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Recommended Citation

Webster, Mackenzie F., "Why Should I Help You? An Exploration of the Contextual and Individual Factors Influencing Capuchin Monkeys' Prosocial Behavior." Dissertation, Georgia State University, 2021.
doi: https://doi.org/10.57709/23988513

Why Should I Help You? An Exploration of the Contextual and Individual Factors Influencing Capuchin Monkeys' Prosocial Behavior

by

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Under the Direction of Sarah F. Brosnan, PhD

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

in the College of Arts and Sciences

Georgia State University

2021

ABSTRACT

Humans are an exceptionally prosocial species, but prosocial behavior is seen across the animal kingdom. Despite widespread observation of such behaviors, however, phylogenies of prosocial behavior have been difficult to establish, and little is known surrounding the proximate mechanisms in animals. This is in part because comparative experimental studies of prosocial behavior have had inconsistent results. There are likely many factors contributing to the variations in prosocial behavior, but the context within which a decision is made may be of particular importance, including experimental design, the social context, and the behavior of the partner. Recent research efforts have also begun to identify effects of immediately prior experiences on prosocial behavior. This dissertation specifically explores the effects of varying the nature of experiences (cooperative, competitive, or non-social tasks) and the outcomes of those experiences (whether a food reward was obtained or not) on subsequent prosocial choices in capuchin monkeys. Monkeys in this study did not overall choose to prosocially provision a partner more when their partner was present than when they were absent, despite demonstrating comprehension of the apparatus contingencies in a knowledge control following testing. Prosocial behavior also did not differ based on the nature or outcome of the prior experience. A measure of displacement behaviors (as a proxy of negative affect) was, however, related to how often subjects selected the prosocial option. Subjects showed increased negative affect after losing a competition compared to winning it, and an interaction with dominance such that any type of competitive experience was more negative than non-social experiences for monkeys who are subordinate to their partner. Finally, partner behavior during the prosocial task did not directly influence prosociality, but there were significant interactions between partner behavior and prior experiences in predicting prosocial choices. While capuchin monkeys did not overall behave prosocially in this study, one possibility is that they received too much training prior to testing that obscured interpretation of the task as a prosocial choice. This may indicate that prosocial behavior is context specific and/or a relatively weak effect. Future research into the interaction of affect and prosocial behavior may prove fruitful.

INDEX WORDS: Prosocial behavior, Cooperation, Competition, Affect, Dominance

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August 2021

DEDICATION

I dedicate this dissertation to my family. To my husband Martin - I could not have done this without you. Thank you for all your support and encouragement over the years, and for always seeing the positives in everything. Thank you to my parents, Ronald and Susan, for being the first to introduce me to science and for always encouraging me to pursue my dreams while helping to make that possible. Your unconditional love and support mean the world to me.

ACKNOWLEDGEMENTS

This dissertation would not have been possible without the help of so many people. I would like to thank my advisor Sarah F. Brosnan for her constant advice and guidance throughout my entire journey at Georgia State University. I would not be writing this today without your continued mentorship and support. Thank you also to Michael J. Beran, committee member and mentor who has always supported me whenever I needed advice, guidance, or just someone to talk to. Thank you to my committee members Sarah J. Barber and Kevin M. Swartout for your help throughout this dissertation, and specifically to Kevin for serving on all my different committees during my time at GSU.

A big shoutout and thank you to Julia Watzek, for her continued statistical, R, and general life advice. Thank you for always believing in me even when I had trouble believing in myself, for slapping the nonsense out of me, and always managing to make me laugh with a perfectly timed gif. I would also like to thank Olivia Reilly and Kelly Leverett for their general support and friendship during my graduate career. Specific thanks to Olivia for helping to collect and organize all the social observational data for this dissertation, and to Kelly to for always answering all my questions, however begrudgingly.

Finally, thank you to the whole CEBUS lab for always supporting one another, and to the entire Language Research Center staff for their commitment to the care and wellbeing of the monkeys.

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1 LITERATURE REVIEW

Humans stand out in the animal kingdom as an exceptionally social and cooperative species. Behaviors for the benefit of others are commonplace, ranging from minimally costly behaviors, such as donating spare change to a charity, to life altering actions with notable costs to the actor, such as donating bone marrow to a stranger. The extent and range of such prosocial tendencies are thought to be an important aspect of our uniquely human levels of cooperation that have contributed to the development of the societies we see today (Chudek & Henrich, 2011; Jaeggi et al., 2010). However, you do not have to look far to see that human prosociality is not ubiquitous, nor is it unique, with prosocial behavior seen to varying degrees across the animal kingdom. So, the question becomes, what determines when individuals are prosocial and what factors are involved in generating prosocial tendencies? Furthermore, how did such behaviors evolve? Regarding the former, extensive research has gone into addressing these questions, and we now know a great deal about when people behave prosocially, why they do, and who does (for reviews see; Mikulincer & Shaver, 2010; Schroeder et al., 1995). The question of the evolution of prosocial behavior remains less well understood, and to address this we must move beyond research with only humans and adopt a comparative approach (Melis, 2018). Comparative research can both inform on the evolutionary history of a behavior as well as help tease out the proximate mechanisms, which may be crucial to understanding human prosociality (Smith et al., 2018).

The desire to unravel the evolutionary history behind prosocial behavior has resulted in a growing comparative literature exploring how some primates and a few other key species show prosocial behavior. Researchers have had difficulty painting a clear picture of the evolution of prosocial behavior, however, due to the apparent inconsistencies in the literature. In particular, while interspecies comparisons have led to hypotheses concerning what important ecological pressures may have led to prosocial tendencies, they often are not supported by all of the available data. The question remains whether this is because they are not good explanations of behavior or whether our experiments lack consistency or are missing key aspects that are important to consider.

For instance, the cooperative breeding hypothesis posits that prosocial behavior is linked to rates of allomaternal care as an important socioecological pressure in the emergence of prosocial behavior (Burkart & van Schaik, 2010). This hypothesis has been supported by comparative research as a good predictor of interspecific variations in prosocial behavior (Burkart et al., 2014). It does not, however, explain occurrences of prosocial behavior in non-cooperative breeding species (which have been readily observed, for instance in chimpanzees; Claidière et al., 2015; Schmelz et al., 2017; Warneken et al., 2007; and capuchin monkeys; Brosnan et al., 2010; Lakshminarayanan & Santos, 2008; Suchak & de Waal, 2012), nor does it do anything to explain *intra*species differences in prosociality. Moreover, of the cooperatively breeding species available, only a small subset, focused in the primates, have been tested, suggesting that more data is needed to see whether this holds more broadly, a widespread problem in prosocial behavior research (Marshall-Pescini et al., 2016).

A key understudied factor that may be leading to the inconsistencies seen in the literature, particularly within species, is the impact of the contextual factors surrounding prosocial decisions in animals. In particular, to what degree are factors such as the quality of the social relationship, the dominance asymmetry, and the communicative behavior between individuals influencing decision-making? Some of these factors may stem from experimental design (i.e., specific subject pairings), while others may be uncontrollable aspects of social-living organisms' lives, such as changes in affective states and positive or negative interactions that may occur prior to testing (e.g., being groomed or being threatened, respectively). Recent evidence suggests these factors are relevant in humans, and elucidating the important factors surrounding prosocial behavior in other species may help generate novel hypotheses about the proximate mechanisms for prosocial behavior and shed light on the evolutionary development.

Thus, the current review summarizes the literature on prosocial behavior in animals with a focus on the contextual factors influencing prosocial behavior. Specifically, I begin with an overview of the primary experimental procedures (a form of context) seen in the literature and discuss the merits and importance of the different methodologies. Next, I provide an updated account of the social factors that have been studied for their influence on prosocial behavior (previously reviewed in; Cronin, 2012). Finally, I summarize the recent literature on the effects of the broader context within which prosocial decisions are made (prior experiences and affective states). I highlight how this area has indicators that it may be of particular importance for understanding prosocial behavior in animals.

1.1 Key Terminology

Research regarding prosocial behavior has garnered interest across disciplines. However, not surprisingly, different disciplines often approach these questions in fundamentally different ways (Bshary & Bergmüller, 2008). It is therefore essential to clarify specific terminology and address the level at which questions are being asked, as there remains semantic confusion in the literature, particularly across disciplines, in regards to implications and levels of explanation (West et al., 2007).

Prosocial behavior is defined as any voluntary behavior by an individual that benefits another, regardless of costs to the actor (Marshall-Pescini et al., 2016). Altruism is sometimes used synonymously with prosocial behavior, but there is an important distinction; altruism involves an immediate cost to the actor, while prosocial behavior does not. Therefore, all acts of altruism can be considered prosocial behavior, but not all instances of prosocial behavior are altruistic. For instance, donating blood or bone marrow to strangers is a costly prosocial behavior that would therefore be considered altruistic, but letting someone into a line of traffic is prosocial but not altruistic, as it costs at best a minor risk of missing the light (a small cost even if it happens). Both terms are further distinguished from cooperation, which can be defined as voluntary actions *by two individuals together* that results in an outcome that could not have been brought about individually (Brosnan & de Waal, 2002). The key difference here is that prosocial behavior and altruism are behaviors exhibited by an actor alone, while cooperation involves joint action, although it may involve a prosocial action by one or both (for instance, in the case of reciprocity).

In addition to an inconsistency in precise definitions, there is also a divergence in the literature on whether the question is being addressed at an ultimate level of explanation or at a proximate level, which can lead to confusion. Ultimate explanations focus on why a behavior exists, while proximate explanations focus on how the behavior works (Scott-Phillips et al., 2011). For instance, researchers interested in *why* prosocial behavior exists may try to compare behavior across several species to determine what ecological pressures have led to the emergence of such behavior (such as cooperative breeding). Researchers interested in *how* the behavior works on the other hand, may be more interested in comparing prosocial behavior across various contexts, to examine when the behavior is displayed and what the psychological mechanisms are behind specific instances of prosocial behavior. Both are important, but address fundamentally different questions, even though superficially they might both might be addressing the question "why are animals prosocial?" For instance, with prosocial behavior, we can hypothesize that an ultimate function is to increase an organism's fitness through reciprocal exchange, and therefore a long-term net benefit for the acting organism, or through increased indirect fitness benefits if the recipient of the prosocial act is related to the actor. On a proximate level, however, the organism need not be aware of how their prosocial behavior benefits themself in the long-term, and could instead be motivated by empathy, affective processes, or an innate other-regarding motivation, or the behavior may be biologically predisposed, and they behave as such without an awareness that their behavior benefits anyone else.

Indeed, the terms 'costs' and 'benefits' are used in both ultimate and proximate explanations of behavior, but in reference to different things. For example, regarding the ultimate question of how a behavior for the sole 'benefit' of another could arise, even at a 'cost' to the actor, evolutionary biologists use processes like kin selection and reciprocity, which allow for an ultimate benefit in terms of *reproductive success* for the actor from an immediately costly behavior. Thus, on an ultimate level it can often be argued that animals are all 'selfishly' motivated. In contrast, proximate explanations focus on the mechanism behind the behavior, and therefore place the emphasis on the immediate costs and benefits, used in the more colloquial sense of gains or losses. Behavior that benefits another may ultimately be evolutionarily beneficial to the actor in the long run (or not), but the actor may be unaware of this benefit and have a proximate mechanism, such as empathy, that motivates the behavior (de Waal & Suchak, 2010). In the current review, we refer to the proximate mechanisms behind behavior in terms of short-term costs and benefits and are not focused on the ultimate explanations for how behavior increases evolutionary fitness or any implications for reproductive success.

To address questions about the evolution of a behavior (both ultimate and proximate), we often look to non-human animals. Phylogenetic comparisons allow us to explore whether particular behaviors or characteristics are evident in species, including humans, with certain ecological or social pressures, and may provide evidence for why the behavior evolved (ultimate explanation). Studying a behavior in other species also helps to pinpoint mechanisms behind the behavior (proximate explanation) by examining species with a range of underlying abilities; species that lack a specific cognitive ability but still show the behavior suggest that the cognitive ability is not essential for the behavior to manifest (although it may nonetheless be involved in species that do have it). In addition, natural selection can, of course, only operate on the materials at hand Thus, when considering humans in particular, an interesting question is how these behaviors evolved, and from what precursors, particularly behaviors seen in other primates (since we ourselves are primates). Finally, at a practical level, studying nonhuman species allows us to exert a greater level of control over subjects and their environments than can be done in research with humans, and may be useful for generating novel mechanistic predictions for a behavior in humans.

1.2 Experimental Studies of Prosocial Behavior

Experimental research is particularly important for investigating the proximate mechanisms and motivations behind prosocial behavior in animals (Sosnowski & Brosnan, 2019). This technique allows for both the isolation and combination of different variables, with control that cannot be achieved in the wild. However, with any experimental research, there is a tradeoff with ecological validity. In particular the stressors and motivations behind behaviors may differ in captivity compared to the wild, which may alter behavior (Stevens & Carlson, 2008). Generally speaking, if a behavior is found in captivity but not the wild, whether or not the captive results are generalizable to how the behavior manifests naturally may be called into question. For instance, if we saw prosocial behavior in experimental contexts but it did not occur in natural settings, we might question if the design accurately reflects ‘prosocial behavior’ in terms of its real context in the world. However, in the case of prosocial behavior, the opposite is true – we see more evidence of prosocial behavior in the wild than in captivity.

Cases of prosocial behavior by animals in the wild take a range of forms, from anecdotal reports of wound cleaning and other forms of helping behaviors (Boesch 1991; de Waal 1996) to systematic accounts of coalitionary support (Boesch et al., 2008; Watts, 1998), food sharing (Boesch & Boesch, 1989) and adoptions (Boesch et al., 2010). Many of these studies are from the primate order, and in particular, chimpanzees; however, anecdotal reports of prosocial behavior have also been widespread among elephants (Bates et al., 2008; Douglas-Hamilton et al., 2006) and cetaceans (Caldwell & Caldwell, 1966; Connor & Norris, 1982). Food-sharing in particular as a form of prosocial behavior has been widely examined in mammals (reviewed in Feistner & McGrew, 1989). Within the primate order, food-sharing is most common within mother-offspring relationships; however in some species, such as callitrichids, capuchins, and chimpanzees, it appears to be more common outside of this relationship than in other species (Feistner & McGrew, 1989; Jaeggi & Van Schaik, 2011).

Despite examples of prosocial behavior being readily observed in the wild, researchers have had difficulty demonstrating prosocial behavior in animals experimentally, even within those species that seem to show prosocial behavior in the wild. Of course, one possibility is that prosocial behavior is simply not common, and/or is over-reported from anecdotal accounts. However, based on the widespread nature of reports from the wild, we assume that prosocial behavior does occur, and on a frequency that is meaningful. Another possibility is that the motivations and stressors that lead to prosocial behavior in the wild are not present in captivity. In prosocial tests that involve the provisioning of food resources, this may be particularly relevant; if the subjects do not think their partner needs any food, they may be less inclined to behave prosocially. While relative assessment of need may indeed affect prosocial behavior, we do not suspect that it precludes it, as numerous studies have found food-sharing behavior within captive environments (reviewed in Jaeggi & Van Schaik, 2011).

Alternatively, it may be that in some prosocial studies the animals do not understand the paradigm the way the human researchers intended. For example, Amici et al. (2014) introduced a comprehension check following their prosocial test and found that most of their subjects (across several species) did not demonstrate understanding of the paradigm’s contingencies. Results such as these call into question both positive and negative results regarding prosocial tendencies in species tested with this paradigm if the researchers did not include comprehension tests of their subjects (de Waal et al., 2008; Horner et al., 2011). Animals almost certainly do not see experimental tests the exact same way as we do (de Waal, 2017), so controls and tests of comprehension are extremely important.

Finally, even in experimental tests with species that behave prosocially in naturalistic settings, and demonstrate comprehension of experimental procedures, subjects may not display prosocial behavior if the experimental paradigm is not a context that inspires prosocial behavior. Indeed, any experimental procedure inadvertently or intentionally controls a lot of different aspects of the context within which a prosocial decision is made. Any of these may affect behavior, including whether there is physical separation between individuals, whether reciprocity is possible, and the identity of the potential recipient (including relatedness, relationship quality, and dominance asymmetry between the actor and their partner). Moreover, these explanations may be interacting; the context of an experimental setting may not be one that evokes prosociality, and thus the animals may not be interpreting the design as a prosocial choice. Below we present the dominant paradigms that have been used to experimentally test prosocial behavior in animals (see Table 1 for summary of studies in the literature), including discussion of the relative merits of each paradigm and the important controls necessary to establish confidence that animals understand the task.

1.3 Prosocial Paradigms

1.3.1 Prosocial Choice (PC) Tasks

The dominant paradigm used to measure prosocial preferences in laboratory research is often referred to as the Prosocial Choice task (PC or PCT: Cronin, 2012; House et al., 2014). In this paradigm, there are typically two choices presented to the decision-making subject (or ‘actor’) that result in various rewards for the actor and a conspecific partner (or ‘recipient’). This choice is most often presented to the actor as the decision between delivering food rewards to themselves as well as the recipient (the ‘prosocial’ option; commonly referred to as the 1/1 option, as in one reward for each individual), or to deliver food to just themselves (the ‘selfish’ 1/0 option). Some variations on this paradigm alternatively present subjects with the option between delivering food *only* to the recipient (the 0/1 option) or to no one (0/0 option), or the option of delivering the same or different values (or quantities) of reward to the recipient (e.g., same [1/1] or lower value [1/1-] rewards to the partner or the same or *higher* value rewards to the partner [1/1+]). The important aspect is that regardless of which tray the actor selects, they get the same reward, so they are only choosing differences for their partner. These tasks lend themselves well to comparative use across species, as they utilize a simple, dichotomous choice option for testing, and allow for different factors within the tasks to be easily manipulated to better get at specific questions (e.g., effects of inequity). Most studies use one of two categories: the platforms task and the tokens task.

In the platforms task, the subject's two choices are presented as platforms, one of which can be pulled to bring food within reach of only themselves (the 1/0 option) and one of which offers food to both subjects (the 1/1 option; Jensen et al., 2006; Silk et al., 2005). These platforms may be side by side or stacked, and each reward is accessible by only one of the participants. The proportion of choices in which the subject, or actor, selects the prosocial 1/1 option when the partner is present is compared to a partner-absent condition, sometimes called a solo control, to verify that the 1/1 choices are based on a preference to bring food to the partner rather than a preference for a platform with more food (2 pieces) than less (only 1 piece). The tokens task is similar in concept, with the exception that the options are represented by two tokens, one of which represents each distribution (de Waal et al., 2008).

