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# The Evolution of Inequity Aversion: Nonhuman Primate Responses to Unequal Reward Distributions

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THE EVOLUTION OF INEQUITY AVERSION: NONHUMAN PRIMATE RESPONSES  
TO UNEQUAL REWARD DISTRIBUTIONS

by

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B.S., Michigan State University, 2010  
M.A., Southern Illinois University Carbondale, 2016

A Thesis  
Submitted in Partial Fulfillment of the Requirements for the  
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A Thesis Submitted in Partial  
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## AN ABSTRACT OF THE THESIS OF

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Inequity aversion, the negative response to receiving an unequal reward, has been intensely studied and is well established in humans. However, why humans developed a profound sense of equity is still enigmatic, and the evolutionary roots of this interesting phenomenon are still largely unknown. The little research that has been completed on nonhuman primates indicates that some species, like humans, are inequity averse, while others are not. Brosnan and de Waal (2003) suggested that an aversion to inequitable outcomes coevolved as a response to an increased emphasis on cooperative relationships, where individuals would respond negatively when their rewards differed from those of a social partner. Chen and Santos (2006), however, suggested that inequity aversion evolved in response to contrast effects, or individual expectations, in which individuals would respond negatively when their rewards differed from those previously received by the individual; this suggests that an animal forms expectations that are irrespective of rewards received by a social partner.

This study aimed to test these two hypotheses by examining responses to inequitable outcomes in three yet untested primate genera (*Gorilla*, *Nomascus*, and *Papio*) and one genus which has been previously tested (*Pongo*). To investigate responses to inequitable outcomes, an established inequity paradigm was used

following Brosnan and de Waal (2003), in which primate subjects were required to complete a task before receiving a reward. Because only responses to differences in reward quality had been tested with nonhuman primates using this paradigm, this study introduced an additional test condition to determine how reward quantity differences would affect individual responses to unequal offerings. It was found that some olive baboons, western-lowland gorillas, and white-cheeked gibbons responded negatively to both individual expectations and social expectations. Orangutans, however, responded to individual expectations, but not to social expectations. This study suggests that there is individual variation in inequity responses of olive baboons, western-lowland gorillas, and white-cheeked gibbons; this is similar to the individual variation in inequity aversion that has been proposed for chimpanzees and bonobos. This study also suggests that orangutans are not inequity averse, which supports results found in previous studies of orangutan inequity aversion.

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# TABLE OF CONTENTS

	<u>PAGE</u>
ABSTRACT .....	i
ACKNOWLEDGMENTS.....	iii
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
CHAPTER 1 – INTRODUCTION.....	1
Inequity Aversion in Humans.....	3
Inequity Aversion in Nonhuman Primates .....	6
The Evolution of Inequity Aversion .....	8
Inequity, Social Organization, and Cooperation.....	13
Alternative Hypothesis for the Evolution of Inequity Aversion.....	15
CHAPTER 2 – STUDY AIMS .....	19
Species Selection.....	19
Adding to the Current Procedural Paradigm.....	22
Hypotheses and Predictions.....	25
CHAPTER 3 – METHODS .....	29
Subjects and Locations .....	29
Baboons .....	30
Apes .....	31
Food Preference Tests.....	32
Baboons .....	32
Apes .....	34

Training .....	35
Baboons and Gibbons .....	35
Gorillas and Orangutans.....	37
Testing.....	37
Test 1: Testing for Contrast Effects .....	39
Test 2: Equitable Reward Quality .....	40
Test 3: Inequitable Reward Quality.....	40
Test 4: Equitable Reward Quantity .....	41
Test 5: Inequitable Reward Quantity.....	41
Interobserver Reliability .....	42
Statistical Analysis.....	42
CHAPTER 4 – RESULTS .....	44
Intraspecific Comparisons .....	44
Food Preference Tests and Training .....	44
Notes on Testing Orangutans.....	45
Testing for Quality Contrast Effects .....	45
Testing for Quantity Contrast Effects.....	46
Disadvantageous Inequitable Reward Quality .....	47
Disadvantageous Inequitable Reward Quantity .....	49
Advantageous Inequitable Reward Quality.....	50
Advantageous Inequitable Reward Quantity.....	51
Overall Results .....	52
Interspecific Comparisons .....	53



Contrast Effects .....	54
Disadvantageous Inequity Aversion.....	55
Advantageous Inequity Aversion .....	55
Individual Trends .....	56
Behavioral Observations .....	57
CHAPTER 5 – DISCUSSION.....	59
Contrast Effects.....	59
Disadvantageous Inequity Aversion .....	62
Advantageous Inequity Aversion .....	70
Addressing the Evolution of Inequity Aversion .....	73
Conclusions.....	77
BIBLIOGRAPHY .....	90
VITA .....	101

## LIST OF TABLES

<u>TABLE</u>	<u>PAGE</u>
TABLE I. Baboon Demographic Characteristics .....	80
TABLE II. Additional Baboon Characteristics .....	80
TABLE III. Ape Demographic Characteristics .....	81
TABLE IV. Conditions and Rewards for all Primate Subjects. ....	81
TABLE V. Test Results for Baboons .....	81
TABLE VI. Test Results for Gorillas .....	82
TABLE VII. Test Results for Gibbons .....	82
TABLE VIII. Test Results for Orangutans .....	82
TABLE IX. Results of Friedman's Tests .....	83

## LIST OF FIGURES

<u>FIGURE</u>	<u>PAGE</u>
FIGURE I. Contrast effects when rewards varied by quality .....	84
FIGURE II. Contrast effects when rewards varied by quantity. ....	85
FIGURE III. Disadvantaegous inequity aversion when rewards varied by quality. ....	86
FIGURE IV. Disadvantaegous inequity aversion when rewards varied by quantity.....	87
FIGURE V. Advantaegous inequity aversion when rewards varied by quality.....	88
FIGURE VI. Advantaegous inequity aversion when rewards varied by quantity .....	89

## CHAPTER 1

### INTRODUCTION

Humans and nonhuman primates must continuously make decisions in order to navigate their social and ecological environments. In order to maximize their fitness, it is generally assumed that individuals would make decisions to maximize the benefits and minimize the costs of behaviors. However, individuals sometimes act in ways which appear not to maximize their individual fitness, and these behaviors could be interpreted as the result of irrational decision-making. For instance, it may seem irrational for an individual to give up an available resource, especially if resources are scarce, only because it is of unequal value compared to a social partner's. This is a behavioral phenomenon known as inequity aversion, and it has been observed in humans and nonhuman primates. Due to the prevalence of inequity aversion in several species of the primate lineage, it is important to understand when and why an individual may make such an 'irrational' decision and why this behavior would evolve and persist throughout evolutionary history.

