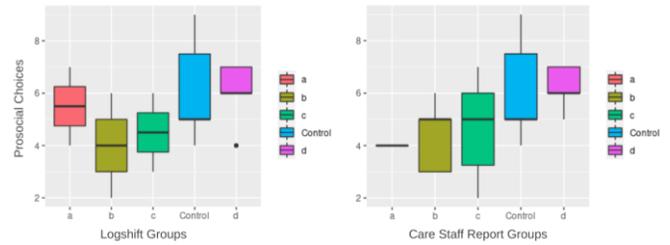
Care Staff Data

Care Staff data was collected using reports and had the same categories as the Logshift data. Care staff rated each combination of participants that was used in this study based on the scale of 1-4 and whether it was a preferred or unpreferred relationship.

RESULTS.

To determine if experimental conditions differed from control conditions, a Wilcoxon signed rank test was conducted. No significance was found between experimental and control conditions (Z= 1.1, p= 0.27). To determine whether the control and experimental conditions differed from chance performance, a Chi-squared test was run comparing the number of prosocial choices made in the control conditions and experimental conditions to 50% (Fig. 1). The control condition did not differ significantly from chance $\chi^2(1, N=70) = 3.66$, p>0.06. The experimental condition did not differ significantly from chance $\chi^2(1, N=170) = 0$, p>1.

Figure 3. Number of prosocial choices grouped into 5 prosociality groups based on the care staff report data (right) and 5 prosociality groups based on the Logshift data (left).

In order to determine if a location bias was influencing subject choice, a Chi-squared test was used to compare the number of right-side choices made in the experiment and control conditions (Fig.2). The control condition was significantly different from chance $\chi^2(1, N=70) = 5.72$, p>0.02. The experimental condition was significantly different from chance $\chi^2(1, N=170) = 9.41$, p>0.002.

A Cohen's Kappa test was run to find the agreeability between the Logshift relationship classifications and care staff relationship classifications (Fig. 3). The agreeability was fair (Cohen's Kappa= 0.3).

DISCUSSION.

Results from the Wilcoxon sign rank test indicate no significant difference in performance between experimental and control conditions, meaning subjects likely did not make prosocial choices or did not understand the prosocial nature of the experimental paradigm. In addition, the chi-square results indicate that subjects were choosing at chance level for both conditions which would be expected for the control conditions in which the outcomes between choices did not differ but was not expected in the experimental prosocial choices with differing outcomes based on tray choice. Furthermore, the side choice chi-square test yielded significant results indicating that subjects had a clear location bias in both experimental and control trials. The reason that the prosocial choice would appear to be at chance is because both tray options are on one side an equal number of times. The participants in the study were found to not have displayed significant prosocial behavior. This would suggest that bonobos are not prosocial concerning food, however this is likely not the case. Both bonobos and chimpanzees have been shown to be prosocial in previous studies [2], [4]. Given that other great apes have been shown to display prosocial behavior, it is more likely that paradigm design is playing an important role in the bonobos' understanding of the nature of the task. Given similar findings in other studies using prosociality tasks, it may be the case that the paradigms that have been created by human experimenters have failed to tap into the prosocial nature of this species.

It is important to examine whether the results of this study were more likely to have been the result of a lack of prosociality or an error in the prosocial choice task paradigm. The previous study found that the main error was that a location bias was found in their prosocial choice task [5]. They believed that it may have been introduced in learning pretests, so this study removed the pretests. However, there was still a location bias found in the data which means that it is more likely a result of the prosocial choice task not being salient enough to subjects. It may be the case that the human experimenter affected the outcome by interfering with the prosocial interaction between conspecifics. Another method that may be more salient might involve having conspecifics interact directly with each other to share tools and food.

The direct act would better simulate how prosocial behavior is exhibited naturally by apes. Studies where apes are required to interact directly rather than by choosing an option tend to show the usage of prosocial behaviors [2,3]. Given this reasoning, it is likely that the prosocial choice task is a flawed methodology that does not yield consistent results, and new methods should be investigated. Additionally, removing the human experimenter but still having a similar choice paradigm may make the outcome of choices more salient. This is shown by a study conducted on chimpanzees that found them to be prosocial using a touch screen guided task [3].

Along with reconsidering the prosocial paradigm design for use with bonobos, the results of the current study also suggest a need to reassess how relationship dyads are considered as well. The Logshift and Care Staff data for social partner preference were very dissimilar. This calls into question the reliability of the data used to quantify the relationship between two individuals. While Care Staff reports are typically used, they seem to not be very reliable when compared to data that is believed to be an indicator of relationship strength between conspecifics. Care staff reports provide multiple perspectives on what a relationship between conspecifics may be; however, they are likely determined by anthropomorphizing the animals being evaluated. Logshift data is able to give quantitative data to determine relationship strength, but it may not actually be an indicator of relationship strength. Shifting with a conspecific could be performed for some other reason or gain to that individual. For example, bonobos have been found to prefer looking at individuals of a higher hierarchical status than themselves [6]. In addition, it has also been found that immature individuals may use harassment behaviors as a way to establish social hierarchy [7]. These are examples of how social behaviors may not indicate relationship strength. More research should be performed to examine how bonobos bond with each other in captivity and how to quantify that for research purposes.

ACKNOWLEDGMENTS.

1. Cronin, Katherine A. "Prosocial Behaviour in Animals: the Influence of Social Relationships, Communication and Rewards." Animal Behaviour, vol. 84, no. 5, 2012, pp. 1085–1093.
2. Krupenye, Christopher, et al. "Bonobos Voluntarily Hand Food to Others but Not Toys or Tools." Proceedings of the Royal Society B: Biological Sciences, vol. 285, no. 1886, 2018, p. 20181536.
3. Nolte, Suska, and Josep Call. "Targeted Helping and Cooperation in Zoo-Living Chimpanzees and Bonobos." Royal Society Open Science, vol. 8, no. 3, 2021, p. 201688.
4. Mendonça, Renata S., et al. "Touch-Screen-Guided Task Reveals a Prosocial Choice Tendency by Chimpanzees (Pan Troglodytes)." PeerJ, vol. 6, 2018.
5. Tan, Jingzhi, et al. "Preference or Paradigm? Bonobos Show No Evidence of Other-Regard in the Standard Prosocial Choice Task." Behaviour, vol. 152, no. 3-4, 2015, pp. 521–544.
6. Lewis, Laura S., et al. "Bonobos and Chimpanzees Preferentially Attend to Familiar Members of the Dominant Sex." Animal Behaviour, vol. 177, 2021, pp. 193–206.
7. Boose, Klaree, and Frances White. "Harassment of Adults by Immatures in Bonobos (Pan Paniscus): Testing the Exploratory Aggression and Rank Improvement Hypotheses." Primates, vol. 58, no. 4, 2017, pp. 493–504.

Seth Shaw is a student at Hillsboro High School in Nashville, TN; he participated in the School for Science and Math at Vanderbilt University.