Each PC task has its own advantages and disadvantages. The platforms task appears at first look to be the most intuitive. The two options available to the subject are laid out for actor and recipient to see at all times, and there is a clear consequence of the actor's behavior that plays out in real-time (they can watch their behavior result in one of the platforms moving towards themselves and the recipient). A disadvantage though, is that the platforms' locations are static, so even if you control for which platform results in each outcome, you risk the subjects developing a side bias or preference for one platform over the other based on something besides the outcomes. In comparison, the tokens task was introduced to control for side biases and a better ability to randomize locations of the options, as tokens can be presented in jumbled piles with more than one of each option (although biases for one token over the other based on color, shape, etc., must also be considered). The outcome of the behavior is more abstract than the platforms task, however. Subjects need to learn the contingencies of selecting each token based on what the experimenter hands out, and not from visual awareness of how their behavior directly manipulates substrates in their environment (and studies have found that subjects do not always demonstrate comprehension of the token contingencies; Amici et al., 2014; but see also; Suchak & de Waal, 2012). It is also considered an important advantage by some that the food rewards are not visible and are less central to the decision in the tokens task, which may reduce impulsive choices in some species. In fact, some researchers have hypothesized that the presence of visible food rewards in the platforms task may be distracting for actors and lead them to only attend to their own outcomes directly in front of them (Burkart et al., 2007; Melis, 2018). Further, the presence of visible food rewards in close proximity with a partner may generate competitive feelings, and obscure any prosocial tendencies (Hirata, 2007).

Initial reports from research on chimpanzees supported this hypothesis, with studies using paradigms in which the food was visible (such as the platforms task) not finding evidence of prosocial behavior in the chimpanzees (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008), but one study using a tokens task, in which the food was wrapped in paper and concealed from the chimpanzees during the decision, finding evidence in favor of prosocial behavior (Horner et al., 2011). In this latter study, however, the authors only compare behavior to a no-partner control that occurred after testing (and with *different* tokens) and did not test whether subjects understood the contingencies of the task, so interpretation of the results are difficult.

Additionally, several studies with capuchin monkeys did not find food visibility to impair prosocial decisions (Brosnan et al., 2010; Lakshminarayanan & Santos, 2008; Takimoto et al., 2010). While this led some to conclude that there may be species differences in the impact of food visibility, which could be driven by species differences in feeding tolerance, more recent studies with chimpanzees have also found prosocial behavior using designs with visible food rewards (Claidière et al., 2015; Schmelz et al., 2017).

Indeed, some studies have directly compared the behavior of actors in scenarios in which their prosocial decision was made both in the presence and absence of a visible food reward (in both cases a token representing a food reward). In one study, chimpanzees could release a peg that would cause an object to roll into the recipient’s enclosure. Subjects were in fact *more* likely to release a food reward for their partners than a token that could be used to obtain food (Melis et al., 2011). These results are obviously incompatible with the assumption that visible food precludes prosocial behavior, although we would note that subjects in this study could never obtain rewards for themselves, which is different from most PC studies and could have an effect on subjects’ interpretations of competition. The direct comparison of capuchin monkey behavior also found evidence of prosociality across several visible food conditions, but not in a token condition in which the monkeys behavior did not differ between testing and the partner absent control (Brosnan et al., 2010), again suggesting that the presence of visible food rewards does not hinder prosocial choices. This indicates that when studying species with particularly low social tolerance surrounding food it may be important to consider the impact of visible food rewards (Cronin, 2012), but that it is not a widespread problem. In fact, this latter study with capuchins indicates that *not* using visible food rewards may in fact be a more influential factor, perhaps reducing the salience of the prosocial decision (Brosnan et al., 2010) or obscuring understanding of the decision at hand.

A more likely disadvantage of having all food rewards visible is the attentional demands it generates (Burkart et al., 2007; Burkart & Rueth, 2013). The presence of several rewards at once means that to understand their choices, actors must attend to all options before making a decision, which typically includes three rewards and the absence of a reward on at least two different platforms. If this proves difficult, it may result in actors choosing between the platforms at random (which, recall, does not affect their personal outcome) or developing a bias for one platform over the other based on a factor outside of the experimental design. Both outcomes may erroneously lead researchers to the conclusion that the animals in their study do or do not demonstrate prosocial preferences.

One way that some researchers have attempted to reduce the attentional demand of the platforms task is to present two platforms with fewer rewards to attend to, such as the option between a platform with a 0/1 reward distribution (only the *recipient* gets a reward) and one with a 0/0 option (no one gets a reward). Thus, the actors need only attend to one reward when making their decision (although they must still check the same number of locations, the assumption is that they are less distracted to those lacking rewards; Burkart et al., 2007). Alternatively, some researchers have tried comparing *rates* of pulling versus not pulling (as opposed to comparing *which* option the actor pulls) between conditions in which behavior can benefit either only the actor (1/0), only the recipient (0/1), both (1/1), or neither (0/0), but actors need only interact with one platform at a time (Amici et al., 2017). While both of these solutions do indeed reduce the attentional demands for actors on a given trial, prosocial behavior in these studies requires behavior on the part of the actor with no immediate personal gain and may reduce motivation to participate at all.

A possible way to increase attention to the choices (when all food rewards are present) may be to give the actors an unattached bar that they use to select between the two platforms they are presented with, before pulling in their selection. This adjustment may slow actors' decisions down, allowing more time to attend to and consider the options before acting. Indeed, in a study with four great ape species, researchers examined tool-use behavior in a paradigm in which rewards were obtained by subjects raking rewards toward themselves. Apes were required to choose between two tables baited with rewards, one of which had a gap that would cause the reward to fall before reaching the subject (meaning there was a 'correct' response, unlike in most prosocial tests). Their responses were compared when the choice was presented to them with a prepositioned tool on each table versus a single tool given to the apes, who had to decide which table they wished to use it on. The apes made significantly more correct choices when given a single tool than when choosing between two prepositioned tools, which the authors argue may be the result of increased bias to grab the first tool seen without considering the decision when presented with pre-positioned tools (Girndt et al., 2008). Thus, a small change in the experimental design can make the task easier for the animals, despite the irony that researchers presumably assumed that prepositioning bars for subjects would be the simpler paradigm. Although this effect of prepositioned bars has not been tested in PC research, allowing subjects a single bar to make their selection in a PC platforms task may similarly slow down decision making and reduce impulsive behavior. Furthermore, this solution could address an additional methodological concern with the platforms task, which is that the context of proximity to conspecifics can influence prosocial choices; prosocial choices in the platforms task often require sitting closer to the recipient than non-prosocial choices (Amici et al., 2014). If actors could choose their preferred platform using a tool that attached at a range of locations on each platform, decisions could be made independent of distance from the recipient.

1.3.2 Necessary Controls

When designing prosocial research, it is important not only to consider how easily animals are able to interpret the paradigm, but also to check for comprehension before drawing conclusions. As demonstrated above, without proper controls it can be difficult to interpret results. The two most essential controls for the PC paradigms are the partner-absent control (also sometimes called the ‘solo control’) and some form of knowledge test for comprehension.

The partner-absent control is a condition in which prosocial choices towards a partner are compared to choices when no partner is present. This control is essential for interpretation of the results because if a subject is interpreting the task as an opportunity to behave prosocially, and we want to conclude that this behavior is indicative of prosocial behavior, they should be selecting the prosocial option more often when tested with a partner than when tested alone. Equivalently high rates of prosocial choices in test conditions and the partner-absent control suggests that subjects’ behavior during testing may not be the result of prosocial tendencies, but instead subjects may either think they could gain access to the other reward, or simply have a bias for the prosocial option (be it the platform or the token) irrespective of prosocial intention. Unfortunately, not all studies have included this control, making it difficult to determine whether high rates of prosocial choices are really due to a preference for behaving prosocially (i.e., Horner et al. 2011).

A knowledge-test control or some criterion for comprehension of the choice contingencies is also essential. In this control, subjects are given the chance to obtain *both* rewards and must prefer that option (the assumption is that all animals would prefer two rewards over one). Since most PC tasks utilize subjects separated by some barrier, removing this and allowing subjects the same contingencies as in testing is a good way to assess comprehension. This control is often included after testing to ensure the subjects understood the task, or as a part of training, to only allow subjects who demonstrate comprehension to participate. However, the timing of this check can introduce its own issues. If presented as a form of training, it may introduce the expectation of both rewards by the subject, and result in a competitive interpretation during testing (Amici et al., 2014). If only presented afterwards, however, it is difficult to determine at what point subjects fully understood the task, so earlier results may be questioned. This is a continued challenge for prosocial research and is a big part of why there is inconsistency in the literature regarding what should be done with this control.

1.3.3 Helping Tasks

A different type of paradigm that has also been widely used to experimentally assess prosocial behavior in the laboratory are the helping or giving assistance tasks (GAT). ‘Helping’ behavior involves an immediate (if sometimes low) cost to the actor, and exclusively benefits the recipient (and therefore is, by our definitions, technically altruistic; Marshall-Pescini et al. 2016). Similar to the PC tasks, these studies have two primary forms; helping via transfer of a desired object or tool to a conspecific or human (“instrumental helping”; Warneken & Tomasello, 2009) or helping via assistance in reaching some otherwise unachievable goal of the other, such as by opening a door to allow access to a reward (“targeted helping”; de Waal, 2008) [1].

Many of these studies have utilized an ‘out-of-reach’ paradigm in which the actor helps the recipient obtain access to an item they cannot reach (Warneken & Tomasello, 2006). Other versions involve the actor having access to a tool or a token that is useful only to the recipient (Skerry et al., 2011; Yamamoto et al., 2009). Alternatively, the help may be a behavior such as opening a door (Bräuer et al., 2013; Tan & Hare, 2013; Warneken et al., 2007), or releasing a blocked reward (Melis et al., 2011) or trapped companion (Bartal et al., 2011; Ben-Ami Bartal et al., 2014; Carballo et al., 2020; Silberberg et al., 2014).

The major advantage to these types of studies is their naturalistic and intuitive appeal. Subjects are presented with a scenario where action on their part clearly benefits another. This behavior is often either mechanically identical to a natural behavior or similar in nature to prosocial behavior that occurs in the wild (i.e., helping others obtain food/access to something desirable). Another often cited advantage to this class of paradigm is that it can be tested without visible food rewards to distract the subject or to inspire competition with the recipient. Indeed, after initial studies using the PC task suggested that chimpanzees were not prosocial, helping tasks were the first to demonstrate that chimpanzees are prosocial in some circumstances, with researchers citing the possible influence of visible food (Warneken & Tomasello, 2006) or competition over food precluding prosociality in the PC studies (Warneken et al., 2007). We already discussed before, however, that more recent research has indicated visible rewards do not preclude prosocial behavior in all circumstances using PC tasks, even in chimpanzees, so this may not be quite the advantage it was once considered.

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[1] Note that in Table 1 we organize the different types of helping tasks further than these two categories, but we group them in text as such in order to be able to draw more meaningful conclusions.

As with the PC tasks, helping tasks also have some disadvantages. Whereas most variations of the PC task present subjects with at least two options to choose between, helping tasks often present the subjects with the option between action and inaction. This could lead to inflated rates of ‘prosocial’ behavior if the subjects prefer action (Melis et al., 2011). It is reasonable to expect this preference, as within these experimental settings subjects are often trained to perform the given behavior prior to testing and may associate it with obtaining a reward. Even if it can be reliably shown that subjects do not expect a reward for their behavior, they may still prefer action to inaction (Smith & Silberberg, 2010), particularly if it progresses them to the next trial in which they might have access to food, or even just gets them through testing faster so that they can rejoin their social group sooner (in most of these studies subjects are isolated from the group during testing).

Some studies have controlled for this by offering the option of alternative behaviors. For instance, in one study with bonobos, researchers found that the subjects chose to unlock a door to release a conspecific and grant them access to a food reward (even one that the subject could otherwise monopolize) over opening a door to an empty cage, suggesting a prosocial preference (Tan & Hare, 2013), although this study did not control for whether subjects might just be inclined to unlock the conspecific just to socialize (regardless of the presence of food). In another study with chimpanzees, researchers offered an alternative to the prosocial behavior, in the form of non-functional ropes, juice-soaked towels, and toothbrushes to play with, and subjects still chose to behave prosocially (Melis et al., 2011). While these controls support the conclusion that the behavior was not just a preference for any action over inaction, the salience of these distractors can be highly variable and alternative explanations such as stimulus enhancement from the location of the recipient, or a desire for social contact are still often difficult to rule out.

The use of the GAT paradigms has been influential in our understanding of primate prosocial behavior, particularly in the great apes. Notably, early helping studies demonstrating prosocial behavior in chimpanzees (Warneken et al., 2007; Warneken & Tomasello, 2006), while PC studies were indicating the absence of such preferences (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008), were likely a driving factor for additional research to closely analyze aspects of the PC experimental design (and generate the necessary controls), as well as to look for a wider range of contexts in which chimpanzees may display prosocial behavior (and evidence of prosocial behavior by chimpanzees in PC task has since been found; Claidière et al., 2015). Recent interpretations suggest that prosocial 'helping' behavior in these GAT studies may be a fundamentally different form of prosocial behavior than prosocial 'sharing' behavior in PC studies (Melis, 2018; Warneken & Tomasello, 2009). If this is the case, both paradigms may be important for understanding the roots of human prosocial behavior but may each do so in different ways. PC paradigms or any prosocial tasks involving food may represent a special domain that is disproportionately influenced by feeding ecology in less tolerant species (Warneken & Tomasello, 2009), and thus requires close consideration in cross-species comparisons. GAT paradigms may therefore be important for modeling the evolutionary history of biological predispositions for instrumental helping, particularly in our closest relatives (the great apes) but may not be as widely applicable to more distant species.

Indeed, capuchins monkeys have been less reliably prosocial in studies utilizing GAT paradigms (Barnes et al., 2008; Skerry et al., 2011; but see also; Drayton & Santos, 2014a) than the PC studies. It is possible that these differences are the result of increased perspective-taking requirements in the GAT paradigms compared to the PC. Capuchin monkeys may show phylogenetic differences compared to chimpanzees in their ability to see past their own outcomes to those of a conspecific under some circumstances (Barnes et al., 2008). This is consistent with research indicating more limited perspective-taking abilities in capuchins than chimpanzees (Hare et al., 2000, 2003). Callitrichids, even more distantly related to humans, have also been the focus of a great deal of prosocial research (fairly consistently demonstrating prosocial behavior in PC studies), but have not been tested on the GAT paradigms. These species likely do not possess the higher-level cognitive abilities required for perspective taking, but nonetheless demonstrate that 'sharing' may be an important part of their ecology (callitrichids are cooperatively breeding species). This further highlights the potential divergence between these different types of prosocial behavior and suggests that PC paradigms may be more widely applicable from a comparative perspective but limited to food-tolerant species.

1.4 Effects of Context

Variable outcomes to GAT and PC tasks even within the same species suggest that other factors may be contributing to prosocial behavior beyond aspects related to experimental design. Such factors may be social (e.g., whether the recipient is familiar, related, bonded, or their relative dominance status to the actor), situational (e.g., the partners behavior towards the actor or reward), or influenced by preceding experiences (including influences on the actors' affective states).

1.4.1 Social Context

1.4.1.1 Familiarity

One of the main ways the social context has been studied explores whether animals behave more prosocially towards "in-group" individuals than towards "out-group" strangers. As may be expected, because out-group members are both less likely to be related or to have the opportunity to reciprocate a prosocial behavior, several studies have found higher rates of prosociality towards groupmates than towards strangers (capuchin monkeys: de Waal et al., 2008; dogs: Dale et al., 2016; Quervel-Chaumette et al., 2015; wolves: Dale et al., 2019; rats: Ben-Ami Bartal et al., 2014). Several other studies, however, have found contradictory results with interesting implications.

For instance, despite multiple studies finding that pet dogs deliver food to a familiar dog more often than towards a stranger dog (Dale et al., 2016; Quervel-Chaumette et al., 2015), *pack* living dogs show no evidence of prosocial behavior (towards pack members or unfamiliar individuals; Dale et al., 2019). Like pet dogs, however, pack living wolves are also only prosocial towards members of their group (Dale et al., 2019). While only a single study has been done with the pack living dogs, these results point to a possible important role of human influence (besides that of domestication) on the observed prosociality of pet dogs. Indeed, humans often actively train their dogs to be socially tolerant of one another, whereas when left to their own devices, the dogs may not exhibit such tolerance. In contrast, wolves are cooperative breeders and hunters, so their ecology itself promotes social tolerance and may be a reason why we see this stark contrast in prosociality towards familiar and unfamiliar individuals.

Other work is less consistent. Capuchin monkeys initially showed evidence of prosocial choices towards familiar individuals (both kin and non-kin), but not towards strangers (de Waal et al., 2008), but then a later study found that the same monkeys behaved prosocially towards all individuals with whom they were tested, strangers included (Suchak & de Waal, 2012). Interestingly, in this second study the experimenters introduced a condition that allowed individuals the opportunity to reciprocate, and rates of prosociality towards strangers greatly increased. Although the capuchins behaved prosocially towards the strangers even when not explicitly able to reciprocate, the results from this additional aspect indicate that prosocial behavior may be tied to expectations of reciprocation in the future, even if outside of the experimental paradigm (such as when released back into the group or introduced to strangers).

Finally, marmosets (*Callithrix penicillata*) may be *more* prosocial towards strangers than towards their pair mates (Mustoe et al., 2015). Importantly, however, the stranger that the subjects were paired with in this study was an opposite-sex partner, and the subjects were not tested in proximity of their current pair mate. Therefore, it is possible that the subjects were treating the strangers as potential future mates, which could explain their prosocial behavior. Supporting this hypothesis, a study with jackdaws (*Corvus monedula*) found a significant interaction between prosocial behavior and sex of the recipient, with the birds behaving more prosocially towards opposite-sex recipients than same-sex recipients, even when compared to sibling relationships. The authors proposed that this may be the result of testing sub-adults who were not yet paired, and thus particularly attracted to opposite-sex, unrelated individuals (Schwab et al., 2012).

Familiarity can clearly play a role in the observation of prosocial behavior, but it is not always straightforward. More work needs to be done to elucidate the relationship between familiarity and prosocial behavior, taking into account species ecology (e.g., whether they are cooperative hunters/breeders) and the status of the out-group individual, particularly whether they could be a potential mate. Furthermore, looking outside of the primate order for species with wider ranges in social ecology may be important for unraveling the mechanism behind these different observed effects.

1.4.1.2 Within-Group Effects: Kinship, Relationship Quality & Dominance

Even within an individual's group, the social context with their partner varies based on relatedness, relationship quality and dominance asymmetry. Such factors are incredibly difficult to test in captive species, however, particularly in primates, where available group sizes are often quite small, and non-invasive testing protocols general dictate that subjects only separate voluntarily, more or less ensuring that only individuals with good relationships are tested together. To directly compare such factors, one would ideally compare prosocial behavior towards kin and non-kin, within high-quality relationships and low-quality relationships, and between dominant and subordinate individuals. In practice, however, when controlling for experience effects and possible reciprocity (i.e., individuals who were recipients of prosocial tests do not later become subjects), there are often not enough individuals to compare these groups with sufficient statistical power. Nonetheless, researchers have attempted to examine these factors and so we have some understanding of their relative effects.