Inequity aversion can be defined as "the aversive reaction to an unequal distribution of resources" (Massen et al., 2012:145) and can be distinguished as either disadvantageous or advantageous (Brosnan and de Waal, 2012). Disadvantageous inequity occurs when an individual receives a "lesser valued outcome than a social

partner,” indicating that individuals who exhibit disadvantageous inequity aversion will reject a reward that is of *lesser* value than a social partner’s reward (Brosnan and de Waal, 2012:337). Advantageous inequity occurs when an individual receives “a more valuable outcome than a social partner,” indicating that individuals who exhibit advantageous inequity aversion will reject a reward that is of *greater* value than a social partner’s reward (Brosnan and de Waal, 2012:337).

A response to advantageous inequity aversion is particularly interesting given the “selfish” nature of Darwinian evolution, in which the individual is the unit of selection. This follows from the idea that natural selection generally only promotes behaviors that benefit the fitness of an actor. Thus, if behaviors are selected upon because they increase the survival or reproductive success on an individual level, it is curious that an individual would give up a resource because it was greater than what a conspecific would receive. It is especially interesting that an individual would behave in a way that benefits non-kin group members at a cost to themselves.

There are at least two scenarios that may explain why individuals express advantageous inequity aversion. A negative response to advantageous inequity may be a prosocial behavior, in which individuals help one another work toward a goal that cannot be achieved individually (Brosnan and de Waal, 2012). It is also possible that individuals who express advantageous inequity aversion may be sensitive to potential future retaliation (Brosnan et al., 2010). A social partner could retaliate if the individual accepts a better reward than what is given to their social partner. Until more is known about how inequity aversion may have evolved, it is difficult to determine why individuals would reject a greater reward than that of a social partner.

The aim of this study was to contribute to the understanding of when and why an individual may be inequity averse and how this trait may have evolved in humans. Extant nonhuman primate species are good models for testing hypotheses about the evolution of inequity aversion in humans for two main reasons. Nonhuman primates are the closest living relatives of humans, indicating that testing nonhuman primates can provide information about whether inequity aversion may have evolved from a common ancestor of humans and other nonhuman primate lineages. Additionally, there is variation in the socioecological environments of nonhuman primates that can be compared and contrasted to those of humans. In this way, hypotheses concerning the social or ecological pressures that may have led to the evolution of inequity aversion can be more easily tested. To better elucidate the evolutionary pressures that may have led to the emergence of inequity aversion, this study examined responses to unequal reward distributions in three yet untested primate species, olive baboons, western-lowland gorillas, and white-cheeked gibbons, and one species that had been previously tested for inequity aversion, orangutans.

### Inequity Aversion in Humans

Previous studies have indicated that both adults and children exhibit negative reactions to inequitable outcomes (Fehr and Schmidt, 1999; McAuliffe et al., 2013), and that inequity aversion occurs at an early age in humans (McAuliffe et al., 2013). At about four years of age, children begin to respond negatively to disadvantageous inequity, and at roughly eight years of age, children begin to react negatively to

advantageous inequity (McAuliffe et al., 2013). This suggests that, in humans, disadvantageous inequity aversion probably develops prior to advantageous inequity aversion (McAuliffe et al., 2013). Disadvantageous inequity aversion also appears to be more common than advantageous inequity aversion, as negative responses to lesser rewards occur more often than negative responses to greater rewards (McAuliffe et al., 2013).

While the above aspects of inequity aversion are consistent among humans, there is also individual variation in responses to inequity among human subjects. For instance, some studies have shown that males and females assign rewards and distinguish fairness differently, indicating that responses to inequity may vary by sex (Pruitt, 1985). Men, for example, will often take a competitive approach to equity games, ensuring that final outcomes between negotiators are unequal; females, on the other hand, more often take a cooperative approach, allowing final outcomes between negotiators to remain relatively similar (Pruitt, 1985).

Peoples' ideas of fairness also vary depending on their goals (Skitka, 2012). For instance, people prefer to distribute equal allocations when given hypothetical scenarios that require affiliation among workers (Leung, 1986). However, people prefer to receive greater rewards than their partner in situations concerned with productivity (Skitka, 2012). When people are given a hypothetical situation in which work accentuates productivity, they prefer an equitable, or profit-making, outcome in which everyone gets rewarded based on the amount of work they put in (Leung, 1986). This could explain why people prefer universities where academic salary distributions are dependent on productivity levels (Konrad and Pfeffer, 1990).

Recent research with children has shown that human responses to inequity aversion also vary by culture. For instance, children 6 to 8 years of age living in the United States or South Africa preferred to discard a resource rather than give the resource to one individual; in this way, the children were maintaining equal rewards across the subject and partner instead of creating an unequal reward distribution (Shaw and Olson, 2012). However, children 6 to 7 years of age living in Uganda preferred to create unequal distributions rather than discard a resource (Paulus, 2015).

Researchers have argued that cultures which are often exposed to environments lacking in resources and which emphasize individual equality to a lesser degree are less likely to respond negatively to reward inequality (Paulus, 2015).