Contrary to expectations from an inclusive fitness perspective, only a few studies comparing prosocial behavior towards kin and non-kin have found significant preferences for directing prosocial behavior towards relatives. Chimpanzees increased rates of tool transfers in a helping study between mother-offspring pairs compared to non-kin pairs (Yamamoto et al., 2009), and long-tailed macaques preferentially delivered food rewards to their relatives more often than to unrelated groupmates (Massen et al., 2010). Capuchin monkeys, however, were as prosocial towards unrelated groupmates as they were to individuals in their group with whom they were related (de Waal et al. 2008), and chimpanzees showed a similar pattern of behavior (they were in fact *less* prosocial towards their kin, although the effect was not statistically significant; Horner et al. 2011). In the only such study in a non-primate species, researchers found no effect of kinship on prosocial behavior in jackdaws (Schwab et al., 2012).

These results indicate that despite predictions from kin selection, animals do not appear to restrict prosocial behavior to kin, or even preferentially direct it towards them. However, interpretation of these results is difficult based on limited evidence from just a few studies. Further, it is possible that inclusive fitness plays a role in prosocial behavior, but that on a proximate level it is over-ridden by other factors of the social group. This may be particularly relevant in captive groups, as these groups are typically smaller and less kin-structured than in the wild, which may lead to the development of different types of relationships.

What other aspects of the social relationship may instead be shaping behavior? For instance, if relationships are less kin-structured in captive groups, perhaps the overall relationship quality is more important than relatedness. Testing this has proven particularly difficult however, as in addition to the same practical difficulties with sample size discussed above, to look at effects of relationship quality it is necessary to have a reliable measure with which to evaluate this. Two studies that looked at whether relationship quality (assessed by behavioral affiliations) was a significant predictor of prosocial behavior in chimpanzees found no effect (Horner et al., 2011; Schmelz et al., 2017). In the latter study, however, the chimpanzee’s social bond was rated as “weak,” “medium-weak,” and a single pairing of “strong” relationship quality, so a larger sample is needed to thoroughly investigate this. Further, in this study the chimpanzees’ behavior was measured after their partner either provided assistance or not, so the relationship quality may have been outweighed by other more immediately-relevant factors (Schmelz et al., 2017). In one study with long-tailed macaques, researchers looked at whether relationship quality was a predictor of prosocial behavior in a dyadic pair, and also introduced a triadic test of prosociality, in which subjects could choose to give to either a ‘friend’ or a ‘non-friend’ (assessed by relationship quality scores; Massen et al., 2011). There was no consistent evidence for an effect of relationship across the study, although there was a non-significant trend for giving to a friend over a non-friend in the triadic test, an effect that went away when controlling for dominance.

Indeed, dominance asymmetry between the actor and recipient in prosocial studies seems like an obvious social factor to consider, but like the other social categorizations, this factor has not produced highly consistent results. In the study just described with long-tailed macaques, the authors found that, in the triadic prosocial test, actors who were lower ranking than both of the possible recipients had a significant preference for giving to the higher ranked of the two recipients, but that rank of the recipients did not matter when the actor was of higher rank than both individuals (Massen et al., 2011). This is consistent with theories that resources should be directed up the hierarchy, from lower ranking individuals to higher ranking individuals (Noë et al., 1991; Seyfarth, 1977a), as the lower rank individuals potentially stand to gain future tolerance or support from the higher ranking individual (Massen et al., 2011). Alternatively, but consistent with resources being directed up the hierarchy, the results could be due to subordinates having an increased tolerance for ‘losing’ resources to dominants, as this may naturally occur, whereas dominants would rarely have experiences in which they relinquished food to a subordinate (Cronin, 2012), and may thus be less likely to do so. These findings are also consistent with results from multiple studies with chimpanzees that similarly found subordinate individuals to be more prosocial towards dominants than the opposite (Horner et al., 2011; Yamamoto et al., 2009).

Other research, however, indicates that the effect of dominance asymmetry on prosocial behavior is not so clear. Two additional studies with chimpanzees did not find any effect of dominance (Jensen et al., 2006; Schmelz et al., 2017), and another suggested the opposite effect; dominant individuals were more prosocial than subordinates, although the difference was not statistically significant (Melis et al., 2011). Indeed, in capuchin monkeys, dominant individuals do appear to be more prosocial than their subordinates (Takimoto et al., 2010), and the same was true in long-tailed macaques (Massen et al., 2010) and rhesus macaques (Chang et al., 2011). In the only study outside of the primate order to examine this, a dominant grey parrot behaved prosocially while a subordinate did not (Péron et al., 2013), although this study only had the two subjects and should therefore be interpreted cautiously.

Researchers have proposed several explanations for these disparities, particularly the finding that dominants are sometimes more prosocial. For instance, it may be that dominants behave more prosocially in order to maintain or display their status (Massen et al., 2010) as a form of honest signaling (Zahavi, 1977). Alternatively, it has been suggested that these effects may be an artifact of the experimental setup, such that reduced anxiety in dominants makes them more likely to approach the apparatus or a greater expectation of getting their partner’s reward (because they do not understand that they are physically separated) are what cause dominant individuals to behave more prosocially than subordinates (Cronin, 2012). Finally, it is also possible that differences are less due to an individual’s place within the dominance hierarchy (such as ‘dominants’ behave more prosocially than ‘subordinates’) and more due to the disparity in dominance rank between individuals, such that animals that are more closely ranked are less prosocial due to increased levels of competitiveness (Massen et al., 2011). Regardless, any of the observed effects of dominance are likely to interact with other social factors, particularly in species with matrilineal social structures, as similarities in rank will be conflated with relatedness in these species.

Indeed, all social effects on prosocial behavior are likely at least in part a combination of various factors of kinship, relationship quality, and dominance asymmetry, and possible interactions may be contributing to the lack of consist patterns within each sub-type. Further research is needed to elucidate in what ways, if any, social context directly influences prosocial behavior. Although it is not always possible to directly compare subjects' behavior towards different individuals within various social contexts, when it is, researchers should report metrics for social relationships and relatedness to allow future researchers to be able to look back for trends in the data (while recognizing that variations in subject numbers and records does not always allow for this).

1.4.2 Behavior of the Recipient

An additional element of the social context in any study of prosocial behavior is the possible interactions between the actors and the recipients. In all the paradigms discussed thus far, actors have at least visual contact with the recipients under most conditions. Thus, the recipient has the potential to engage in their own behavior that could influence the actor. In particular, the recipient may direct behavior towards the reward or towards the actor, making the goals of the recipient more salient.

Recipients expressing interest in the reward by directing behavior towards it is the most common form of recipient behavior reported. This is unsurprising, as behavior of this sort necessitates no cognitive requirements of perspective-taking or understanding of the task setup and the actor's role in obtaining the reward by the recipient (who often has not received any training and is merely a passive partner). These reward-directed behaviors, such as reaching or positioning oneself in front of the reward on the part of the recipient, may inadvertently direct the actor's attention to the recipient's goals or act as a form of stimulus enhancement.

Research on the out-of-reach paradigm supports this conclusion, as reaching for the reward enhances rates of object retrieval in chimpanzees (Warneken et al., 2007) and capuchin monkeys (Barnes et al., 2008; Drayton & Santos, 2014a), although additional results in capuchin monkeys indicate that personal reward may be a more influential factor (Barnes et al., 2008). Further, these studies all examined reaching behavior by a human experimenter instead of a conspecific. The only study to find a significant effect with a conspecific recipient showed that jackdaws were significantly more prosocial towards a conspecific who approached the apparatus first, which always corresponded with the recipient visibly trying to gain access to the reward prior to the actor's decision (Schwab et al., 2012).

Other studies have found no effect of recipient reaching behavior on prosocial choices (Burkart et al., 2007; Dale et al., 2016), and perhaps more surprisingly, several have found a significant *decrease* in prosocial behavior after the recipients' expressed interest in the reward by reaching (Burkart & van Schaik, 2013; Cronin et al., 2009) or trying to access the reward (Tan & Hare, 2013). These results are inconsistent with the hypothesis that recipient behavior directed at the reward signals the recipients' goals and thus inspires prosocial behavior. It has instead been suggested that behavior directed towards the reward may focus the actors' attention on the desirable item, and therefore away from the recipient and their needs. Alternatively, if the actors mistakenly think they can access the reward themselves, the recipients directing behavior towards the reward may make that possibility seem less likely, because the partner may steal it (Cronin, 2012). The limited number of studies and species in which researchers have measured recipient behavior prior to prosocial choices makes it difficult to draw conclusions on the potential impact. Furthermore, it is unclear from the literature how common such behavior may truly be; in studies where recipient behavior is not mentioned, we do not know if it was unmeasured or simply never observed.

Additionally, the recipient also may perform behaviors other than reward-directed behavior that shed more light on the impact of recipient behavior on prosocial choices. While these other behaviors can take several forms, in an effort to compare across studies, we group them here into two categories; subject-directed behaviors (behaviors directed towards the actor, such as begging or direct requests) and attention-getting behavior (behavior that may attract the actors' attention to the recipient, such as vocalizations or noisy behaviors). Unfortunately, however, within the literature these behaviors are not always differentiated, so while we attempt to discuss them separately here, we cannot always accurately distinguish these two possible forms.

Cronin (2012) defined direct requests for assistance as behaviors unambiguously directed towards the actor. These actor-directed behaviors have only been observed in great apes to date and involve behaviors such as open-palm reaching requests and vocalizations. These open-palm requests are the most often reported form of direct requests, seen primarily in object-transfer studies (although not universally across species or subjects), and generally increase the rate of object exchange (Pelé et al., 2009; Yamamoto et al., 2009, 2012), although this effect may be reduced over time (Dufour et al., 2009). In some of the reported studies, however, these 'request' behaviors were also lumped with behaviors such as the clapping of hands or beating the caging, which would perhaps better be categorized as attention-getting behavior. It is thus difficult to say if the requests are the driving factor in the studies that do not differentiate.

Indeed, Horner et al. (2011) included hitting the caging as a form of attention-getting behavior that is not specifically directed at the subject, while distinguishing this behavior from direct requests and pressure, which included behaviors like the open-palm begging directed at the actor. Interestingly, in this study the authors found that attention-getting behavior following a trial led to an increase in prosocial choices, whereas direct requests (like the open-palm reach) or pressure did not. The authors did not distinguish between requests and pressure (such as display behavior), however, so we also cannot rule out that the pressure behaviors hid any effect of request behaviors on prosocial choices. The enhancing effect of attention-getting behaviors by the recipient on actor prosocial choices was also seen in a study in which chimpanzees were more likely to provide help in the form of releasing a chain to deliver a food reward to a conspecific when the partner shook the chain and made a loud noise (Melis et al., 2011).

In contrast, in one study measuring ‘begging’ behavior in capuchin monkeys, the authors did not report direct effects of behavior on subsequent prosocial choices, but found much higher rates of begging by dominant recipients, and less prosocial behavior directed towards these dominants (Takimoto et al., 2010). Begging behavior in this study, however, included waiting near the high-value container, reaching towards it, and touching it (which we would define as reward-directed behavior), and pounding on the front panel (which we would consider attention-getting behavior). Therefore, it is difficult to untangle what may be driving the effect. Similarly, Vonk et al. (2008) found that ‘begging’ behavior did not influence prosocial choices, but they do not define what behaviors this includes.

Thus, it appears that behaviors directed towards the reward may not have much of a facilitating effect on prosocial behavior. Other forms of recipient behavior, such as attention-getting behavior, may be more likely to increase prosociality, but additional work is needed to clarify. Moreover, it will be important in future research to differentiate between the different types of recipient behavior, whether the attention-getting behavior is directed at the actor or not, and whether it may be considered ‘pressure.’ Indeed, one of the main hypotheses to explain food-sharing behavior in the wild is the ‘sharing-under-pressure’ hypothesis, which posits that individuals share in an effort to avoid beggar harassment (de Waal & Suchak, 2010; Stevens & Stephens, 2002). While there is a good deal of research that does not support this hypothesis (reviewed by; de Waal & Suchak, 2010), it remains that differentiating between behaviors directing the actor’s attention to the recipients’ need as opposed to pressuring the actor to behave a certain way may be important, as they could have opposite effects that negate any significant findings when grouped together. Finally, these effects could also interact with social factors, such as differences in the effects of pressure or attention-getting behavior displayed by a dominant compared to a subordinate recipient relative to the actor, but this interaction has not been examined.

1.4.3 Prior Experiences

An additional context that could both interact with as well as subvert social context effects, and has remained relatively unexplored, is the possible impacts of prior experiences. Particularly within small, relatively stable captive groups, and within pairs composed of only socially tolerant individuals, the influence of social relationships on prosocial behavior may be more subtle and nuanced. Instead, the effects of temporally recent experiences (both social and non-social) may have potentially greater impacts on prosocial tendencies. These effects could be important to untangle, as they may point to possible prosocial mechanisms, such as emotional book-keeping, empathy, or an underlying affective mechanism. While the possible influences of prior experiences cannot be pulled from the existing literature (as these factors are not reported), recent efforts to explicitly examine such impacts have found significant effects.

For instance, immediately preceding events showed a clear effect on capuchin monkeys' subsequent prosocial behavior in a study exploring "paying-it-forward" behavior in the monkeys. Their interest was whether being the recipient of generosity contributed to the likelihood of future generosity (prosocial behavior; Leimgruber et al. 2014). In a modified version of the platforms task, monkeys could choose between two reward allotments for themselves and a recipient that gave the recipient either a high-value reward or a very low one, while the actor's reward remained constant. The *recipient* would then go on and immediately become the *actor* in another, different pair. There was a significant relationship between the behavior received and the subsequent behavior displayed, such that rates of prosocial behavior were significantly higher after being the recipient of prosocial behavior and significantly lower after being passed over for receiving prosocial behavior. Their findings are consistent with a 'give-what-you-get' strategy that does not factor in the specific recipient (i.e., not returning the factor to the actor that previously helped you) and is not only for positive outcomes (i.e., not just pay-it-forward, but also pay-it-back). The authors hypothesize that this tendency could stem from an affective motivation, but were unable to directly test this (Leimgruber et al., 2014).

Prosocial behavior also may be shaped by prior experiences of prosocial behavior directed towards the actor even when not immediately preceding the choice (Claidière et al., 2015). After experiencing the prosocial task as an actor to determine baseline levels of prosocial behavior by the subject towards a conspecific, the subject was the *recipient* of a prosocial choice by a different individual (to rule out reciprocity). Next, they were again the actor to see if prosocial behavior towards the original recipient was different than in the baseline. The researchers found that chimpanzees and seven-year-old children, but not capuchin monkeys or five-year-old children, showed increased rates of prosocial behavior after having prosocial behavior directed towards themselves. This study is important because it again revealed that there can be a notable effect of prior experiences, in this instance from a much earlier experience, on subsequent prosocial behavior. The authors proposed that the effects observed may be due to actors learning more about how the task works from being a recipient on the other end (Claidière et al., 2015).

It seems odd that capuchins failed to change their behavior in the above study while they did so in Leimgruber et al.'s (2014). The capuchins in this latter study were also, however, less prosocial to begin with than the chimpanzees, which contrasts with the broader literature. It is possible that there was some other factor influencing capuchin prosociality in this study that prevented the observation of an effect of prior experiences. It is not immediately clear, however, what that factor may be. Additionally, a key difference between this study and the earlier 'give-what-you-get' study is the timeline of events. In the first capuchin study, actors were immediately tested for their own prosocial choices following being the recipient of a prosocial behavior, within a single session (Leimgruber et al., 2014). In the other study, Claidière and colleagues (2015) examined prosocial behavior after being the recipient on a different day. We suspect it is possible that the impact of prior experiences observed in chimpanzees in this study is the result of an improved understanding of the task (which may not have occurred for the capuchins), while in the 'give-what-you-get' study we are seeing impacts more directly related to the immediately prior experience and the perhaps subsequent affective changes that resulted from the different outcomes.

This can be more carefully studied by manipulating recipient behavior prior to an actor's prosocial choice. Using a variation on a platforms PC task, Schmelz et al. (2017) found that, consistent with much of the previous literature on prosocial behavior in chimpanzees, subjects were not prosocial after the recipient provided no assistance to the subject (i.e., passively waited for subject decisions, as in most PC studies). However, in a series of conditions in which the recipient provided assistance to the actor, in the form of granting them access to the prosocial task (and therefore subsequent rewards), rates of prosocial behavior increased even when there was a *cost* to the actor in picking the prosocial option compared to controls in which an experimenter controlled access. This was particularly true if the recipients' assistance was 'risky' (when the recipient chose to forgo a definite reward for themselves to grant the actor access to the prosocial task). In effect, it seemed that chimpanzees increased their rate of prosocial behaviors when the recipient "deserved" it.

1.5 Conclusions and Future Directions

One of the major patterns that has emerged from research on prosocial behavior in animals is that no species, including humans, demonstrate clear prosocial tendencies across all contexts. Within animals, when context effects on prosocial behavior are even examined, the relationship between the actor and recipient has been received the most attention. While evidence for significant effects of factors such as familiarity, kinship, relationship quality, dominance, and partner behavior have emerged, clear patterns across species tested on such factors have not. Limited evidence and the practical challenges of testing these factors have contributed to the difficulty in drawing definitive conclusions regarding possible impacts. Based on the human literature indicating the importance of relationship quality and social factors on prosocial choices

(Barry & Wentzel, 2006; Padilla-Walker et al., 2015), researchers should continue to provide data on as many of these factors as they can when testing animal models, whether they plan to look at that factor directly or not, so that future research can compare trends across studies. Furthermore, researchers should explicitly look for interactions between social contexts when possible. For instance, a social factor like dominance asymmetry may play a role on the impact of partner behavior on prosocial choices, with the behavior of a dominant (and perhaps more threatening) partner influencing choices more than subordinate partner behavior.

It seems that, particularly within captive social groups in which differences in social dynamics may not vary dramatically, the importance of recipient behavior, prior experiences, and the interaction of these factors may be discovered to play a more important role in prosocial choices than general aspects of the social relationship (such as relatedness). Indeed, actively investigating these factors and their interactions should be a driving goal of future research. Developing hypotheses based on the human literature may prove fruitful for identifying areas of the context surrounding prosocial decisions that may be most important to investigate in animals. Of particular interest may be research investigating how prosocial behavior is impacted be prior experiences of agonistic of affiliative social interactions, as these are important categories of social interactions that may be influential in both captive and wild settings. Initial efforts indicate these types of experiences may be important (Leimgruber et al., 2014; Schmelz et al., 2017), but more work is needed to untangle the effects of possible underlying affective mechanisms from more complicated mechanisms that may be involved in reciprocity and assessments of effort and intent. In general, we predict that future research on prosocial behavior may shed light on important mechanisms behind and the evolutionary trajectory of such behavior, from its most rudimentary forms to the complex and flexible prosocial behavior seen in humans.

Table 1. Review of experimental design and other factors that have been examined in prosocial research.

			Social context				Experimental Context														Controls	
Citation	Species	Prosocial Behavior	Relationship Quality	Kinship	Dominance	In-group/out-group	PC (Platforms)	PC (Tokens)	PC (Other)	Helping (Object Retrieval)	Helping (Object Transfer)	Helping (Rescuing)	Helping (Access)	Helping (Other)	Conspecific or Experimenter?	No-cost	Some cost	Reward Distributions	Behavior of recipient measured?	Actors ever recipients?	Knowledge Test	Solo Control
Silk et al. (2005)	*Pan troglodytes*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1. 1/0	-	-	x	x
	Pan troglodytes	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	x	x	x
Jensen et al. (2006)	*Pan troglodytes*	n	-	-	n	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0, 0/0	-	-	x	x
Warneken & Tomasello (2006)	*Pan troglodytes*	y	-	-	-	-	-	-	-	x	-	-	-	-	E	-	x	-	-	-	-	-
	Pan troglodytes	n	-	-	-	-	-	-	-	-	-	-	x	x	E	-	x	-	-	-	-	-
Warneken et al. (2007)	*Pan troglodytes*	y	-	-	-	-	-	-	-	x	-	-	-	-	E	-	x	-	-	-	-	-
	Pan troglodytes	y	-	-	-	-	-	-	-	-	-	-	x	-	C	-	x	-	x	-	-	-
Vonk et al. (2008)	*Pan troglodytes*	n	-	-	-	-	-	-	x	-	-	-	-	-	C	-	x	1/0 *and* 0/1	x	-	-	x
	Pan troglodytes	n	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	1/0 *and* 0/1	-	-	-	x
Yamamoto et al. (2009)	*Pan troglodytes*	y	-	y	y	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	-
	Pan troglodytes	y	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	-

Yamamoto & Tanaka (2010)	*Pan troglodytes*	n	-	n	-	-	-	-	x	-	-	-	-	-	C	x	-	1/0, $1/1^+$, 0/0	-	x	x	x
Melis et al. (2011)	*Pan troglodytes*	y	-	-	n	-	-	-	-	-	-	-	x	-	C	-	x	-	x	-	x	x
Horner et al. (2011)	*Pan troglodytes*	yh	n	n	n	-	-	x	-	-	-	-	-	-	C	x	-	1/0, 1/1	x	x	-	x
Yamamoto et al. (2012)	*Pan troglodytes*	y	-	-	-	-	-	-	-	x	-	-	-	-	C	-	x	-	x	x	-	-
House et al. (2014)[1]	*Pan troglodytes*	y	-	-	-	-	-	-	x	-	-	-	x	-	C	x	x	1/3, 1/2, 1/0, 0/1, 0/0, 0/0(1)	-	x	x	-
	Pan troglodytes	n	-	-	-	-	-	-	x	-	-	-	-	-	C	x	x	1/1, 1/0, 1/0 (1), 0/1, 0/0	-	x	x	-
Amici et al. (2014)	*Pan troglodytes*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Pan troglodytes	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Claidiere et al. (2015)	*Pan troglodytes*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1 vs 1/1+, 1+/1+ vs 1+/1	-	x	x	x
Schmelz et al. (2017)	*Pan troglodytes*	y	n	-	n	-	x	-	-	-	-	-	-	-	C	x	x	1/1, 1/0, 0/1 [3]	x	-	x	-
Mendonca et al. (2018)	*Pan troglodytes*	y	-	-	-	-	-	-	x	-	-	-	-	-	C	x	x	1/1, 1/0, 0/1	-	x	x	-
Tan & Hare (2013)	*Pan paniscus*	y	-	-	-	n	-	-	-	-	-	-	x	-	C	-	x	-	x	-	x	x
Amici et al. (2014)	*Pan paniscus*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Pan paniscus	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Amici et al. (2014)	*Pongo abelii*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Pongo abelii	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Kim et al. (2015)	*Pongo spp.*	n	y	-	-	-	-	-	x	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Emigh et al. (2019)	*Pongo pygmaeus*	y	-		-	-	-	x	-	-	-	-	-	-	C	-	-	1/1, 1/0	-	-	-	-

Amici et al. (2014)	*Gorilla gorilla*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Gorilla gorilla	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Massen et al. (2010)	*Macaca fascicularis*	y	-	y	y	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0(1)	-	x	-	x
Massen et al. (2011)	*Macaca fascicularis*	y	n	-	y	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0(1)	-	x	-	x
Burkart & van Schaik (2013)[1]	*Macaca fuscata*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	0/1	-	x	-	-
de Waal et al. (2008)	*Sapajus/Cebus apella*	y	-	n	-	y	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0, 1/1+	x	x	-	-
Barnes et al. (2008)	*Sapajus/Cebus apella*	y	-	-	-	-	-	-	-	x	-	-	-	-	E	-	x	-	-	-	-	-
Lakshminarayanan & Santos (2008)	*Sapajus/Cebus apella*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1 vs 1/1-, 1-/1- vs 1-/1	-	?	x	x
Takimoto et al. (2010)	*Sapajus/Cebus apella*	y	-	-	y	-	-	-	x	-	-	-	-	-	C	x	-	1/1+ vs 1/1-, 1+/1+ vs 1+/1-	x	-	-	x
Brosnan et al. (2010)[2]	*Sapajus/Cebus apella*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	x	x	1+/1+, 1-/1-, 1-/1+. 0/1-, 0/1+	-	-	-	x
Skerry et al. (2011)	*Sapajus/Cebus apella*	n	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	-	-	-	x
Suchak & de Waal (2012)	*Sapajus/Cebus apella*	y	-	-	-	n	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	x	x	x
Burkart & van Schaik (2013)[1]	*Sapajus/Cebus apella*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	0/1	-	x	-	-
Amici et al. (2014)	*Sapajus/Cebus apella*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Sapajus/Cebus apella	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Drayton & Santos (2014a)	*Sapajus/Cebus apella*	n	-	-	-	-	-	-	x	-	-	-	-	-	C	x	-	1/1 vs 1/0, 0/1 vs 0/0	-	-	x	x

Drayton & Santos (2014b)	*Sapajus/Cebus apella*	y	-	-	-	-	-	-	-	x	-	-	-	-	E	-	x	-	-	-	-	-
Claidiere et al. (2015)	*Sapajus/Cebus apella*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1 vs 1/1+, 1+/1+ vs 1+/1	-	x	x	x
Amici et al. (2014)	*Ateles geoffroyi*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
	Ateles geoffroyi	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0	-	-	x	x
Burkart et al. 2007	*Callithrix jacchus*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	0/1, 0/0	x	?	x	x
Burkart & van Schaik (2013)[1]	*Callithrix jacchus*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	0/1	x	x	-	-
Burkart & van Schaik (2020)[1]	*Callithrix jacchus*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	-	x	0/1	x	x	-	x
Mustoe et al. (2015)[2]	*Callithrix penicillata*	y	-	-	-	y	x	-	-	-	-	-	-	-	C	-	x	1/0, 0/1, 0/0	-	x	-	x
Cronin (2009)	*Saguinus oedipus*	n	-	-	-	-	x	-	-	-	-	-	-	-	C	x	x	1/1 vs 1/0, 0/1 vs 0/0	x	x	-	x
Stevens (2010)	*Saguinus oedipus*	n	-	-	-	n	x	-	-	-	-	-	-	-	C	x	x	1/3, 0/3	-	x	x	x
Nakahara et al. (2017)	*Tursiops truncatus*	y	-	-	-	-	-	-	x	-	-	-	-	-	C	x	x	1/1 vs 1/0	x	x	-	x
	Tursiops truncatus	y	-	-	-	-	-	-	-	-	-	-	x	-	C	-	x	-	x	x	-	x
Lalot et al. (2021)	*Tursiops truncatus*	y	-	-	-	-	-	-	x	-	-	-	-	-	C	x	-	1/0, 1/1, 0/0	-	x	-	x
Brauer et al. (2013)	*Canis familiaris*	y	-	-	-	n	-	-	-	-	-	-	x	-	E	-	x	-	-	-	-	-
Quervel-Chaumette et al. (2015)	*Canis familiaris*	y	-	-	-	y	x	-	-	-	-	-	-	-	C	-	x	0/1, 0/0	-	-	x	x
Quervel-Chaumette et al. (2016)	*Canis familiaris*	n	-	-	-	n	x	-	-	-	-	-	-	-	E	-	x	0/1, 0/0	-	-	x	x

Dale et al. (2016)	*Canis familiaris*	y	-	-	-	y	-	x	-	-	-	-	-	-	C	-	x	0/1, 0/0	x	-	x	x
Dale et al. (2019)	*Canis familiaris*	n	-	-	-	n	-	-	x	-	-	-	-	-	C	-	x	0/1, 0/0	-	x	x	x
Van Bourg et al. (2020)	*Canis familiaris*	y	-	-	-	-	-	-	-	-	-	x	-	-	E	x	-	-	x	-	x	-
Carballo et al. (2020)	*Canis familiaris*	y	-	-	-	-	-	-	-	-	-	x	-	-	E	-	x	-	-	-	-	-
Dale et al. (2019)	*Canis lupus*	y	-	-	-	y	-	-	x	-	-	-	-	-	C	-	x	0/1, 0/0	-	x	x	x
Ben-Ami Bartal et al. (2011)	*Sprague-Dawley rats*	y	-	-	-	-	-	-	-	-	-	x	-	-	C	-	x	-	x	?	-	x
Ben-Ami Bartal et al. (2014)	*Sprague-Dawley rats*	y	-	-	-	y	-	-	-	-	-	x	-	-	C	-	x	-	x	-	-	-
Hernandez-Lallement et al. (2015)	*Long-Evans rats*	*y*	-	-	-	-	-	-	*x*	-	-	-	-	-	*C*	x	-	1/1, 1/0	-	-	-	*x*
Ueno et al. (2019)	*C57Bl/6N mouse strain*	*y*	-	-	-	n	-	-	-	-	-	x	-	-	*C*	x	x	-	*x*	-	-	*x*
Amici et al. (2017)[1,2]	*Suricata curicatta*	n	-	-	-	-	-	-	x	-	-	-	-	-	C	-	x	1/1, 1/0, 0/1, 0/0	-	x	-	x
Di Lascio et al. (2013)	*Corvus corax*	n	-	-	-	-	-	-	x	-	-	-	-	-	C	x	-	1/1, 1/0	-	x	-	x
Massen et al. (2015)	*Corvus corax*	n	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	x
	Corvus corax[1]	n	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	-
Lambert et al. (2017)	*Corvus corax*	n	n	-	n	-	x	-	-	-	-	-	-	-	C	-	x	0/1, 0/0(1)	x	?	x	x
Wascher et al. (2020)	*Corvus corax*	n	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	-
Wascher et al. (2020)	*Corvus corone*	n	-	-	-	-	-	-	-	-	x	-	-	-	C	-	x	-	x	x	-	-
Schwab et al. (2012)	*Corvus monedula*	y	-	n	-	-	-	-	x	-	-	-	-	-	C	x	x	1/1, 1/0, 0/1	x	-	-	x

Horn et al. (2016)[1]	*Cyanopica cyana*	y	-	-	-	-	-	-	-	-	-	-	x	-	C	-	x	-	x	x	-	-
Duque et al. (2018)[2]	*Gymnorhinus cyanocephalus*	y	-	-	-	-	x	-	-	-	-	-	-	-	C	x	x	1/1, 0/1	-	-	x	x
Peron et al. (2013)	*Psittacus erithacus*	y	-	-	y	-	-	x	-	-	-	-	-	-	C	x	x	1/1, 1/0, 0/1, 0/0	x	x	-	-
Krasheninnikova et al. (2019)	*Psittacus erithacus*	n	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1 vs 1/0, 1/1+ vs 1/0	x	x	x	x
Heaney et al. (2020)	*Nestor notabilis*	y	-	-	-	-	-	x	-	-	-	-	-	-	C	x	-	1/1, 1/0, 0/0	-	x	-	x

Note: y/n’s indicate that the study looked for an reported on a particular effect (‘y’ if that effect was significant, ‘n’ if it was not). x's indicate the specified methodologies and controls were used.

[1] Behavior was measured in a group setting, not a controlled dyad

[2] Rates of pulling behavior recorded instead of a choice between two options

[3] Unique methodology presented in some conditions in which the recipient was able to select the options presented to the subject

2 INTRODUCTION

While cooperation is seen widely across the animal kingdom, the depth and breadth of human cooperation is unique (Massen et al., 2019; Melis & Semmann, 2010). One aspect of human nature thought to play a role in the development of such extensive cooperation is our tendency towards prosocial behavior (Chudek & Henrich, 2011; Jaeggi et al., 2010). Indeed, humans regularly engage in behavior that benefits others (Penner et al., 2005), often at great personal cost, and other animals regularly display prosocial behavior as well. The display of such prosocial and altruistic[2] behavior has long been difficult to reconcile by the theory of evolution through natural selection, as it is not immediately clear how a behavior solely benefiting another (regardless of cost to the actor) could be selected for (Darwin, 1871). While ultimate evolutionary explanations such as kin selection (Axelrod & Hamilton, 1981; Hamilton, 1964) and reciprocity (Axelrod & Hamilton, 1981; Trivers, 1971) have broadly addressed how prosocial behaviors could evolve, many questions remain regarding the proximate mechanisms for such behavior (Melis, 2018).

Despite readily observing prosocial behavior in the wild across numerous species (Boesch & Boesch, 1989; Caldwell & Caldwell, 1966; Feistner & McGrew, 1989; Jaeggi & Van Schaik, 2011), experimental tests of such behavior have turned up much more varied results. Two primate species that have been the target for much of the work on animal prosocial behavior, chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Sapajus* [*Cebus*] *apella*), have both demonstrated prosocial behavior in the wild as well as captivity, and in a variety of contexts. One challenge, however, is that prosocial behavior has not been consistent across

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[2] Here we define altruistic behavior as behavior that benefits another with some cost to the actor, while prosocial behavior refers more widely to any behavior benefiting another, regardless of cost.

experimental studies. A possible explanation for this inconsistency is the diversity of designs used to assess prosocial decisions (Cronin, 2012; Marshall-Pescini et al., 2016). Indeed, research including the necessary controls and checks for comprehension suggests that some of the designs either do not measure prosocial behavior or are not understood by the species being tested in the way that the experimenters intended (Amici et al., 2014; Brosnan, 2018; reviewed in; Marshall-Pescini et al., 2016).

Intraspecies differences in prosocial behavior may also be the result of the context within which prosocial decisions are made, particularly the social context. The social dynamics (such as relationship quality and dominance asymmetry) between the actor and the recipient and the overt behaviors of the potential recipient – both immediately before and surrounding a prosocial decision, have been investigated for their possible contribution to intraspecies differences in prosocial behavior (reviewed in Cronin, 2012). More recently, the impacts of experiences prior to the decision have been explored (Leimgruber et al., 2014; Schmelz et al., 2017). Together these factors may be critical to interpreting the results of previous studies and understanding the evolution of prosocial behavior more broadly. Furthermore, these factors are likely interacting with one another in their impact on prosocial decisions and untangling these effects may be essential to elucidating the mechanisms behind prosocial decisions.

Consider the first of these, social dynamics; while prosocial behavior towards strangers is common in humans, one would not expect most people to behave as prosocially towards a stranger as towards their closest friend (Padilla-Walker & Christensen, 2011). Indeed, when children are given an opportunity to share resources, they are more likely to allocate these to friends than to non-friends (Moore, 2009). While this seems intuitive, data from the animal literature does not as clearly support a strong connection between relationship quality and prosocial behavior. Long-tailed macaques (*Macaca fasicularis*) preferentially provided resources to a ‘friend’ over a ‘non-friend’ in a triadic prosocial test, but the effect went away when controlling for dominance. Chimpanzees have also not shown an effect of relationship quality on prosocial decisions (Horner et al., 2011; Schmelz et al., 2017). This is somewhat surprising since if prosocial behavior was motivated by mechanisms related to expectations of future reciprocity, we might expect prosocial acts to occur more within close relationships in which there are increased future opportunities for reciprocation. One challenge to this literature is that these studies typically take place among captive groups with relatively small sample sizes. It is possible that the frequency of interaction (and therefore opportunity for reciprocity) among all pairs swamps the effects of relationship quality.

An additional aspect of the social dynamic that may have an influence on prosocial behavior is the dominance asymmetry between individuals. Most animals establish some form of dominance hierarchy in which higher ranking individuals have priority access to resources (food, mates, locations, etc.), although this can vary dramatically in terms of linearity and strictness. The majority of research has found that dominant individuals tend to be more prosocial to their subordinates than vice versa (Chang et al., 2011; Massen et al., 2010; Takimoto et al., 2010), although others have found no effect of dominance (Jensen et al., 2006; Schmelz et al., 2017) or effects in the opposite direction (Yamamoto et al., 2009). This is somewhat surprising, as you might expect subordinates to behave more prosocially towards dominants with whom they can curry favor (Noë et al., 1991), as is seen for grooming direction (dominant individuals receive more grooming than subordinates; Seyfarth, 1977). Alternatively, food sharing may be a form of honest signaling of the dominant’s status (Massen et al., 2010; Zahavi, 2004). It has also been proposed that dominance effects could be the result of experimental procedures, such that dominant individuals are more likely to approach the apparatus or to expect to gain access to their partner's reward (Cronin, 2012). However, all of these proximate mechanisms remain to be tested. Additionally, while factors like rank and relationship quality undoubtedly could affect prosocial choices, they also likely interact with shorter-tern effects, such as the pairs' interactions prior to the prosocial choice or current affective states, and these interactions may explain some of the inconsistency in the literature.

Furthermore, most prosocial studies allow for communication (intentional or not) between the partner who is the possible beneficiary of a prosocial act and the individual making the prosocial decision. Interestingly, and somewhat counterintuitively, much of the research has found that when recipients indicate interest in the reward, actors *reduce* rates of prosocial behavior (Burkart & van Schaik, 2013; Cronin et al., 2009; Tan & Hare, 2013; but see also: Burkart et al., 2007; Dale et al., 2016; Schwab et al., 2012). It has been hypothesized that this effect may be due to actor's misinterpretation of the task. Recipients reaching towards the reward might be interpreted as an independent solution to obtaining the food, and an indication that the recipient no longer needs the actors help (Burkart & Rueth, 2013). Alternatively, if actors thought they could gain access to both rewards after a prosocial choice, that expectation may be diminished if the recipient is indicating desire for the reward (Cronin, 2012). Moreover, an effect like the latter may be exasperated by social dynamics like dominance; if a dominant individual indicates desire for the reward, this may decrease a subordinate's expectation of accessing that reward more than when a subordinate indicates interest (since dominants may be more likely to assume they can take food from a subordinate). Again, to our knowledge this has not been tested.