In addition to culture, other social factors, such as relationship strength, have been shown to influence inequity aversion. For example, humans' decisions regarding the distribution of payoffs are contingent upon the strength of relationship between the subject and partner (Loewenstein et al., 1989). The study by Loewenstein and colleagues (1989) indicated that humans respond more strongly to inequity when they have a strong relationship with their social partner as opposed to a relatively weaker relationship. People also tend to split distributions more evenly on occasions when partners have spent more time together (Skitka, 2012). This may indicate that the value of a particular relationship may be important in the maintenance of inequity aversion in humans. Thus, the goal of maintaining a social relationship may cause people to behave in what appears to be an unselfish manner. Inequity aversion, and particularly advantageous inequity aversion, may therefore be a behavior humans use to avoid relationship damage.



## Inequity Aversion in Nonhuman Primates

Although much research on inequity aversion has been completed with humans, only a small number of primate species has been tested to elucidate the evolutionary roots of humans' sense of inequity. As of yet, only chimpanzees (*Pan troglodytes*) (Brosnan et al., 2010), capuchin monkeys (*Cebus apella*) (Brosnan and de Waal, 2003), and macaques (*Macaca mulatta* and *Macaca fascicularis*) (Hopper et al., 2013; Massen et al., 2012) have been shown to be inequity averse, while orangutans (*Pongo pygmaeus*) (Brosnan et al., 2011), squirrel monkeys (*Saimiri sciureus* and *Saimiri boliviensis*) (Freeman et al., 2013; Talbot et al., 2010), owl monkeys (*Aotus spp.*) (Freeman et al., 2013), marmosets (*Callithrix jacchus*) (Freeman et al., 2013), and tamarins (*Saguinus oedipus*) (Neiworth et al., 2009) did not respond to inequitable outcomes. Evidence concerning inequity aversion in bonobos (*Pan paniscus*) is currently inconclusive, because some bonobos responded negatively to receiving unequal rewards in one study, but the results were not statistically significant (Brauer et al., 2009).

While some nonhuman primate species are inequity averse, they do not respond negatively to inequitable outcomes when they are given rewards in the absence of a task (i.e., something the primates must successfully complete in order be rewarded) (Brosnan et al., 2010). To elicit a response to inequity, many researchers have incorporated a token-exchange task into the experimental design; this requires that the subject first accept and trade a harmless, inedible object before receiving a food reward from an experimenter (Brosnan and de Waal, 2003; Brosnan et al., 2010;

Brosnan et al., 2011; Chen and Santos, 2006; Freeman et al., 2013; Hopper et al., 2013; Massen et al., 2012; Talbot et al., 2011; van Wolkenten et al., 2007). This token-exchange procedure usually involves at least two conditions. In the equity condition, the experimenter gives the subject and a social partner the same reward after both individuals trade a non-food token for a designated food item (Brosnan, 2013). In the inequity condition, the experimenter gives one individual a more preferred reward after the token exchange and the other individual a less preferred reward after the inedible token has been traded (Brosnan, 2013). In this paradigm, the experimenter observes the response of a subject when they receive an unequal distribution and have no control over their partner's outcomes; the researcher then compares this reaction to the same individual's response after receiving an equal reward as their partner (Brosnan, 2013).

While most researchers now agree that a task is required to elicit a negative response to inequity in nonhuman primates, there is still conflicting evidence about the effects of effort, or how much an individual is required to work in order to receive a reward. It is possible that nonhuman primates are more concerned with the quality or amount of rewards received as opposed to the amount of work the individual had to complete before receiving the rewards. For instance, some studies showed that responses to inequity were not affected by the level of effort that was required to complete a task (Brosnan et al., 2010; DeAngelo and Brosnan, 2013). Brosnan (2013) stated that a response to inequity may not be affected by effort, and therefore sensitivity to inequitable outcomes is due to differences in rewards earned rather than differences in the amount of work completed.

However, Brosnan and de Waal (2012) acknowledged that the combination of unequal effort and inequitable distribution may enhance responses, as nonhuman primates responded negatively to disadvantageous inequity more often when they were required to complete a task involving greater effort. This claim was supported in one study, in which capuchins were required to exchange a token either once or three times before receiving a less preferred food reward than their social partner; the social partner, in this case, always received a more preferred reward without having to complete a task (van Wolkenten et al., 2007). In that study, the monkeys participated in the task significantly less often when they were required to exchange a token three times for a less preferred reward, as opposed to when they made only one exchange for that same reward (van Wolkenten et al., 2007). An individual's sensitivity to effort in relation to rewards gained would make sense in terms of an animal's foraging choices in their natural environment. An animal would need to determine whether the benefits of gaining access to specific food sources, such as those of preferred taste or those that provide a greater abundance of food, would outweigh the costs of gaining the food, such as predation risk, energy consumed by traveling, and competition with conspecifics.

### The Evolution of Inequity Aversion

As it appears as though negative responses to unequal reward distributions are not unique to humans, it is important to understand how the trait may have evolved. However, understanding the evolution of inequity aversion is a complicated process for

a number of reasons. First, it is often difficult to determine whether a behavioral trait, including inequity aversion, is a homology (a trait shared by two or more species based on descent that was inherited from a common ancestor) or a homoplasy (a trait shared by two or more species based on similar function that evolved independently in different lineages). This is because behavioral traits are not as apparent as morphological traits, for example. Additionally, when considering whether or not a species is inequity averse, it is important to note that the absence of a response to unequal distributions does not equate to the absence of an ability to recognize disparity between resource allocations. Observing an expected response in a species provides a clear demonstration that an individual is capable of recognizing and responding to inequity; however, the lack of performance does not necessarily indicate that they are not capable of doing so. An individual may recognize that their outcome is unequal to a social partner's outcome, but they may still accept the unequal reward. Although behavioral traits, such as inequity aversion, may be difficult to interpret, it is nonetheless imperative to try to understand how inequity aversion evolved.