There are some indications that there may be species differences in the effects of partner behavior on prosocial choices. For instance, 'direct requests' for prosocial decisions have only been observed in some great ape species, increasing rates of prosocial behavior (Pelé et al., 2009; Yamamoto et al., 2009, 2012). Attention-getting behaviors such as banging on caging have been observed in capuchin monkeys as well as great apes (Takimoto et al., 2010), but only led to an increase in prosocial behavior in the chimpanzees (Horner et al., 2011; Melis et al., 2011). These effects, however, are difficult to review across studies that grouped behaviors differently and found different – and non-comparable results. For example, Horner et al. (2011) found ‘attention-getting’ behavior by the partner to increase prosocial behavior, but inexplicably included self-scratching as a behavior in that category. Takimoto et al. (2010) found cage-banging behavior in the capuchins, but lumped it with several reward-directed behaviors into a ‘begging’ category, and did not find an effect. We urge researchers to clearly outline their rationale for grouping behaviors, and when possible, report on the effects of individual behaviors so that future research can better untangle the effects.

The last context that may be important are the immediate experiences prior to prosocial decisions. This has been only minimally studied in animals, but fairly widely explored in humans – particularly in the developmental literature with regards to gaming contexts (Toppe et al., 2019). Children tend to behave more prosocially during and after playing cooperative games compared to competitive games (Finlinson et al., 2000; Toppe et al., 2019), and increase rates of sharing following collaboration (Hamann et al., 2011). In fact, the effect of cooperative gaming on prosocial behavior is notable enough to be used as an intervention to promote prosocial behavior in children (Garaigordobil & Echebarría, 1995; Toppe et al., 2019). In a comparative study, 2- and 3-year old children, but not chimpanzees, were more likely to share rewards with a partner to make outcomes equal after working collaboratively to obtain the rewards (Hamann et al., 2011). Only one chimpanzee pair was tested in this study, however, and the inequitable outcome following collaboration was the result of a complicated experimental procedure, not the direct result of either chimpanzee's behavior. Thus, the subject may not have felt equitable rewards were 'earned.' Indeed, chimpanzees have been found to assist partners in acquiring food, even at a cost to themselves, when the partner previously provided assistance (Schmelz et al., 2017), and in fact behaved the most prosocial following a scenario in which the partner risked their own reward to provide the assistance. These results indicate that chimpanzee prosocial behavior is impacted by the partners' perceived effort and risk as well.

Capuchin monkey prosocial behavior has not yet been studied in the context of a partner's prior collaboration or assistance, but they, too, are impacted by immediately prior experiences. Following being the recipient of a prosocial act, capuchins behaved more prosocially, while after being passed over for a prosocial opportunity they behaved *less* prosocially, towards a third-party (Leimgruber et al., 2014). This indicates that the effect of such experiences may be due to a general mechanism, such as a give-what-you-get strategy (Leimgruber et al., 2014), and not a direct reciprocation – although research has not compared prosocial behavior towards a third-party to the original actor. Furthermore, these results could also be the result of a simple affective mechanism, from positive or negative affect generated from being the recipient (or not) of prosocial behavior, respectively (Leimgruber et al., 2014). Indeed, the role of affect in prosocial decisions has received little attention in the animal literature, which is particularly surprising given the emphasis placed on such aspects in human research. For instance, it is considered well-established that humans are more generous and helpful when they are in a positive mood (Aknin et al., 2018; George, 1991; Kayser et al., 2010). To our knowledge, however, the effects of affective state (positive or negative) on prosocial behavior has not been explored in any animal model, likely because affect in animal models has barely been explored in general, and positive affect in particular is not well understood (Boissy et al., 2007). Either of these proposed mechanisms for the effect of prior experiences in capuchin monkeys is in contrast with the study on chimpanzees suggesting that there may be more complicated mechanisms involved in decisions, with the partners' role and effort impacting decisions to behave prosocially or not (Schmelz et al., 2017).

To this end, the current study aimed to untangle the effects of the valence of prior experiences (positive or negative outcomes) from the effects of the type of experience (cooperative, competitive, or non-social) and a partner's involvement in the outcome in a way more closely parallel to the human literature. Importantly, we utilized a very similar procedure across the three contexts, allowing for direct comparison of behavior and limiting alternative impacts. Capuchin monkeys are an interesting species to test because there have been observed effects of prior experiences on their prosocial behavior (Leimgruber et al., 2014) and they have widely demonstrated prosocial tendencies across multiple paradigms (Drayton & Santos, 2014a; Lakshminarayanan & Santos, 2008; Suchak & de Waal, 2012), but research has not yet investigated how a partner's specific role in a prior interaction may influence behavior.

To test prosocial choices, we adopted a variation on the platforms prosocial choice task (Jensen et al., 2006; Lakshminarayanan & Santos, 2008; Silk et al., 2005), in which subjects choose between the option of a platform that delivers food rewards to themselves and a partner (1/1; prosocial option) or just to themselves (1/0; selfish option). To control for biases in sitting closer to (or further away from) the partner, we adopted a novel methodology in which subjects connected a metal rod to magnets along the length of their preferred platform (allowing for prosocial and selfish choices from both far and close, respectively). Furthermore, this addition was expected to slow down decision-making and reduce biases towards grabbing the first pre-positioned bar seen (Girndt et al., 2008).

We predicted that capuchins would make more prosocial decisions following a positive experience (obtaining a food reward; regardless of context) compared to following a negative experience (failing to obtain an available reward). We also predicted that both positive and negative *social* experiences would have a greater impact on prosocial behavior than positive/negative non-social experiences if subjects were accounting for partner involvement. Finally, we predicted that capuchin prosocial behavior would be impacted by and interaction of the partner's role in the experience and the outcome. Specifically, we predicted the highest rates of prosocial behavior would be directed towards partners who had just helped bring about a cooperative outcome, and the lowest rates directed towards partners who had just outcompeted the subject for a reward in the competitive scenario.

An additional goal of the study was to contribute to the literature on the impacts of the animals' relationships, particularly regarding the dominance asymmetry and relationship quality between the subject and partner, and partner behavior on prosocial decisions. Since the literature on this is quite varied, particularly between species, this aspect of the study was intended to be more exploratory. While consistent effects of relationship quality have not been found, we predicted that if relationship quality influences prosocial choices, it would be such that rates of prosocial behavior are higher towards individuals in higher quality relationships. We did not have any specific predictions on the effects of dominance. The literature most often indicates dominants behave more prosocially to subordinates than vice versa, but the results have been mixed, and the mechanism behind such effects is unknown. Finally, we also did not have any specific predictions about how partner behavior would impact prosocial decisions. The literature would indicate that reward-directed behavior may decrease prosocial choices, while attention-getting behaviors might increase prosocial behavior, but neither effect has been found in capuchin monkeys.

3 METHODS

3.1 Subjects

Subjects included nine adult capuchin monkeys (4 male, 5 female) from five different social groups housed at the Language Research Center (LRC) at Georgia State University. All subjects were raised in captivity and housed in social groups with indoor and outdoor access and environmental enrichment (climbing structures and other toys). All subjects had ad libitum access to water, received a daily diet of fruits, vegetables, and primate chow (regardless of the day's testing), and received peanuts, grapes, and apples as supplemental food for participation in this study.

Each subject was tested with a designated partner for the duration of the study (5 additional monkeys: 4 females, 1 male). Designated partners were assigned to rule out any effects of possible reciprocity in the study (partners did not become subjects and no subject had prior experience as a partner). The designated partner acted as such for the all the subjects in their group, to limit the number of possible subjects automatically eliminated from our subject pool to one per group (Table 2). Designated partners were chosen based on the following factors when possible; the partner was of middle rank, the partner was not mother or offspring of any of the subjects, and the partner readily entered the joint testing box. Not all of these factors were possible for each group. The exceptions are; in Griffin's group, Lily (partner) is the highest ranking female, and in Gabe's group, Atilla (subject) is the offspring of Applesauce (partner). These exceptions were made due to a lack of alternatives that fit more criteria for the designated partner.

Table 2. Subject and partner designations with the pairs' composite sociality index as a measure of relationship quality, and dominance status relative to their partner (either dominant

or subordinate to the partner). CSI's ≥1 reflect stronger affiliative relationships with scores ≤1 reflecting weaker relationships.

Group	Subject	Partner	CSI	Dominance
Logan				
	Ivory	Paddy	0.67	Dominant
Griffin				
	Griffin	Lily	1.23	Dominant
	Wren	Lily	0.36	Subordinate
	Widget	Lily	0.85	Subordinate
Nkima				
	Nkima	Gambit	1.52	Dominant
	Nala	Gambit	0.95	Dominant
	Lychee	Gambit	0.12	Subordinate
Liam				
	Liam	Albert	-	Dominant
Gabe				
	Atilla	Applesauce	0.33	Dominant

3.2 Dyadic Composite Sociality Index

A Dyadic Composite Sociality Index (CSI) was calculated for each pair as a measure of the strength of their affiliative relationship (Silk et al., 2013; Silk et al., 2006) using the following formula where *d* is the number of behaviors used to calculate the scores (in this case 3; grooming, contact, and proximity behavior), f_{ixy} is the rate of behavior *for the dyad*, and *fi* is the rate of behavior across *all* dyads in the group:

$$DSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{f_i}}{d}$$

Using this formula, each dyad was assigned a number between 0 and infinity, with higher values representing dyads with more affiliative behavior relative to their group, and thus as a stand-in measure of relationships of higher quality (Table 2). The average CSI is 1, and anything greater than 1 represents dyads that have a stronger affiliative relationship than average in the group (Kalbitz et al., 2016).

Affiliative data were collected during routine observational group scans. State behavior of all subjects was recorded at 3 min increments over the course of 30-minute scans. Specifically for the current use, every 3 minutes it was recorded whether subjects were grooming, in contact, or in proximity (approximately a monkey's arm reach) with another individual in their social group. Scans were recorded using an in-house application on Kindle Fires (WhatsOb; Watzek & Brosnan, 2016). These routine scans were typically conducted at minimum once per week, however due to research restrictions during the 2020 Covid-19 pandemic, there is a period during which scans were less frequent. All scans collected six months prior to the start of data collection and through the period of data collection were included, resulting in a total of 33 scans for Logan's group, 31 scans for Griffin's group, 32 scans for Nkima's group, and 36 scans for Gabe's group. We could not calculate a CSI score for Liam and Albert, as the pair-housed subjects are not part of the routine observations.

3.3 Dominance

Rank determinations could not be calculated from the observational data, as agonistic encounters were far too infrequent. Instead, two alternative, independent measures of dominance were obtained.

3.3.1 "Peanut Test"

To determine the relative rank of subjects within our pairs, specifically in a food context, a 'peanut test' was conducted to assess which individual in the pair has priority access to food. To measure this, subjects entered the joint box with their partner and were moved to a single side together, *not* physically separated from one another. The pair was then simultaneously presented with a single peanut on a tray. The peanut was displayed out-of-reach for five seconds before being moved towards the enclosure, and which individual obtained the peanut was recorded. Pairs experienced three sessions with four trials each for a total of 12 measures of dominance. All subjects considered dominant to their partner (Table 2) obtained the peanut on at least 10/12 peanut tests. One partner, Lily, chose not to separate into the joint box after testing so we were unable to run the peanut test for the pairs in Griffin's group. Results from the rank survey (see 3.3.2, below) for these pairs were 100% in agreement, however, so the rank determination from the survey was used alone.

3.3.2 Rank Survey

As an alternative measure of dominance, individuals (researchers and care staff) that frequently worked closely with the monkeys were surveyed for their opinions of dominance based on their regular observations (see Appendix A for example questionnaire). Individuals were asked to indicate which monkey within a pair they would consider dominant and provide a rating of their confidence of their judgment (on a scale of 1-7). If a rater was uncertain for a particular pair or had not been closely working closely with that group recently, they were asked not to rate that pair. In all pairings, the data from this survey corresponded with the dominance rating that came from the peanut test.

3.4 General Procedure

Subjects were presented with 12 test sessions, two of each experimental condition (see Table 3), and four control sessions for a total of 16 sessions. During each session, subjects entered a joint testing box with their designated partner (or alone for the partner-absent control and knowledge-test sessions). Subjects and partners were separated within the joint box by a clear barrier with small holes (approximately 2.5 inches in diameter) that allowed for visual, vocal, and limited tactile contact through the holes. Prosocial testing was preceded by various experimental manipulations involving the opportunity for subject and partner to engage in either a competitive, cooperative, or nonsocial task, rigged for a predetermined outcome (successful or failed acquisition of a food reward), depending on condition. Following this task, the *subject* was presented with a solo, no-cost prosocial task (12 trials), in which they chose between two reward distributions (Figure 2); one where both they and their partner got a high value reward (apple slices; 1/1) and one where only the subject got a reward (1/0). The subject received the same reward regardless of which tray they pulled on every trial. Choices during the prosocial task were recorded live, and all sessions were video recorded for inter-rater reliability assessments and behavioral coding.

Table 3. Experimental conditions and descriptions of the outcomes for the subject and their partner

		Descriptive Outcome	
Task	Outcome	Subject	Partner
Cooperation	+	Obtained food reward	Obtained food reward
	-	Did *not* obtain food reward	Did *not* obtain food reward
Competition	+	Obtained food reward	Did *not* obtain food reward
	-	Did *not* obtain food reward	Obtained food reward
Non-Social	+	Obtained food reward	No reward possible
	-	Did *not* obtain food reward	No reward possible

Subjects experienced all four sessions of each experimental task manipulation (competitive, cooperative, or non-social) in succession. To control for possible order effects of the task, task presentation was randomized between subjects. To control for the effects of outcome (successful or failed reward acquisition, +/- *for the subject*), outcome presentation was pseudo-randomized between subjects so that half the subjects experienced the positive outcome of each task first and the other half experienced the negative outcomes first.

In addition to the test sessions following the experimental manipulations, subjects were also presented with four control sessions; a satiation control, two partner-absent controls (or solo controls), and a knowledge-probe control (see Figure 1). All subjects experienced the satiation control before the onset of any testing sessions. In this control, the session proceeded identically to test sessions (general procedure described above), but instead of experiencing an experimental task prior to prosocial testing, subjects were gifted directly with three half grapes (the same reward as the positive outcomes for the various tasks). The two partner-absent controls (or solo controls) were interspersed between the three experimental testing conditions. While these controls are often included at the start or end of an experiment, the inclusion or more than one solo control presented throughout testing limited the possibility that differences between the control and test conditions could be attributable to testing experience. In the partner-absent controls, subjects entered the joint-testing box alone, and were presented with the same prosocial choice options as in testing but with no partner present (subjects were *not* able to access extra rewards; 12 trials). Finally, a knowledge-test control was included at the end of testing for all subjects. In this session, subjects again entered the joint box alone; however, in this control they had access to *both* the subject side and the recipient side of the joint box. Thus, if subjects selected the ‘prosocial’ option, they would have access to two rewards instead of one (12 trials). This control was included to assess whether subjects understand the task contingencies.

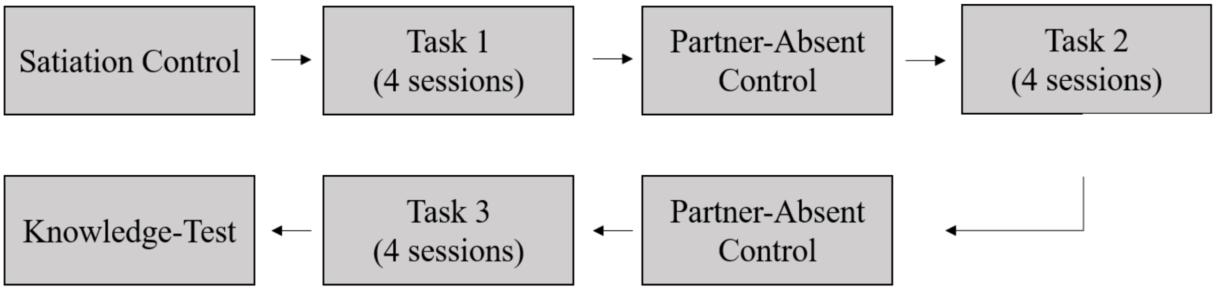

Figure 1. General order of session presentation
Note: Order of task presentation randomized by subject

3.5 Behavioral Measures

All sessions were video recorded for later behavioral analysis. Both subject and partner behavior was analyzed independently. Data was collected for rates of scratching, urine-washing, body shaking, stereotypic behavior, threatening (each other, the experimenter, or other), attention-getting (variations on cage-banging, see Appendix B), reaching towards the reward, reaching towards their partner, grabbing the tray, and pulling behavior. Locations were recorded for choices in the prosocial task (subjects only) and feeding behavior (see Appendix B for complete ethogram of behavior). Behavior was recorded using the BORIS behavioral annotation software (Friard & Gamba, 2016). To increase power and reduce the number of analyses run, scratching and body-shaking were grouped together into a ‘displacement’ behavior category. This is consistent with the literature (Maestripieri et al., 1992; Troisi, 2002) and supported by our results indicating a significant correlation between scratching and body-shaking for both the subject (r = 0.373, p < .001) and partner (r = 0.374, p < .001). We also grouped reaching for the reward and tray grabbing behavior, as they were very similar motions (both involved extending the arm towards the reward) and were significantly correlated for both the subject (r = 0.25, p = .002) and partner (r = 0.37, p < .001). Finally, we eliminated any behaviors that were extremely low occurring from analyses (if they were displayed less than five times across all sessions by the majority of the individuals, which we defined as at least 5/9 subjects or 3/5 partners). This eliminated from future analysis reaching for the partner, urine-washing, stereotypic, and threatening behaviors for the subjects, and reaching for the subject, stereotypic, and threatening behaviors for the partners. All of the behaviors eliminated based on these criteria were found to never be observed in some of the monkeys, and even those that were occasionally displayed (less than five times across 16 sessions for more than half of the subjects/partners) meant there were too many zero cells to run meaningful analyses.

Twenty percent of the videos were double-coded by a second rater blind to the study's hypotheses to establish inter-rater-reliability. IRR was calculated for each behavior using correlations between the number of observed behaviors observed per session indicated by the primary experimenter compared to the IRR coder. IRR is reported for each behavior in the Results section.

3.6 Prosocial Task

3.6.1 Apparatus

Figure 2. Experimental setup for the prosocial task

The prosocial choice task (PC) apparatus consisted of four identically sized wooden trays connected to sliding rails upon a movable platform/table (Figure 2). Each of the trays was connected to another tray (A to B and C to D), such that when tray B or C was moved forward or backward the connected tray moved congruently. The apparatus was like a bar pull setup that subjects were already familiar with, but instead of having a permanently attached bar, the apparatus was moved via a detachable tool connected by strong magnetic strips (Figure 2). The magnetic strips were placed along two of the trays (trays B and C, Figure 2) on both the top and the bottom, so subjects could either place the bar on top of the tray or slide it underneath to make the connection. During testing, subjects were given the tool and allowed to reach for one of the trays. Once the magnet attached to a tray, the subjects were able to pull the selected tray (and rewards) within reach. This methodological consideration was included in an effort to increase subjects' attention to the options available to them. Additionally, placement of the magnetic strips along the entire length of both the option trays (and underneath) allowed subjects to have a wide range of distance from their partner's enclosure from which to select their preferred tray, to ensure selection was not based on preferred proximity to their partner.

3.6.2 Training – Prosocial Task

3.6.2.1 Training A

Subjects were first trained on how to use the magnetic tool. The experimenter baited a single tray (B or C) in view of the subject, and then attached the tool to the magnetic strip and allowed the subject to pull the apparatus towards themselves to retrieve the reward. During the first session, the experimenter attached the tool for the subject (while they watched) on the first two trials, and then handed the subject the tool for the remaining 10 trials (12 total). Subjects were given 1 minute to pull in the tray and retrieve the food reward using the tool. During this first session, if the subject was unable to retrieve the food after 1 minute on any of the trials, the experimenter would shape the subject towards the proper behavior (i.e., after 1 minute the experimenter would connect the tool to the tray and give the subject another 30 seconds to pull it in). Due to unexpected difficulty with the tool during this first session, an additional training step was added to facilitate subjects' learning to use the tool.

During these Training A sessions, the two tray options (B and C) were randomly baited and the tool was balanced between the joint box faceplate and the platform between the two trays such that subjects only had to push the tool towards their chosen tray for it to connect and be able to pulled in to retrieve the reward (subjects had no trouble learning to pull the tray in once the bar was connected, they only had difficulty with manipulating the tool). This training was gradually built up until the tool could be handed to subjects in the manner of testing (passed to subjects from the back of the caging) and the tray was successfully pulled in. The side of the joint box that the apparatus was pushed up to was alternated between sessions. Subjects passed Training A if they successfully manipulated the tool to the correct tray (the one baited with food) on 10/12 trials over two consecutive sessions. Subjects took, on average, 9.8 ± 5.2 sessions to pass Training A.

3.6.2.2 Training B

After the initial tool training, subjects were then presented with two additional forms of training to ensure they understood the PC apparatus contingencies. During Training B one of the four trays (only the accessible ones) was randomly baited. Subjects were alone in the joint box and able to access both sides of the enclosure and had 30 seconds to use their tool to select one of the trays. The side of the joint boxed that the apparatus was pushed up to was alternated between sessions. Subjects reached criterion if they pulled the correct tray (tray B if A or B was baited or tray C if C or D was baited) on 10/12 trials over two consecutive sessions. It took subjects, on average, 4.3 ± 2.2 sessions to pass Training B (it took a minimum of two sessions to pass).

3.6.2.3 Training C

In the final type of training sessions, subjects were again alone in the joint box with access to both sides of the enclosure. This time, however, all four trays were baited on every trial. Subjects had 30 seconds to make a selection and passed training if they successfully pulled the ‘prosocial’ tray (the inside tray, which differed depending on which side of the joint box the apparatus was positioned and resulted in two rewards instead of just one) on 10/12 trials over two consecutive sessions. The side of the joint boxed that the apparatus was pushed up to alternated between sessions. This training was to ensure that subjects understand that pulling the prosocial tray moved two rewards within reach of the joint box, and that rewards on the outside tray were never accessible. It took subjects, on average, 12.7 ± 8.1 sessions to pass Training C. The knowledge-test control at the end of testing mimicked this training identically to ensure that subjects maintained their understanding of the task contingencies throughout testing, and to match the literature (knowledge-tests such as this are often included after testing as a check of comprehension). Training was included to demonstrate subjects understood *before* testing to prevent loss of data that would occur if subjects did not demonstrate comprehension after-the-fact.

3.7 Cooperative Task

3.7.1 Apparatus – Cooperative Task

Figure 3. Experimental setup for the cooperative task

The cooperative task apparatus consisted of two connected trays on sliding rails placed on a moveable table (Figure 3). Attached to the center of each tray was a rope. The tray was weighted such that (except for in training), subjects were unable to pull the tray in alone. Once subjects and their partner pulled the tray into arm-reach distance, the tray would lock into place so that the monkeys could reach the rewards on the colored plates without maintaining tension on the ropes. The apparatus for this task was chosen because capuchin monkeys are very good at working together to achieve rewards using similar apparatuses (Brosnan et al., 2006, 2010; Claidière et al., 2015; Lakshminarayanan & Santos, 2008). Using ropes to pull in the platforms as opposed to the often-used bar-pull was selected to increase the difference between the prosocial and experimental tasks.

3.7.2 Training – Cooperative Task

Subjects were trained on the cooperative rope-pull alone in the joint box, with access to both sides of the enclosure. Subjects were not expected to require much training, as all participants had extensive experience using both rope and bar-pull apparatus and had already been trained on the prosocial bar-pull. Training was included, however, to ensure that subjects understood the task.

Training sessions consisted of 12 trials. On each trial, subjects watched as one side of the apparatus (randomly determined) was baited with a high-value food reward (grape half). The apparatus was then pushed towards the subject and two ropes were simultaneously extended towards the center of each side of the enclosure. The subject was given 1 minute to pull either rope towards the cage, moving the tray to within reach. If the subject successfully pulled the tray and retrieved the reward on 10/12 trials, they passed training. All subjects passed training during their first session. Before testing, subjects were also presented with one social experience with the apparatus. For the cooperative task, the apparatus was baited such that subjects required their partner’s strength to pull the tray in, and they had one minute to cooperate to do so for 12 trials. All pairs were successful on at least 10/12 trials.

3.7.3 Testing – Cooperative Task

Test sessions followed the general procedures outlined above. After entering the joint testing box, subjects and their partner were presented with the cooperative apparatus for a single high value reward trial. Both sides of the apparatus were baited with the same high value food reward (3 grape halves) in full view of both individuals. Ropes were then simultaneously handed to both monkeys in the center of their respective testing areas, and they had 1 minute to cooperatively pull the apparatus in, resulting in a food reward for both individuals. On no sessions in which cooperation was possible did the subject and partner fail to retrieve their rewards. In the planned unsuccessful cooperation sessions, the apparatus was weighted such that even with both monkeys pulling they were unable to move the tray all the way towards the test box, and a lock was placed that prevented the trays from moving all the way forward. The pair had 1 minute to attempt the (impossible) cooperation before the apparatus was pulled away and the food rewards were removed. Immediately following the cooperative task, the apparatus was removed and replaced by the prosocial apparatus for testing to proceed.

3.8 Competitive Task

3.8.1 Apparatus – Competitive Task

Figure 4. Experimental setup for the competitive task

To maintain consistency, the competitive task apparatus was the same as the cooperative task apparatus with a few key changes. For the competitive task, the latch connecting the two trays (which made it move forward or back as a single unit in the cooperative task) was removed, and the trays were connected via a pulley system such that when one of the trays was pulled toward the caging the other tray moved away from the caging the equivalent amount. Therefore, if the monkeys were both pulling, they were pulling against one another. Additionally, the colors of the ropes and the plates on which the food rewards were placed were different (Figure 4).

3.8.2 Training – Competitive Task

As in the cooperative task, subjects were not expected to require training, but underwent one session to be certain of high rates of pulling behavior. Subjects were trained by themselves after entering the joint test box alone with access to both sides of the enclosure. Sessions consisted of 12 trials. On each trial, subjects watched as one side of the apparatus (randomly determined) was baited. The apparatus was then pushed towards the subject and ropes were placed in the center of both sides of the joint box simultaneously. Subjects were given 1 minute to select a rope to pull towards the cage and move a tray to within reach. If they pulled the rope connected to the tray that was baited towards the cage, the tray locked into place allowing subjects to retrieve the food reward. If they pulled the rope on the side of the tray that was not baited, it would similarly move towards the enclosure and lock, and subjects were not able to access to the reward on that trial (unless they switched sides before the tray was pulled all the way into the lock position, in which case they were still free to attempt to reach the reward). Once the tray locked into position the subject was not able to change their decision. If the subjects successfully pulled the baited tray and retrieved the reward on 10/12 trials, they passed training. All but two of the subjects passed training on their first session. Two subjects (Paddy and Ivory) passed training on their second session. Before testing, subjects were also presented with one social experience with the apparatus. For the competitive task (12 trials), subjects were allowed to compete naturally using the apparatus, such that the winner of each trial was not predetermined. In all pairs both the subject and the partner were successful on some of the trials.

3.8.3 Testing – Competitive Task

Test sessions followed the general procedures outlined above. For the competitive task specifically, after entering the joint test-box, subjects and their partner were presented with a single trial with the competitive apparatus. Both sides of the apparatus were baited with the same high value food reward (3 grapes halves) in full view of both individuals. Ropes were then simultaneously handed to both monkeys in the center of their respective testing areas. In positive competition sessions, the apparatus was manipulated such that the partner’s tray was blocked from being pulled all the way in. This allowed the subject the chance to pull their tray in fully (until it latched) and ‘win’ the competition. In the negative competition sessions, the apparatus was manipulated in the reverse way, such that it was the subjects’ tray that was blocked from being pulled all the way in. In all testing sessions both the subject and the partner pulled on their ropes and engaged in ‘competition,’ and the winner proceeded as was outlined by the condition.

3.9 Non-Social Task

3.9.1 Apparatus – Non-Social Task

Figure 5. Experimental setup for the non-social task

The non-social task apparatus was identical to the cooperative and competitive apparatus, but the apparatus was manipulated to only have a single tray (Figure 5). The tray was weighted such that it was somewhat challenging, but possible, for each subject to pull the tray towards their caging and reach the food reward by themselves. Both rope and plate upon which the rewards were placed were unique from the cooperative and competitive conditions.

3.9.2 Training – Non-Social Task

Subjects had experience with multiple variations of this rope-pull paradigm and were thus not expected to require any training for this task. Subjects were presented with one session of 12 trials to ensure understanding when presented with the solo task. Subjects had 1 minute per trial and passed training if they successfully retrieved the reward on 10/12 trials. All subjects passed on their first session. Before testing, subjects were also presented with one ‘social’ experience with the apparatus (their partner was present but uninvolved), so they could see that the task did not involve their partner. All subjects successfully retrieved their food rewards on 12/12 trials.

3.9.3 Testing – Non-Social Task

Test sessions followed the general procedure outlined above. After entering the joint box with their designated partner, subjects were presented with the non-social task alone (their partner was present but uninvolved). If it was a positive outcome session, subjects were presented with the apparatus with no intervention. In the negative outcome sessions, subjects were given 1 minute to complete the task, but the apparatus was weighted so that it could not be pulled in by the subject alone, and thus the food remained out of reach. After the minute was up, the apparatus and food reward were removed, and the session proceeded to the prosocial test.

3.10 Data Analysis

All statistical analyses were run in R version 3.6.0 (R Core Team, 2019) and figures were produced using the package ggplot2 (Wickham, 2016). Model analyses were conducted using the *lme4* package (Bates et al., 2014). All models were compared using the Akaike information criterion (AIC) to determine best-fit models, and P-values were calculated by using likelihood ratio tests comparing full models with fixed effects to a null model with just the random effects.

Estimated marginal means were calculated using the *emmeans* package (Lenth, 2021) to make specific pairwise contrasts and obtain odds ratios between the different variables and their interactions.

Subjects' choices in the prosocial task were recorded live (and later confirmed from video) as either prosocial (selecting the 1/1 option) or selfish (1/0 option). First, to assess whether subjects demonstrated knowledge of the contingencies of the task, I compared subjects' proportion of prosocial responses in the knowledge test control (in which subjects could double their reward if they selected the 'prosocial' option) to the two control conditions and the testing sessions collapsed together. I ran a generalized linear mixed model (GLMM) with proportion of prosocial responses as the dependent variable (DV). Condition (knowledge test, partner absent control, satiation control, and testing sessions) was entered as a fixed effect, and subject ID entered as a random term to account for repeated measures. I then compared this model to a null model (which included only the random effect) using a likelihood ratio test and used package *emmeans* to make pairwise comparisons between the conditions.

Next, to determine whether the proportion of prosocial responses changed over time (across sessions), I ran a GLMM with proportion of prosocial responses as the DV and session entered as a fixed effect, with subject ID as a random effect. Since this effect was significant, session was included in the 'null' model for the rest of the model comparisons.

To determine whether the experimental manipulations impacted prosocial responses, I ran a GLMM with proportion of prosocial responses as the DV, session, outcome, task, and an interaction term (outcome*task) entered as fixed effects, with subject ID as a random effect.

To investigate the effects of the social dynamics on prosocial behavior I ran separate GLMMs with proportion of prosocial responses as the DV, and either dominance (whether the subject was dominant or subordinate to their partner) or relationship quality (CSI score) as fixed effects, with subject ID as a random effect. Models were kept separate because they were based on slightly different datasets (since a CSI score could not be calculated for one pair - Liam/Albert). Additionally, to investigate whether the social dynamics influenced prosocial behavior as a factor of the prior experiences, I constructed models with three-way interaction terms with the social factor (relationship quality & dominance) and task*outcome. I then reduced the models down to only the significant terms. Pairwise comparisons of the significant terms were calculated using the package *emmeans*.

Next, to examine the effects of partner behaviors on subjects' prosocial decisions, I ran a series of GLMMs with proportion of prosocial responses as the DV and subject ID as a random effect, with the rates of partner behaviors (attention-getting and reward-directed behavior) and their interaction terms with task and outcome (as well as a three-way interaction with task*outcome). I compared the null model to a simple model with only main effects and the full model with interactions for each behavior, and then reduced the models down to only the significant terms.

To examine whether the display of any behaviors by the *subject* were significant predictors of their prosocial choices, a series of GLMMs were run with the same terms as the partner-behavior analyses, but with rates of subject behavior as fixed effects instead (attention-getting, reward-directed, and displacement behaviors) and all their possible interaction terms, and the models were reduced to their best-fit.

A final, best-fit model for predicting prosocial behavior was constructed combining all the significant terms from the previous analyses. This was then compared to a null model and each of the previously significant models for predicting prosocial behavior to find the best model with the lowest AIC.

Finally, to examine how the experiences influenced both subject and partner behavior (particularly their displacement behavior, indicative of negative affect), I ran a series of GLMMs comparing rates of subject and partner displacement behaviors (each independently as a DV), with subject ID as a random effect, task, outcome, and their interaction term (task*outcome) as fixed effects, as well as dominance and its interaction terms, and the proportion of prosocial responses by the subject as fixed effects (the last one being only applicable when looking at rates of *partner* behavior). These were all reduced down to best-fit models with only significant terms.

4 RESULTS

4.1 Influences on Prosocial Behavior

4.1.1 Controls

Comparing the controls and testing sessions, there was a significant effect of condition (knowledge test, partner absent control, satiation control, testing sessions) on the rate of prosocial choices made by subjects ($\chi^2(3) = 69.92$, $p < .001$; Figure 6). Subjects demonstrated understanding of the apparatus contingencies, maximizing personal reward in the knowledge test. On average, comparing the control conditions and the collapsed testing sessions, subjects chose the prosocial option at a higher rate in the knowledge test (9.56 ± 0.44) than the partner-absent controls (6.89 ± 0.90, β = 1.07, t = 3.85, *p* < .001), satiation control (3.33 ± 1.31, β = 2.40, t = 7.36, *p* < .001), and testing sessions (5.84 ± 0.34, β = 1.44, t = 5.84, *p* < .001). Rates of prosocial behavior in the satiation control were also significantly lower than the partner absent solo controls (β = -1.33, t = 5.07, *p* < .001) and the testing sessions (β = -0.96, t = -4.22, *p* = < .001), but rates of prosocial behavior did not significantly differ between the testing sessions and the partner absent controls (β = -0.37, t = 2.41, *p* = .075).

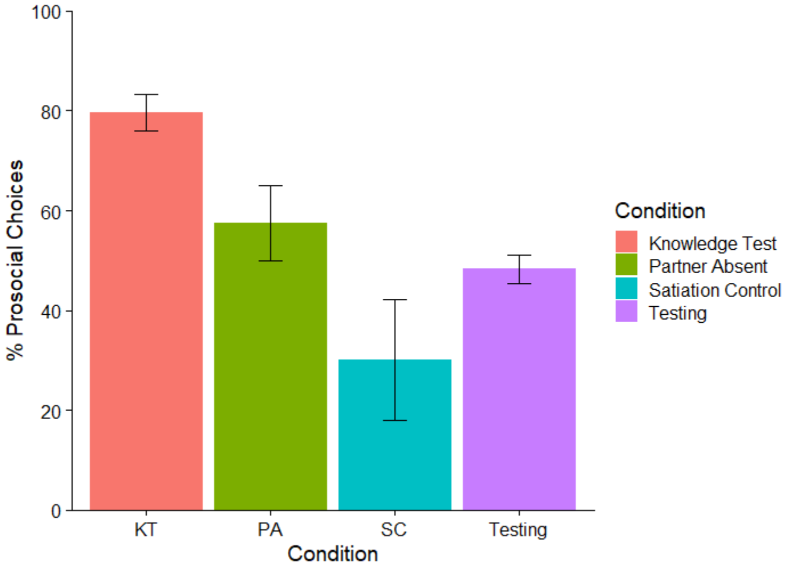

Figure 6. Percent of prosocial choices across the control conditions and collapsed across the testing sessions. Error bars reflect SEM

4.1.2 Prior Experience

Session number was a significant predictor of prosocial choices ($\chi^2(1) = 6.99$, $p = .008$). Over the course of the testing sessions, subjects' rates of prosocial behavior increased (β = 0.04, t = 2.64, $p = .008$; Figure 7). All additional model comparisons were thus compared to a 'null' model that included session as a fixed effect.

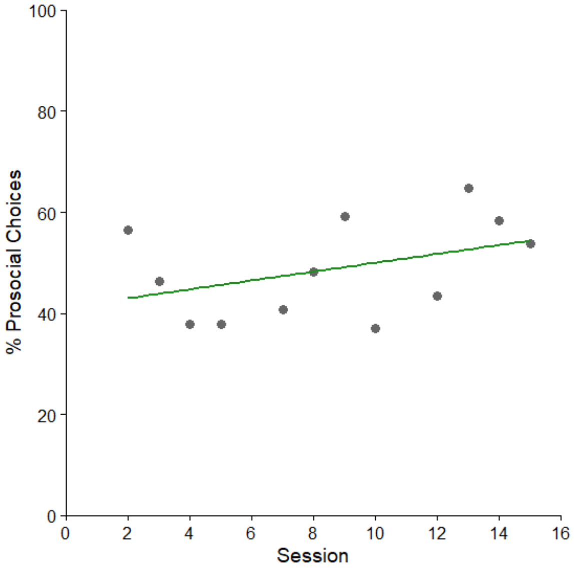

Figure 7. *Average percent of prosocial behavior across the testing sessions. Control sessions (sessions 1, 6, 11, and 16) were excluded from this graph and the accompanying analyses.*

Comparing rates of prosocial choices between the testing conditions, prosocial behavior did not significantly differ across the conditions, revealing no significant effect of task (cooperative, competitive, and non-social; $\chi^2(2) = 0.10$, p =.950), outcome (positive and negative; $\chi^2(1) = 2.52$, p =.112), or an interaction between task*outcome ($\chi^2(5) = 7.11$, p =.213; Figure 8).