While humans and some nonhuman primate species show negative reactions to inequitable outcomes, researchers have stated that inequity aversion does not appear to be a homology for the order Primates, as not all primate species tested thus far have exhibited an aversion to unequal rewards (Brosnan and de Waal, 2014). However, only a limited number of primate species have been tested for inequity aversion, and a homology of the trait for the order Primates cannot be completely ruled out at this time. It is therefore imperative to test additional primate species for the presence or absence of inequity aversion. If later research supports the homology of inequity aversion in

Primates, further analysis would have to address the common behavioral and cognitive characteristics among all primate species that may have led to the evolution of a sense of inequity. Furthermore, research would have to be completed in order to understand why the behavior was secondarily lost in some primate species. Importantly, even if inequity aversion is not homologous in the order Primates, the trait could still be a homology for certain primate subgroups.

Researchers have suggested that a common origin of inequity aversion is unlikely for the hominoid clade, as orangutans do not respond to inequitable outcomes (Brosnan et al., 2011). However, it is still difficult to make this claim, because there is conflicting evidence about bonobo inequity aversion (Brauer et al., 2006), and gorillas and hylobatids, such as gibbons, have not been tested with an established inequity paradigm. It is possible that bonobos, gorillas, and hylobatids respond negatively to unequal outcomes, which could indicate that the last common ancestor of extant hominoids already possessed inequity aversion, and orangutans lost it secondarily, perhaps due to their semi-solitary nature.

Further assessments have been made about the evolution of inequity aversion among additional primate subgroups, as well. Whether inequity aversion is a homology in the superfamily Cercopithecoidea is currently unknown, because the only Old World monkey genus that has yet been tested is *Macaca* (Hopper et al., 2013; Massen et al., 2012). The evolution of inequity aversion in the parvorder Platyrrhini is a little clearer, considering more species in this subgroup have been tested. It appears as though inequity aversion is not homologous in New World monkeys, because capuchin monkeys do respond negatively to inequity, whereas marmosets, tamarins, squirrel

monkeys, and owl monkeys do not (Brosnan and de Waal, 2014). However, the apparent absence of inequity aversion in callitrichids, squirrel monkeys, and owl monkeys could be attributed to the limited amount of data that has been collected for these species. Furthermore, the absence of data on strepsirrhines and tarsiers renders the evolution of inequity aversion even more nebulous.

If inequity aversion is not homologous in Primates, then this trait evolved independently multiple times during the evolutionary history of this group. Such independent evolution of inequity aversion would suggest that similar evolutionary pressures led to convergent solutions in distantly related species. In this context, the importance of testing additional primate species becomes even more apparent.

Researchers agree that regardless of whether inequity aversion is homologous or homoplastic, this behavioral trait most likely evolved in different species in a series of stages (Chen and Santos, 2006; Brosnan, 2013). The presumption is that each stage promoted the reproductive success and/or the survival of individuals. After interpreting Brosnan's explanation of inequity aversion, Chen and Santos (2006) suggested that the first stage involves the evolution of an organism's cognitive ability to realize that the value of resources of others can diverge from the value of the individual's own resources. The second stage is the evolution of an organism's capability of responding to unequal outcomes (Chen and Santos, 2006). The third and final stage, according to Chen and Santos (2006), is the organism's tendency to give up their own rewards in order to create a more equal reward distribution.

However, at least one significant stage in the evolution of inequity aversion is omitted from this scheme. Before an organism can realize that their own rewards differ

from those of another individual, that organism must first distinguish the self from the other. For instance, Mitchell (2015) argued that an organism must recognize that their body and behaviors are separate from those of their conspecifics, and the organism must distinguish when their body movements and behaviors either resemble or differ from the movements and behaviors of others. Only then can the organism complete stages one through three as suggested by Chen and Santos (2006).

While the ultimate causes of inequity aversion (those which explain how and why the trait came to be) are of greatest interest to most researchers, it is also important to understand the proximate causes of inequity aversion (those which explain the mechanisms facilitating an individual to exhibit the behavior). Therefore, the aim of this thesis is not to simply explain the evolution of inequity aversion at the ultimate level, but is rather to better understand the underlying mechanisms of inequity aversion (at the proximate level).

If inequity aversion is not a homologous trait for the order Primates, then it must be considered as to why this trait appears in certain primate species and not others. Why would inequity aversion evolve separately several times in evolutionary history? What function does inequity aversion fulfill? If inequity aversion is a homoplastic trait for the order Primates, this allows for the testing of hypotheses regarding the evolution of this trait, with each lineage or subgroup acting as a contrast for the others. If inequity aversion is homoplastic within primate subgroups, such as at the superfamily, family, or genus level, hypotheses for the evolution of inequity aversion should focus on species' socioecological environment.

### Inequity, Social Organization, and Cooperation

It is possible that inequity aversion evolved in order to maintain cooperative relationships among group members (Brauer et al., 2006; Brosnan, 2013; Brosnan and de Waal, 2012; Massen et al., 2012; Skitka, 2012; van Wolkenten et al., 2007), which would be plausible considering that so far only species that live in large, complex societies and which cooperate with non-kin and non-pair-bonded group members have been shown to respond negatively to unequal rewards (Brosnan and de Waal, 2014). For example, capuchin monkeys, macaques, and chimpanzees, all species which are inequity averse, rely on the cooperation of non-kin group members for forming coalition alliances in aggressive situations (Higham and Maestriperi, 2010; Nishida, 1983; Perry, 1996; van Noordwijk and van Schaik, 1985). Chimpanzees also show cooperative mate-guarding (Watts, 1998), cooperative hunting (Boesch, 1994), and meat-sharing (Mitani and Watts, 2001) with non-kin conspecifics. Additionally, capuchin monkeys cooperate to gain food resources (Rose, 1997) and show food-sharing behavior (Perry and Rose, 1994) with non-kin individuals.

Furthermore, it is fairly easy to see how inequity aversion may have evolved to increase cooperation and social interaction among group members in species where individuals have repeated interactions, long-term relationships, mutual benefits, and dependency with non-kin and non-pair-bonded group members. Massen and colleagues (2012) suggested that individuals who cooperate with conspecifics may evade unequal outcomes by using complex decision-making abilities to monitor the outcomes of social partners. If one individual is consistently receiving fewer benefits than their cooperative partner, that individual may cancel their cooperative relationship



with that particular partner, assuming the individual recognized the disparity in their outcomes. This is because cooperative partners may only want to invest in cooperation if the rewards are equally beneficial. Thus, an awareness of equal sharing is useful for maintaining a high level of cooperativeness (Massen et al., 2012).

Similarly, it has been suggested that aversive reactions to inequity may have evolved as a way to determine the reliability of a potential social partner (Brosnan, 2013; Brosnan and de Waal, 2012; Brosnan et al., 2011), in which individuals test whether social partners will give as equally as they receive. For instance, an interest in another's well-being could enhance an individual's reputation of being a "fair" partner and may ensure later reciprocity in the individual's favor (Brosnan, 2013). Research with capuchin monkeys supports this idea, as the monkeys appear to recognize and anticipate future necessary cooperation with their partners (Brosnan, 2013). However, due to the limited data regarding the relationship between inequity aversion and future cooperation, this theoretical explanation needs to be further explored before definitive conclusions can be made.

While there is strong evidence that inequity aversion evolved in tandem with an increase in cooperative relationships, it is less clear why cooperative breeders such as marmosets (Freeman et al., 2013) and tamarins (Neiwirth et al., 2009) would not be inequity averse. Species in which both the male and female participate in rearing offspring obviously must socially cooperate with one another (Brosnan, 2013). However, these species do not appear to be inequity averse, perhaps because responding to unequal outcomes is costly to those with close, *exclusive* social relationships (Brosnan, 2013; DeAngelo and Brosnan, 2013). This is plausible because

inequity aversion is assumed to be a method for determining the value of a social partner. However, switching partners is more costly in pair-bonded species who have already invested significant time and resources into their partnerships; therefore, responding to inequitable outcomes would be less beneficial for these individuals (Brosnan, 2013). It has been predicted that pair-living partners with a newly formed relationship are more likely to respond negatively to unequal outcomes than partners with a longer relationship history, because replacing a social partner is more difficult and costly for the latter individuals (DeAngelo and Brosnan, 2013). This may explain why pair-bonded species, such as gibbons, do sometimes switch social partners (Reichard, 1995).

Inequity aversion may be a trait that is only maintained where there are direct fitness consequences of maintaining it. Those who are inequity averse should enjoy higher fitness than those who are not when an absence of the trait is consequential to one's survival or opportunity to reproduce. Perhaps in species where individuals have the opportunity to cooperate with multiple non-kin conspecifics, an individual receives greater fitness benefits from choosing the conspecific that provides the most equal partnership. However, species which typically only cooperate with kin or few non-kin individuals do not benefit from reacting negatively to unequal resource distributions.

#### Alternative Hypothesis for the Evolution of Inequity Aversion

Although it is plausible that inequity aversion evolved as a response to cooperation among non-kin group members, alternative hypotheses have been proposed. For example, Chen and Santos (2006) criticized Brosnan's hypothesis that

suggested that the underlying mechanisms of inequity are related to sociality; they argued that Brosnan's approach is too domain-specific, or too narrow. Chen and Santos (2006) instead proposed that inequity aversion occurs in contexts irrespective of a social domain.

It was hypothesized that a negative response to unequal outcomes is a reply to a violation of previous expectations (Chen and Santos, 2006), known as "contrast effects" (Brosnan and de Waal, 2012), "frustration effects" (Roma et al., 2006), or the "food-expectation hypothesis" (Brauer et al., 2006). In these models, an animal expects to receive a reward that they have previously been shown or have previously been given. When the animal does not receive that expected reward, they respond negatively. In compliance with the "food-expectation hypothesis" (Brauer et al., 2006), inequity aversion should occur if expectations are violated, regardless of the presence or absence of a social partner.

Chen and Santos (2006) therefore hypothesized that inequity aversion evolved in response to a more general environment based on a reference-point that may or may not have a social component. They suggested that one apparent evolutionary advantage to recognizing another individual's rewards is to determine whether others living in the same environment are receiving more payoffs than one's own environmental rewards (Chen and Santos, 2006). Chen and Santos (2006) theorized that understanding the payoffs of others could indicate important changes occurring in the organism's environment that may affect an individual's behavior, especially regarding feeding patterns. For example, an animal who recognizes that other individuals receive better food from a shared environment should more actively seek

this food themselves, regardless of the presence or absence of cooperative partners (Chen and Santos, 2006). However, it could be argued that as long as an individual's environmental needs are met, there is no benefit to knowing whether their group members are gaining more "payoffs" from their environment.

It must be considered that the hypothesis proposed by Chen and Santos is not entirely plausible as currently stated, and it remains rather theoretical, as it is difficult to test empirically. For example, environmental resources are constantly changing in response to several variables, including season, temperature, rainfall patterns, and sometimes environmental destruction by humans. Similarly, natural resources, such as food items, are almost always different from one another in some way, even when food rewards are of the same species. For instance, it seems highly unlikely that two fruits even on the same tree will ever have the exact same size, shape, density, ripeness, and nutritional content. Similarly, the internal state of the individual, such as hunger or satiation, in addition to other factors—such as dominance status, distance to food sources, the presence of competing conspecifics, and the presence of predators—play into an individual's decision to leave a food source in search for a better resource. The consequence of the immense variation in ecological variables is that primates should be constantly changing their expectations to fit their environment. An animal can almost never expect to receive the same exact food item that the individual received in the past, and because of this, should not react negatively *a priori* when a current reward does not match those of past rewards.

Brosnan and de Waal (2012) also countered the argument that negative responses to unequal rewards are due to contrast effects rather than social

expectations. Contradicting evidence to the claim of contrast effects has been shown experimentally for several species which are inequity averse (Brosnan and de Waal, 2012). For instance, nonhuman primates refused to participate in a task with a social partner when the subject received a less preferred reward than their partner; however, in the absence of a social partner, these same animals fail to respond negatively after receiving a different reward than one previously shown to them (Brosnan and de Waal, 2012). If the primates were only responding to the contrast between past and present rewards, these animals should have responded negatively in both scenarios.