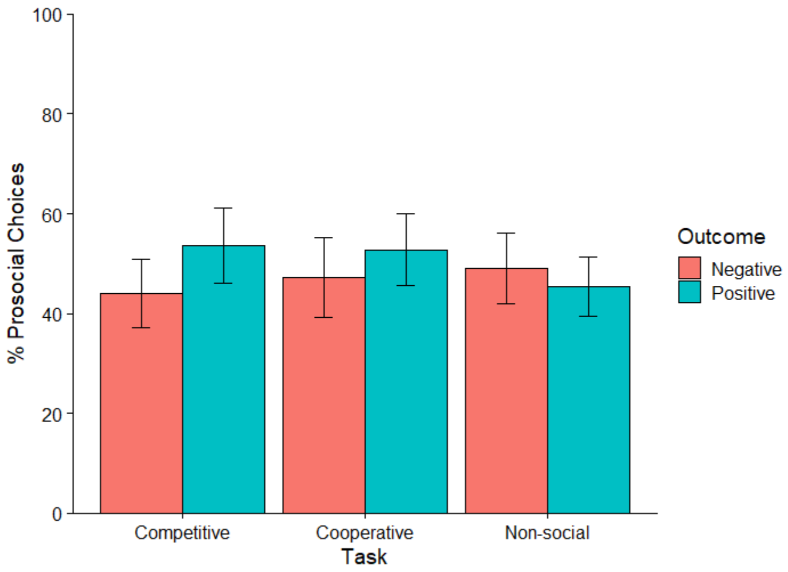

Figure 8. Percent of prosocial choices in the testing conditions, collapsed across all subjects. Error bars reflect SEM.

4.1.3 Social Dynamics

4.1.3.1 Dominance

Dominance alone did not have a significant effect on prosocial behavior ($\chi^2(1) = 1.42$, $p = .234$), and models with two- and three-way interactions with task and outcome were not significantly better than a null model (two-way model; $\chi^2(12) = 13.44$, $p = .144$, three-way model; $\chi^2(11) = 16.16$, $p = .139$).

4.1.3.2 Relationship Quality

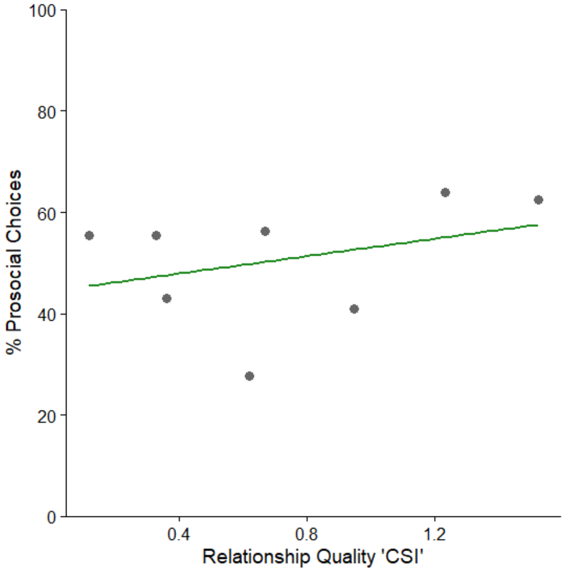

Figure 9. Plot of the average prosocial responses as a factor of their relationship quality as indicated by a composite sociality index (CSI) score.

Relationship quality alone was not a significant predictor of prosocial behavior ($\chi^2(1) = 0.99$, $p = .321$; Figure 9), and models with two- and three-way interactions with task and outcome were not significantly better than a null model (two-way model; $\chi^2(9) = 6.51$, $p = .688$, three-way model; $\chi^2(11) = 7.34$, $p = .771$).

4.1.4 Partner Behavior

There was no main effect of attention-getting behavior (IRR; r = .99) by the partner on the subjects' prosocial choices ($\chi^2(1) = 3.19$, $p = .074$). There was, however, a significant two-way interaction effect of partner attention-getting behavior with the prior task ($\chi^2(2) = 24.06$, $p < .001$) in predicting prosocial behavior (Figure 10), but this was not improved by a three-way interaction ($\chi^2(3) = 4.41$, $p =.220$).

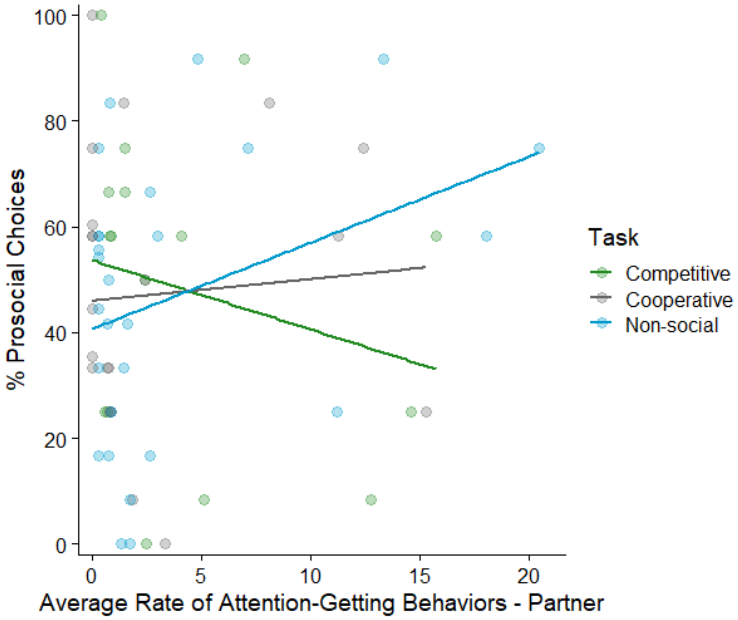

Figure 10. Graph depicting the two-way interaction between partners' attention-getting behavior and task for predicting prosocial choices.

Additionally, there was a significant three-way interaction between partner rates of reward-directed behavior (IRR; r = .88), task, and outcome (reward-directed*task*outcome; $\chi^2(11) = 97.10$, $p < .001$; Figure 11), that was not improved by reducing to the two-way interactions. Together, these results indicate that the effect of the partners’ behavior (both attention-getting and reward-directed) on subject prosocial choices was dependent on both the prior tasks and outcomes, however, we urge caution in interpreting complicated two- and three-way interaction with limited data points.

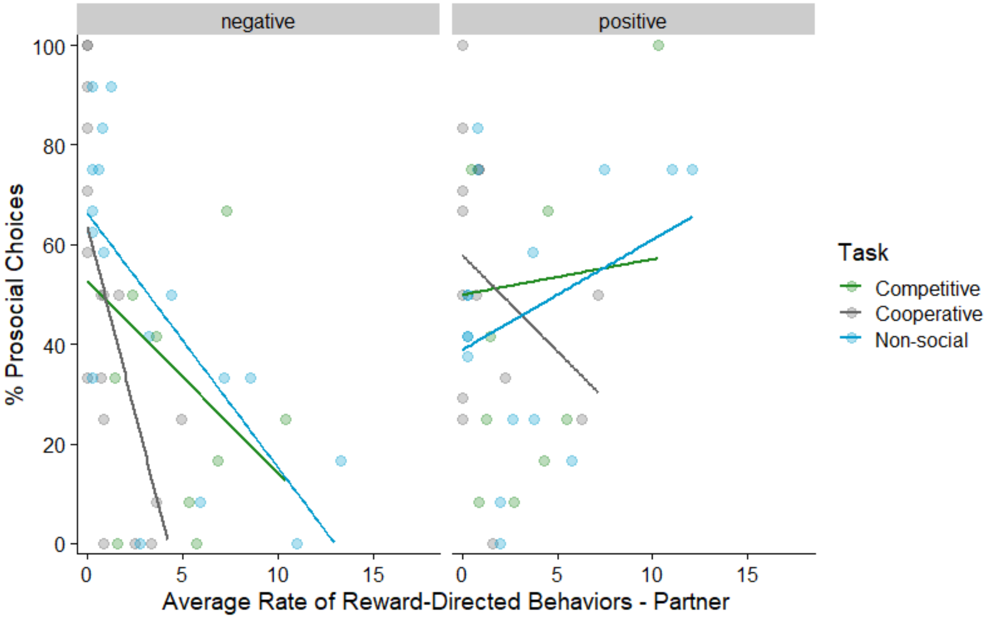

Figure 11. *Graph depicting the three-way interaction between partners' reward-directed behavior, task, and outcome.*

4.1.5 Subject behavior

The rate of subject displacement behavior (IRR; r = .99) was significantly related to prosocial behavior ($\chi^2(1) = 10.12$, $p = .001$), that was not improved by any interaction effects ($\chi^2(10) = 6.55$, $p = .767$). As rates of displacement behaviors increased, prosocial behavior decreased ($\beta = -0.07$, $t = -3.17$, $p = .001$; Figure 12).

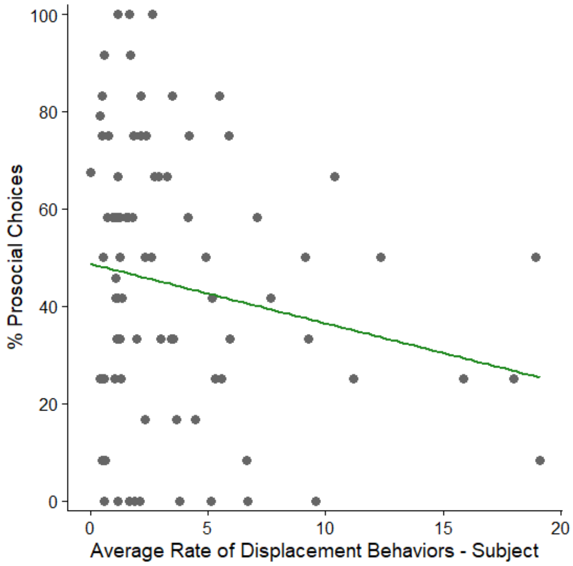

Figure 12. Relationship between average rates of displacement behavior displayed by the subject and their average prosocial choices.

4.2 Best overall model

A full model including all of the significant terms from the models listed above was compared to each previous models, and found to be the best-fit model, significantly improving predictions of prosocial behavior compared to any of the others ($\chi^2(15) = 124.17$, $p < .001$). This full model included the average rate of subject displacement behaviors and session as fixed effects, as well as partner attention-getting*task and partner reward-directed behavior*task*outcome interaction terms, controlling for subject ID as a random effect (Table 4). These results indicate that each of these fixed effects individually contributes significantly to overall predictions of prosocial behavior.

Table 4. Comparison of the significant models used to predict prosocial behavior

Model	Df	AIC	χ^2	*p*
Null (with session #)		751.31		
Displacement model (subject displacement behavior)	1	743.19	10.12	.001*
Partner behavior model (reward-directed*task*outcome + attention-getting*task)	13	659.00	110.18	<.001*
Full model (all the above terms)	1	657.13	3.87	.049*

*indicates significance at p-value of <.05a

4.3 Effects of Prior Experiences on Displacement Behavior

4.3.1 Subject behavior

A model predicting rates of displacement behavior by the subject (as the DV), revealed significant two-way interactions between task and dominance ($\chi^2(2) = 7.12$, *p* = .028; Figure 14) and a trending interaction between task and outcome ($\chi^2(2) = 5.87$, *p* = .053; Figure 14). These results suggest that following the different tasks (competitive, cooperative, and non-social), subject rates of displacement behavior (commonly used as a behavioral indicator of negative affect) differed depending on the outcome of the task and the subjects' dominance relative to their partner. Specific pairwise comparisons revealed that, for subordinates, following a competitive experience, rates of displacement behavior were significantly higher than after a non-social experience (β = 1.65, t = 3.17, *p* = .004). Incidence ratios indicate that compared to the non-social experiences, following a competitive experience, subordinates displayed 5.2 times the rate of displacement behaviors. Additionally, contrasts revealed that following a competitive experience, across all dominance levels, displacement behavior was significantly higher when the subject lost the competitive experience (outcome: negative) compared to when the subject won the competition (outcome: positive; β = 0.89, t = 2.00, *p* = .045). Compared to winning competition, rates of displacement behavior were 2.4 times the rate after losing a competitive experience.

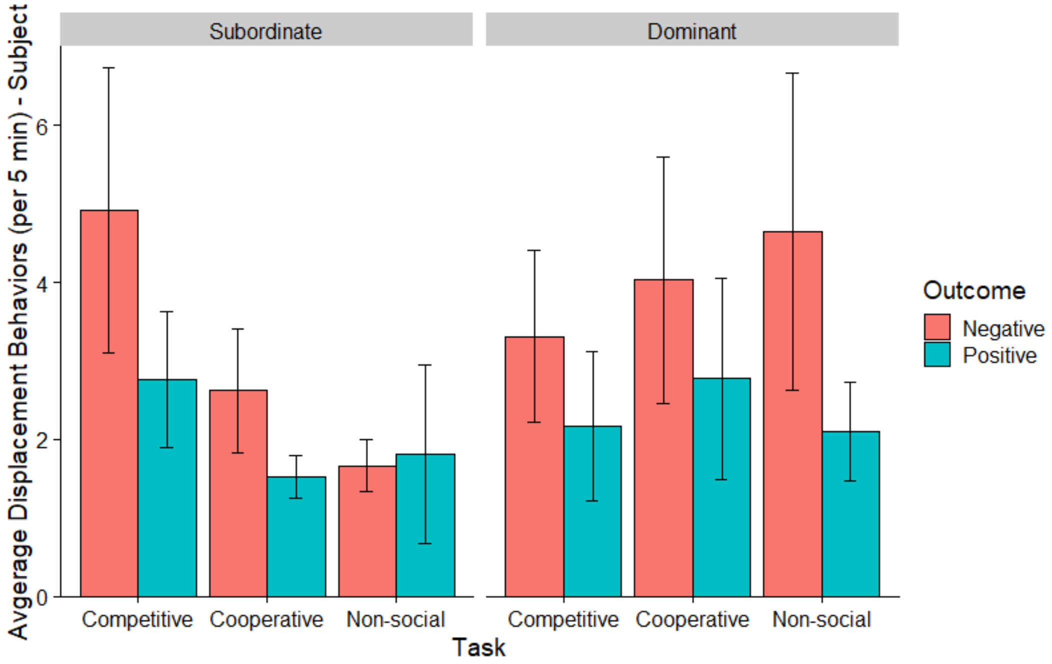

Figure 13. Graphs of the average display of displacement behaviors following the different tasks and outcomes, grouped by and dominance. Note: graph reflect aggregate sums of behavior rates (not accounting for individual differences) while model statistics. Error bars reflect SEM.

Interestingly, examining behavior across the control conditions and the testing sessions collapsed across task and outcome revealed significant differences in the rate subjects displayed displacement behaviors ($\chi^2(3) = 10.66$, *p* = .014; Figure 15). Rates of displacement behavior were significantly lower during the knowledge test than the satiation control (β = -1.35, t = 2.82, *p* = .025) and testing sessions (β = -1.15, t = -2.95, *p* = .017).

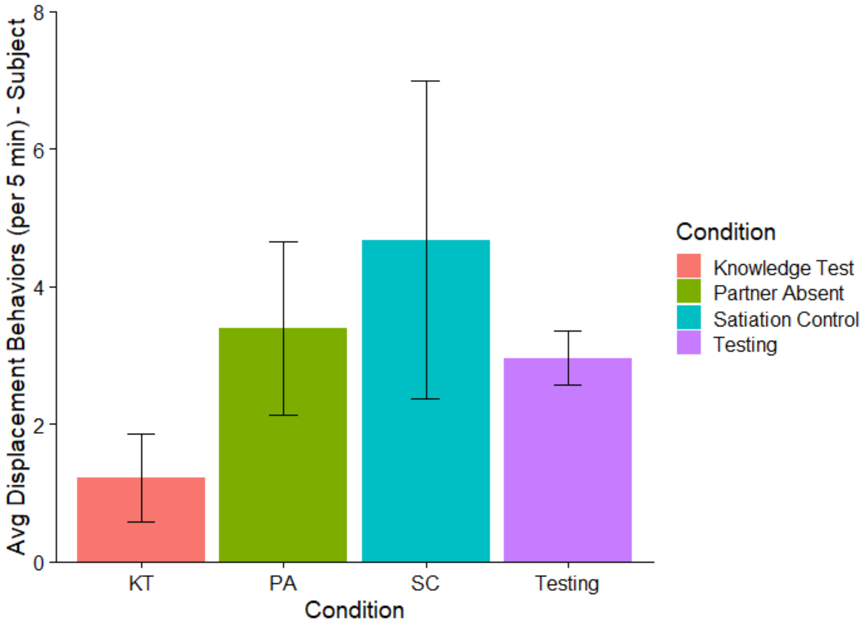

Figure 14. Average rates of displacement behaviors in the control conditions and collapsed across testing sessions. Note: graph depicts aggregated rates of behavior across subjects, while analyses control for individual differences in behavior. Error bars reflect SEM.

4.3.2 Partner behavior

Partner rates of displacement behavior (IRR; r = .98) were not significantly affected by the conditions (task or outcome), and there were no significant interaction effects with dominance. There was a significant main effect of prosocial choices (made by the subject) on partner displacement behavior, however ($\chi^2(2) = 7.21$, $p = .027$). Rates of displacement behavior by the partner decreased as subject prosocial choices increased ($\beta = -0.90$, t = 1.88, $p = .059$; Figure 15).