## CHAPTER 2

### STUDY AIMS

As the study of inequity aversion is rather recent in primatology, there is still much to learn about the mechanisms and function that govern this behavior. An obvious need is to increase the number of primate species tested for inequity aversion under controlled conditions. In order to better understand the evolution of inequity aversion, this study aimed to examine this phenomenon in three yet untested primate genera. This study also included a species which has been previously tested in order to check for consistency in intraspecific responses to inequity and to provide validity for this study's methods. While an established inequity paradigm (Brosnan and de Waal, 2003) was used to allow for easier comparison of behavioral responses across studies, a new test condition was added to provide a better understanding of species' responses to unequal reward distributions.

### Species Selection

One of the most pertinent areas of future research pertaining to the expansion of nonhuman primate inequity studies is to test the remaining ape species to better understand the behavior's prevalence among hominoids. This includes studying

individuals of the family Hylobatidae and those of the genus *Gorilla*, as little is known about either group's responses to inequity. Although it appears as though not all primates in the superfamily Hominoidea are inequity averse (Brosnan et al., 2011), studying hylobatids and gorillas could increase the understanding of how a species' socioecological environment plays a role in inequity aversion. Similarly, if both hylobatids and gorillas do respond negatively to unequal outcomes, it could indicate that the last common ancestor of extant hominoids already possessed the capacity for inequity aversion, and orangutans may have lost this ability secondarily.

As macaques are so far the only Old World monkeys that have been tested in regards to inequity aversion (Hopper et al., 2013; Massen et al., 2012), completing similar inequity experiments on additional Old World monkeys, such as baboons of the genus *Papio*, is of paramount importance for understanding the evolutionary roots of inequity aversion. Studies of baboons can help to determine possible socioecological factors driving inequity responses in humans and nonhuman animals. Studying baboons also puts us one step closer to understanding whether or not there could be homology of inequity aversion in Cercopithecoidea.

While orangutans have been tested for inequity aversion in one study, it is important to include this species in additional studies on this topic for a number of reasons. As of yet, orangutans are the only ape species that has been definitively declared as non-aversive to unequal distributions. It is therefore important to determine whether the absence of inequity aversion in the small number of orangutans tested (N=5; Brosnan et al., 2011) is anomalous or whether the absence of the behavior is characteristic of the species as a whole. Additionally, including a species already tested

for inequity aversion provides a source of validation for the research methods, as observed behaviors of this species can be compared across studies.

Orangutans, hylobatids, gorillas, and baboons are good model species for the study of inequity aversion not only due to these groups' phylogenetic relationship with previously tested species, but also due to the socioecological differences among them. Researchers agree that it is necessary to increase our knowledge about the similarities and differences of inequity responses in socially cooperative species as opposed to those which do not typically cooperate with non-kin group members (Brosnan and de Waal, 2012). Testing species which vary in the amount of cooperation that occurs among conspecifics would be beneficial for understanding the social implications of inequity aversion.

Orangutans, gibbons, gorillas, and baboons are excellent model species to determine the relationship between species cooperation and inequity aversion. Orangutans are considered solitary foragers which have only brief social interactions with non-kin conspecifics (Mitani et al., 1991; te Boekhorst et al., 1990). Hylobatids typically live in bonded pairs with dependent offspring (Reichard and Boesch, 2003; Palombit 1996). Gorillas often live in family groups averaging nine individuals (Yamagiwa et al., 2003), consisting of all adult males or one or two males and multiple females (Doran and McNeilage, 1998). Baboons of the genus *Papio* are characterized by high sociality as expressed in their multi-male, multi-female social organization, averaging between 15 and 150 individuals (Barton et al, 1996; Dunbar and Dunbar, 1974; Ray and Sapolsky, 1992; Rowel, 1966), Due to the varied social interactions these four primate groups have with non-kin group members, testing orangutans,



hylobatids, gorillas, and baboons would make an excellent comparison for understanding the social influences driving inequity aversion.

### Adding to the Current Procedural Paradigm

In order to allow for cross-species comparison of nonhuman primates, it is important to use similar procedures with each species tested (Brosnan and de Waal, 2012). As the majority of studies investigating inequity aversion involve a token-exchange or targeting paradigm (Brosnan et al., 2010; Brosnan et al., 2011; Brosnan and de Waal, 2005; Freeman et al., 2013; Hooper et al., 2013; Massen et al., 2012; van Wolkenten et al., 2007), it would be beneficial to mimic these methods when examining inequity in a species that has yet to be tested. To control for contrast effects, a contrast condition should be used in which the subject and partner complete a task and are both given a less-preferred reward than the one previously shown to them, as prior studies have done (Brosnan, 2013).

While it is important to use procedures similar to those used in previous inequity aversion studies in order to allow for cross-species comparison, it is equally necessary to explore how responses to inequity vary with differences in methodology (Brosnan and de Waal, 2012). Therefore, it would be beneficial for researchers to use an established inequity paradigm involving a task (Brosnan and de Waal, 2003), while adding one procedure not yet tested in nonhuman primates. As it appears as though differences in quantitative, as opposed to qualitative, reward distributions have not been

analyzed in relation to nonhuman primate inequity aversion, this would be a valuable addition to future experimental procedures.

While many species clearly demonstrate their aversion to unequal qualitative distributions (Brosnan et al., 2010; Brosnan et al., 2011; Brosnan and de Waal, 2003; Chen and Santos, 2006; Freeman et al., 2013; Hooper et al., 2013; Massen et al., 2012; Roma et al., 2006; Talbot et al., 2011; van Wolkenten et al., 2007), it would be interesting to see whether individuals respond negatively to receiving a lesser amount of the same food rewards than a social partner. It is obvious that recognizing the type of food obtained by oneself and one's conspecific is important in an animal's natural environment, as different foods cause animals to be more satiated than others. However, recognizing the abundance or scarcity of food gained by social partners compared to themselves seems equally, if not more, important for an animal's survival. If it is assumed that inequity aversion evolved in response to a species' ecological environment, it is essential to assess whether negative responses to unequal quantitative distributions exist in primate species.

Although adding a difference in quantitative distributions to the procedure is clearly important for the study of inequity aversion, there are several aspects one must consider before doing so. For instance, some rewards may be interpreted as so high in value that receiving a smaller amount of a high-value reward than a conspecific partner may not elicit a negative response. Therefore, distributing different amounts of the low-value reward would be a better indicator of the role quantity plays in response to unequal outcomes.

Another important consideration to make before introducing a quantitative component into the current inequity paradigm is whether or not nonhuman primates are able to recognize numerical differences in resources. Researchers have found that several nonhuman primate species are able to distinguish between two sets of items that differ numerically, including chimpanzees (Beran, 2001; Beran et al., 2008; Boysen and Berntson, 1995; Hanus and Call, 2007), bonobos (Hanus and Call, 2007), rhesus macaques (Beran, 2007; Brannon and Terrace), hamadryas baboons (Smith et al., 2003), and squirrel monkeys (Smith et al., 2003). Research has also suggested that nonhuman primates understand numerosity used in naturalistic contexts, such as vocal communication (Kitchen, 2004) and intergroup conflict (Wilson et al., 2001).

Importantly, all nonhuman primate groups tested in this study have been shown to have numerical abilities. For instance, in one study, gorillas and orangutans were able to select the larger of two amounts of the same food item when the quantities were presented at the same time and when the quantities were presented one after the other (Hanus and Call, 2007). Similarly, gibbons were able to select the larger of two quantities at a greater percentage than expected by chance when the ratio between quantities was  $4/3$ ,  $3/2$ ,  $5/3$ , or  $5/2$  (Yocum, 2010). In another study, olive baboons were able to distinguish between two small amounts of food (both less than four items), two large amounts of food (both greater than four items), and between one small amount and one large amount of food (Barnard et al., 2013).

## Hypotheses and Predictions

The current consensus among most scholars researching inequity aversion is that a negative response to inequitable outcomes evolved in tandem with an increase in cooperative relationships among conspecifics (Brosnan and de Waal, 2012; Brosnan et al., 2010; Brosnan et al., 2011; Brosnan and de Waal, 2003; Freeman et al., 2013; Hooper et al., 2013; Massen et al., 2012; Talbot et al., 2011; van Wolkenten et al., 2007). Therefore, hypotheses can be made about the presence or absence of inequity aversion in those primate species that have yet to be studied. It was hypothesized that “social” species would show aversive reactions to disadvantageous inequitable outcomes, whereas “semi-social” species would not. “Social” species were defined here as those which cooperate with non-kin and non-pair-bonded group members and have an average group size consisting of greater than four individuals. “Semi-social” species were considered to be those which do not cooperate with non-kin, non-pair-bonded conspecifics and have average group sizes including four or fewer individuals.

Additionally, predictions can be made about nonhuman primate responses to advantageous inequity aversion. Studies of human inequity aversion have shown that humans respond more strongly to inequity when they have a strong relationship with their social partner (Loewenstein et al., 1989) and when partners have spent more time together (Skitka, 2012). Therefore, it was hypothesized that individuals with a strong relationship with their social partner, who were members of species which cooperate with non-kin group members, would show aversive reactions to advantageous inequitable outcomes.

Lastly, it was predicted that none of the nonhuman primate species tested would exhibit contrast effects. This is because environmental resources and an animal's internal state are constantly changing in response to several variables, and food items in a natural environment are almost always different from one another in some way, even when food rewards are of the same species. In the wild, an animal can almost never expect to receive the same exact food item that the individual received in the past, and because of this, should not react negatively *a priori* when a current reward does not match those of past rewards. Additionally, captive nonhuman primates often receive food items that differ from those once shown or given to them, and should therefore not react negatively to receiving a reward different from one previously given to them.

The following predictions can then be made following the hypotheses discussed above:

Hypothesis 1: Primate species which typically cooperate with non-kin and non-pair-bonded group members *will* show aversive reactions to disadvantageous inequitable outcomes, whereas primate species which do not cooperate with non-kin, non-pair-bonded conspecifics *will not*.

Predictions:

- 1a) Orangutans *will not* respond negatively after receiving a lesser reward than their social partner after both individuals complete the same task.
- 1b) Hylobatids *will not* respond negatively after receiving a lesser reward than their social partner after both individuals complete the same task.

1c) Gorillas *will* respond negatively after receiving a lesser reward than their social partner after both individuals complete the same task.

1d) Baboons *will* respond negatively after receiving a lesser reward than their social partner after both individuals complete the same task.

Hypothesis 2: Individuals which have a strong relationship with their social partner and are members of species which cooperates with non-kin group members *will* show aversive reactions to advantageous inequitable outcomes; those individuals which do not have a strong relationship with their social partner and/or are not members of a species which cooperates with non-kin group members *will not*.

Predictions:

2a) Orangutans *will not* respond negatively after receiving a greater reward than their social partner after both individuals complete the same task.

2b) Hylobatids *will not* respond negatively after receiving a greater reward than their social partner after both individuals complete the same task.

2c) Gorillas *will* respond negatively after receiving a greater reward than their social partner after both individuals complete the same task. (This prediction is based on the fact that the pair of gorillas tested are full-siblings, have lived together for 13 years, and presumably, have a strong social relationship.)

2d) Baboons *will not* respond negatively after receiving a greater reward than their social partner after both individuals complete the same task. (This prediction is based on the fact that none of the baboons tested had prior contact with the individual they were paired with until the onset of this study;

therefore, the baboon subjects did not presumably have strong social relationships with their partners.)

Hypothesis 3: Nonhuman primates which often receive rewards that differ from previous rewards given to them will not exhibit contrast effects.