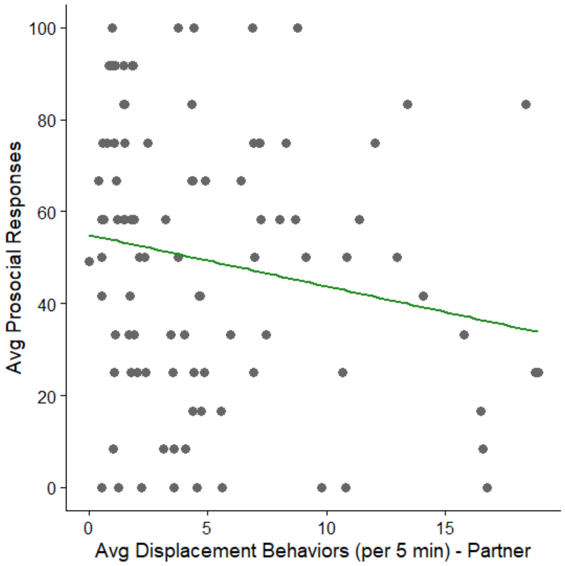

Figure 15. *Relationship between average rates of displacement behavior displayed by the partner and the average rate of prosocial choices made by the subject.*

5 DISCUSSION

Capuchin monkeys given the option to prosocially choose an outcome that rewarded their partner did not do so more often when there was a partner present compared to a partner-absent control. This contrasts with studies that have found capuchins to exhibit prosocial tendencies (Brosnan et al., 2010; de Waal et al., 2008; Lakshminarayanan & Santos, 2008; Suchak & de Waal, 2012; Takimoto et al., 2010), although it is consistent with other findings (Amici et al., 2014; Burkart & van Schaik, 2013; Drayton & Santos, 2014b; Skerry et al., 2011). Importantly, our results are not due to a failure of subjects to understand the paradigm, as they all passed a knowledge control in which they could access both sides of the apparatus by choosing the option that brought them two rewards, rather than one. Contrary to our predictions, but perhaps not surprisingly given their indifference towards the prosocial option, subjects' tendency to choose the prosocial option was also not impacted by immediately prior experiences that were cooperative, competitive, or non-social, nor were they affected by whether the subject got the food reward during those experiences. However, whether monkeys more often chose the prosocial option did relate to rates of displacement behavior (which is a measure of negative affect; Maestripieri et al., 1992; Troisi, 2002). Further analyses of displacement behaviors found them to increase after losing a competitive experience compared to winning, and an interaction effect between dominance and the type of prior experience. Monkeys subordinate to their partner displayed higher rates of displacement behavior following a competitive experience (win or lose) relative to a non-social experience. These changes in behavior did not, however, directly translate to changes in prosocial behavior following the different tasks. Finally, we found several interactions between the prior experiences and partner behavior in impacting prosocial choices. The limited sample size means such interactions must be interpreted cautiously, but these are valuable in highlighting the likelihood that interactions among different individual and contextual factors may be underlying the variability seen across studies of prosocial decision making. Below we discuss these findings in more detail.

Overall, the capuchin monkeys in this study did not change their choices when a partner was present versus absent, instead choosing the prosocial option at chance levels in both conditions. This suggests that the subjects were indifferent to what their partner received, neither changing their behavior to reward their partner (prosocial) or not (spiteful). This result adds to a literature that has shown inconsistency in responses. Considering just variations on the platforms task, capuchins demonstrate prosocial tendencies in some studies (Brosnan et al., 2010; Claidière et al., 2015; Lakshminarayanan & Santos, 2008) but not others (Amici et al., 2014; Burkart & van Schaik, 2013). One factor that may play a role is reward distribution. Two of the studies that found prosocial tendencies in the monkeys (Claidière et al., 2015; Lakshminarayanan & Santos, 2008) allowed subjects to choose between an option that delivered the same reward as the subject received to the partner, or to receive a *lower* value reward (1/1 vs 1/1-), whereas the current study compared the same reward to *no* reward (1/1 vs 1/0). Indeed, previous work using this distribution with capuchins also found no evidence of prosocial behavior (Amici et al, 2014). In retrospect, while we chose this distribution to maximize the contrast between the prosocial and selfish options, and indeed, the knowledge test showed that the monkeys could discriminate between them when it was in their personal interest, this may have been a poor choice. These results suggest that future work should focus on distributions in which the partner receives a lesser reward.

One challenge all studies of prosocial behavior face is training the subjects on the prosocial paradigm, and ours was no exception. We had to train our subjects that one of the trays resulted in two rewards moving within reach of the enclosure, while for the other tray the second reward was unreachable. To do so, we gave the monkeys access to both sides of the "prosocial" apparatus. This turned out to not be easy for our monkeys to learn, so they received an average of 13 (range 2-27) training sessions. This much experience may have inadvertently trained subjects to expect both rewards, increasing their competitiveness when they were with the partner (Amici et al., 2014). Supporting this, our lowest rates of prosocial choices and highest rates of displacement behavior were unexpectedly in the satiation control, in which the subject was handed three grape halves prior to prosocial testing. This was, importantly, the first test session for all subjects, raising the possibility that they were reacting to either frustration at suddenly not being able to get the other reward, or perceived competition with the partner who was to receive it. If this is the case, it suggests that our monkeys did not perceive this as a prosocial task, despite passing the knowledge control, but instead as a bait-and-switch in which previously available rewards were no longer accessible. Indeed, the slight increase in prosocial behavior across test sessions may suggest that the monkeys are becoming less frustrated with this change over time. In general, this is not a discrimination the monkeys easily understood, suggesting that without training it is difficult to interpret monkeys' choices (if the knowledge test was only at the end of the study, they may pass it, but not have had the same level of understanding in earlier sessions).

The absence of impact of the tasks or outcomes prior to prosocial testing contrasts the limited existing literature, although with a general lack of prosocial behavior it is difficult to know if prior experience would have led to an effect in another context. Capuchin monkeys previously demonstrated increased rates of prosocial behavior following being the recipient of a prosocial act, and decreased rates following an experience where they themselves were not the recipient of a possible prosocial action (Leimgruber et al., 2014). Children tested in a similar paradigm to the current study, in which prosocial behavior was measured following cooperative, competitive, and non-social ('solitary') games, showed decreased rates of prosocial behavior after a competitive experience, although no difference between a cooperative and non-social experience (Toppe et al., 2019). A key difference between the current study is that we measured prosocial behavior towards the same individual involved in the prior experience, whereas the other two studies measured behaviors towards a third-party. However, we intentionally chose a direct reciprocity paradigm because theory (Axelrod, 1984; de Waal & Brosnan, 2006) and data (de Waal, 1989; Molesti & Majolo, 2017; Schino & Aureli, 2008) predict that subjects should show a stronger reaction towards the individual with whom they were directly involved rather than a third party. Indeed, Schmelz et al. (2017) found direct influences of chimpanzee partners' assistance on the subjects' subsequent prosocial behavior towards that individual, and this was even sensitive to the perceived 'risk' of their partner's assistance. It will be interesting to see if these differences are the result of species differences, or if future studies with capuchin monkeys using a different population or measure of prosocial behavior will find similar effects.

As an additional measure, we looked at displacement behaviors as a proxy for negative affect (Maestripieri et al., 1992; Troisi, 2002)[3]. Overall, we found that outside of the specific tasks or outcomes, there was a general correlation of increased displacement behavior with decreased rates of prosocial choices, which suggests an effect of negative affect on decision-making. Regarding the different conditions, we did not see the predicted increase in displacement behaviors following all of the negative outcomes (across tasks), but we did find increased displacement behavior after losing competition compared to winning. Moreover, we found that monkeys who were subordinate to their partners showed higher levels of displacement

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[3] It is important to note that the absence of negative effect is not a measure of positive affect, but there are currently no behavioral measures of positive affect within the animal literature.

behavior following any competitive as opposed to non-social experience, whereas monkey’s dominant to their partners did not. Taken together, these findings suggest that at least our competitive manipulation influenced affect in the expected direction, however it is notable that this did not translate to significant changes in prosocial behavior. We cannot differentiate whether this is because negative affect is not influencing prosocial choices or because our monkeys did not treat this task as an opportunity to be prosocial.

Previous research has also indicated that the partner’s behavior can influence prosocial choices. One such behavior is ‘reward-directed behavior,’ which involves the partner reaching towards the reward or grabbing at the platform on which the rewards were located. This behavior has been linked with fewer prosocial choices in other species (Burkart & van Schaik, 2013; Cronin et al., 2009; Tan & Hare, 2013; see also; Burkart et al., 2007; Dale et al., 2016; Schwab et al., 2012), but we found no effect on our monkeys’ responses. We also saw ‘attention-getting’ behaviors, which manifested in the form of banging on the caging and manipulating the barrier between subject and partner (lifting or sliding this back and forth created a loud banging noise). These behavior have been found to influence prosocial decisions in chimpanzees (Horner et al., 2011; Melis et al., 2011), but not capuchins (Takimoto et al., 2010) and consistent with this, we found no influence on prosocial decisions. Whether this is due to a species difference in the effect of attention-getting behavior on prosocial choices is difficult to say given the limited prosocial behavior in the current study.

Moreover, interpreting this is complicated by the inconsistency in classification of these behaviors across studies. Specifically, while all three studies reporting attention-getting behavior observed and recorded hitting the caging behavior, both chimpanzee studies classified it as ‘attention-getting,’ while the capuchin study grouped it with displays of sitting near, reaching towards, and touching the high-value container, and classified this constellation as ‘begging.’ In addition, one of the chimpanzee studies included self-scratching as attention-getting behavior (Horner et al., 2011), which does not follow other classifications of self-scratching as a stress response. Lumping multiple behaviors with different causes into the same category can inflate responses and obscure the true effect of each behavior, making it difficult to draw conclusions regarding the effects of any of these behaviors on prosocial choices. Nonetheless, the consistent finding that none of these are impacting choices in capuchins may suggest that they are less attentive to their partners’ actions than chimpanzees.

Finally, while we saw no overall effect of any one type of behavior, we did see significant interaction effects with the prior experiences in predicting prosocial choices. Our sample size is so small that we cannot interpret these with any confidence. However, the take-home message may be that it is not any one context or individual state influencing prosocial decisions, but an interaction among many, including affective state and the partner’s behavior. If so, this reiterates the need to carefully distinguish behaviors so that we can determine which are playing a role, and a need for larger studies that have the power to identify these potential interactions.

5.1 Future Directions

While it remains possible that the subjects in our study are simply not prosocial, we suspect that the paradigm used in this study was not interpreted by our subjects as a choice to behave prosocially or not. We suggest that future research addresses this through two considerations. It may be that the choice between the option to provision a partner with the same reward as the subject or a *lesser* reward is easier for capuchins to interpret than the option between the same reward or *no* reward. We also believe that while our results indicate training may be essential for interpreting results from early sessions (a knowledge test at the end cannot determine what subjects understood at the beginning of the study), this training should be limited. Moreover, this could be used to directly assess which of the different reward contingencies (a lower value reward or no reward as the non-prosocial option) are easier to learn. Researchers may also consider including a social session with the apparatus as part of training as well (which could be done with a stooge partner not involved in testing), to ensure subjects understand they will not always be able to access both rewards.

While the current study intentionally strove to create prior experiences that were as similar as possible to one another while only manipulating specific factors to change the nature and outcome of the prior experience, thus reducing alternative explanations, subjects may not have interpreted all the experiences the way we intended. While there is evidence for the expected change in affect following the competitive task, we did not find similar evidence following the cooperative task. It is not clear if this is simply because we do not have a measure of positive affect, or because subjects did not see successful cooperation as a positive outcome, but one way to address this may be to use a more salient task. For instance, subjects were very good at cooperating to pull in the rewards in this study, and in most instances did so rather quickly. The speed in reaching this outcome may have obscured their partner’s role in bringing it about. A rope pull that takes substantially more effort and time to achieve may increase salience of the experience. Additionally, while there is evidence for the expected interpretation of the competitive scenario, salience could also be increased by a paradigm in which individuals compete over the same resource instead of competing over access to their own rewards as in the current study. While this might introduce some alternative explanations for possible differences in outcomes, it would be a useful start to determining if prior experiences such as these influence prosocial behavior.

More broadly, systematically testing and comparing the effects of contextual and social factors such as partner behavior, dominance, and relationship quality may yet prove key to understanding the mechanisms behind prosocial behavior. We also encourage researchers to explicitly examine how these effects may be interacting with one another, although acknowledge the challenges of doing so with sample sizes as small as most primate research. These efforts may be aided if researchers could collaborate, and when possible, increase transparency with data, so that future researchers can gain power by having access to that information. For instance, presenting the effects of individual partner behaviors on prosocial choices, even if behaviors are grouped for the main analyses, would help with understanding the relative effects of such behaviors across species, particularly when behaviors are grouped differently.

Finally, we hope future research will continue to strive to untangle the effects of prior experiences, and the partner's role, from possible affective influences on prosocial behavior. Furthermore, we hope to see efforts to elucidate whether there are species differences in the mechanisms behind these effects of prior experiences. The current study aimed to explicitly examine part of this distinction in capuchin monkeys, by providing various experiences in which both positive and negative outcomes were brought about through partner involvement, and others in which the outcome was independent of a conspecific (in the non-social conditions). While our results are unable to speak to these impacts due to an overall lack of prosocial behavior, we hope future research will continue along these lines. We expect that collectively this research will help contribute to a better understanding of the proximate mechanism(s) and evolutionary history behind prosocial behavior, particularly the flexible, context-specific, prosocial behavior seen in humans.

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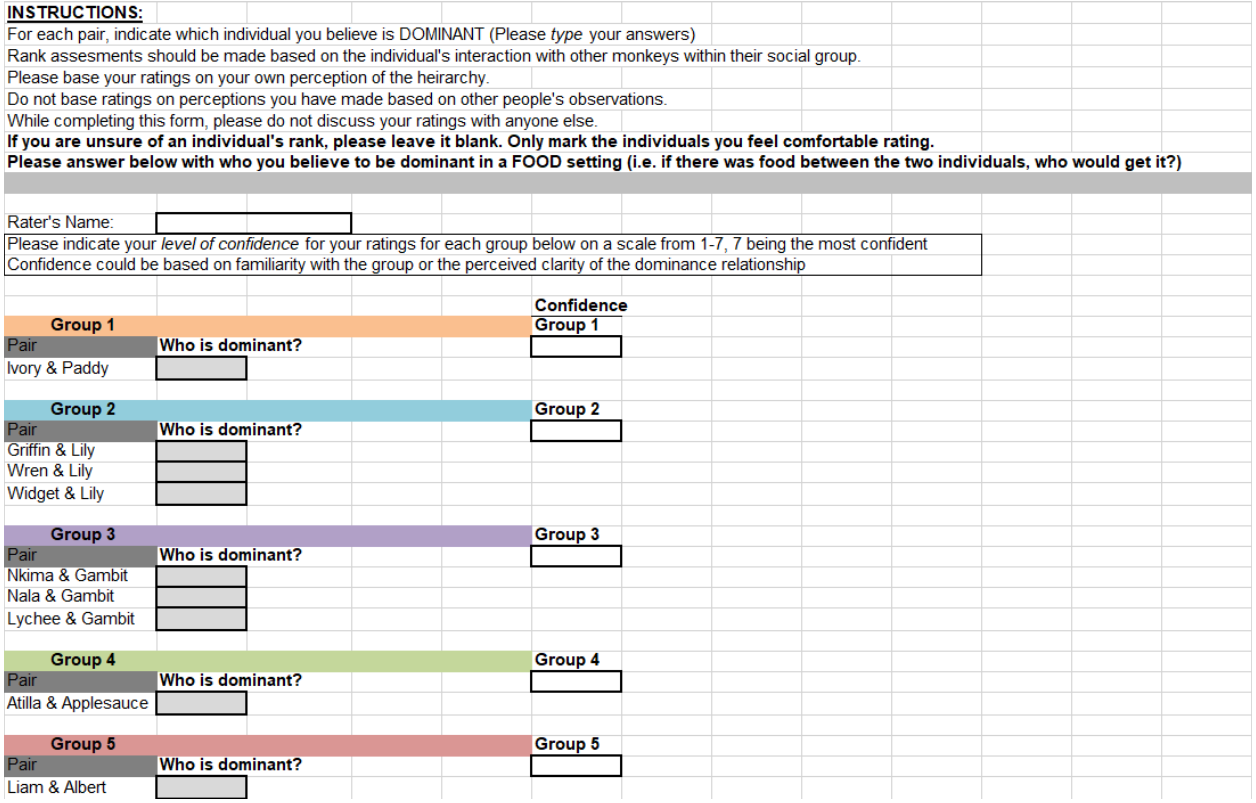
7 APPENDIX A



INSTRUCTIONS:
For each pair, indicate which individual you believe is DOMINANT (Please *type* your answers)
Rank assesments should be made based on the individual's interaction with other monkeys within their social group.
Please base your ratings on your own perception of the heirarchy.
Do not base ratings on perceptions you have made based on other people's observations.
While completing this form, please do not discuss your ratings with anyone else.
If you are unsure of an individual's rank, please leave it blank. Only mark the individuals you feel comfortable rating.
Please answer below with who you believe to be dominant in a FOOD setting (i.e. if there was food between the two individuals, who would get it?)

Rater's Name: ☐
Please indicate your *level of confidence* for your ratings for each group below on a scale from 1-7, 7 being the most confident
Confidence could be based on familiarity with the group or the perceived clarity of the dominance relationship

		Confidence
Group 1		**Group 1**
Pair	**Who is dominant?**	☐
Ivory & Paddy	☐	
Group 2		**Group 2**
Pair	**Who is dominant?**	☐
Griffin & Lily	☐	
Wren & Lily	☐	
Widget & Lily	☐	
Group 3		**Group 3**
Pair	**Who is dominant?**	☐
Nkima & Gambit	☐	
Nala & Gambit	☐	
Lychee & Gambit	☐	
Group 4		**Group 4**
Pair	**Who is dominant?**	☐
Atilla & Applesauce	☐	
Group 5		**Group 5**
Pair	**Who is dominant?**	☐
Liam & Albert	☐	

Figure 1. Image depicting the survey filled out by researchers and care staff familiar with the subjects to obtain relative dominance ranks within the pairs

8 APPENDIX B

Table 1. Ethogram used for behavioral coding

Behavior		Type	Definitions
Reward-Directed behavior			
	Reaching	Point	Extending of the arm towards the food reward or apparatus on which the reward is located, in a manner that is not resting (i.e. not just dangling the arm outside of the caging)
	Table/Apparatus grabbing	Point	Grabbing or pushing of the apparatus including, but not limited to, any occurrences involving movement of the apparatus
	Rope pulling	State	Active pulling behavior. Begins when rope tension is engaged and ends when it is loosened.
Partner-Directed behavior			
	Reaching	Point	Extending of the arm towards the partner or partner’s enclosure through the divider or in front of the caging.
	Threatening	Point	Open mouth display accompanied by rigid posture and erect tail. Often, but not always, accompanied by threatening vocalizations.
	Attention-getting	Point	Noisy displays including; hitting the faceplate, joint box door or barrier between subject and partner, or moving the barrier to the side or up and down producing a loud noise.
Self-directed behavior			
	Scratching	Point	Behavior in which the hand or food is engaged in rigorous contact with any other part of the body. Considered the same behavior if the motion is stopped and started within 3 seconds in the same location by the same limb. If scratching moves to a new location on the body or the same spot is scratched by a different limb, it is considered a separate occurrence.
	Body shake	Point	Rapid side to side movement of the full body. Often begins or ends with rapid tail movement.
	Urine washing	Point	Activity in which the subject urinates into hand and then rubs or scratches it into fur. First scratch that occurs, if it occurs immediately following the urine catching, is considered part of the urine washing behavior.
Stereotypic behavior		Point	Repetitive or invariant behavior without apparent function. Examples include: head tossing (abrupt lift of the head upwards and backwards), regurgitate and re-ingest (spitting up food and eating it again), cage head tossing (repeated head tossing while hanging on the cage siding), twirling (rapid and repeated spinning in circles).