Predictions:

- 3a) Orangutans *will not* respond negatively to receiving a different reward than one that was previously shown to them.
- 3b) Hylobatids *will not* respond negatively to receiving a different reward than one that was previously shown to them.
- 3c) Gorillas *will not* respond negatively to receiving a different reward than one that was previously shown to them.
- 3d) Baboons *will not* respond negatively to receiving a different reward than one that was previously shown to them.

## CHAPTER 3

### METHODS

#### Subjects and Study Locations

Subjects included twelve olive baboons (*Papio anubis*), two western-lowland gorillas (*Gorilla gorilla*), four orangutans (*Pongo* spp.), and two white-cheeked gibbons (*Nomascus leucogenys*). All nonhuman primate subjects were novel to inequity testing. No subject was deprived of food or water, which was available *ad libitum* to all subjects during experimentation. Additionally, subjects were given two more extensive meals per day, once in the morning and once in the afternoon. With the exception of small food rewards given during experimentation, no changes to the subjects' regular feeding schedules or diet were made prior to, during, or after testing. This study was approved by the Institutional Animal Care and Use Committee of Southern Illinois University Carbondale (IACUC 15-008), the Institutional Animal Care and Use Committee of Texas Biomedical Research Institute (IACUC 1495 PC 0), and the Institutional Animal Care and Use Committee of Smithsonian National Zoological Park (NZIP-IACUC 15-17).



## Baboons

During the study, all twelve olive baboon subjects were temporarily individually housed in the veterinary clinic at the Southwest National Primate Research Center (SNPRC) in San Antonio, Texas. Baboons were housed in hanging cages, approximately 1 x 1.2 m in size, with the exception of one male subject housed in a cage stationed on the ground that was approximately 1.5 x 1.8 m in size (Table 2). At the initiation of the study, ten of the baboon subjects had been located in the veterinary clinic for 3 to 31 days due to minor illness and/or injury (Table 2). The remaining two baboons had been located in the clinic for 78 and 85 days respectively, and these two individuals formed a pair. Importantly, while the amount of time located in the clinic varied by individual, baboons were only placed next to their partners at the initiation of the study, and therefore, pairs were exposed to each other for the same amount of time. Prior to and following clinic visits, baboon subjects were housed in social groups comprised of between 4 and 14 individuals (Table 1).

To ensure that baboons' familiarity with their social partner did not affect the baboon's performance, these subjects were tested in pairs consisting of two individuals from different social groups. All pairs remained consistent throughout all trials and test sessions. Male subjects were each tested with another male subject, and female subjects were each tested with another female subject. This was because male subjects were located in one room containing only male baboons, and female subjects were located in a separate room containing only female baboons. This procedure also mimicked additional studies of nonhuman primate inequity aversion, in which male

subjects were tested only with other males, and female subjects were tested only with other females (Brosnan and de Waal, 2003; Brosnan et al., 2010).

During training and test sessions, baboon pairs were located in separate, adjacent cages placed approximately 15 cm apart. Cage sides were comprised of vertical bars spaced approximately 7 cm apart, indicating that the baboons in each pair were visible to one another at all times. Because the baboons have been reported by the facility as being both familiar and comfortable with the isolation cages, especially when receiving food rewards, this set-up was not expected to significantly influence the subjects' behavior.

### Apes

Two western-lowland gorillas, four orangutans, and two white-cheeked gibbons were housed in social groups at the Smithsonian National Zoological Park (NZP) in Washington, D.C. One gorilla social group was tested, which consisted of two full-sibling black-back males. Two orangutan social groups were tested, which each included one mating pair of orangutans. One gibbon social group was tested, which consisted of one mating pair of gibbons.

Because gorilla, orangutan, and gibbon subjects were limited, individuals of these species were tested in pairs consisting of two individuals from the same social group. All pairs remained consistent throughout all trials and test sessions. Gorillas, orangutans, and gibbons were temporarily separated from their partner into adjacent cages prior to each training and test session. Mesh doors separated the adjacent enclosures, and therefore, subjects were visible to one another for the duration of

experimentation. Following each session, the subjects were reintroduced to their group mate. Separating subjects from their social partners allowed for more control over the experimental conditions and prevented aggressive interactions between group mates during testing. Importantly, gorilla and orangutan subjects separate daily into individual cages for their afternoon meals, so separating from their social partners was not unusual. Additionally, the gorilla, orangutan, and gibbon subjects all separated from one another willingly and showed no signs of stress due to separation. Therefore, this set-up was not expected to significantly influence the subjects' behavior.

### Food Preference Tests

Prior to inequity testing, food preference tests were completed in order to determine which food items each primate pair considered to be high and low-value rewards. A dichotomous choice test (Brosnan and de Waal, 2004a, b) was used in which an assortment of foods was sequentially offered to the subjects, two food items at a time. All food items were preapproved by the facilities' administrations and were foods that the subjects were familiar with prior to this study.

#### Baboons

For food preference tests with baboons, the experimenter began by holding a piece of carrot (approximately 2.5 cm x 2.5 cm x 3 mm) in one hand and piece of grape (approximately 2.5 cm x 2.5 cm x 3 mm) in the other hand, keeping their hands centered on the primate subject and approximately 30 cm apart. The experimenter then

stepped forward approximately 30 cm from the first subject's cage. The baboon subject was required to gesture with their hand, foot, or head toward one of the two food items, at which point the experimenter handed the baboon the food item that was gestured toward by the subject (Brosnan and de Waal, 2004). The experimenter marked which food item the subject gestured toward and then repeated this process with the second subject. To control for side biases, the experimenter alternated food items between their left and right hands between trials (Brosnan et al., 2010).

This food preference test was completed a total of 5 times, followed by 5 trials of carrot vs. mini marshmallow and 5 trials of grape vs. mini marshmallow (15 trials per subject). The food item that was chosen the most by the pair of baboons was marked as the high-value food; the food that was chosen the least was considered the low-value food. Each baboon pair had to prefer the high-value food item over the low-value food item in at least 80% of the trials in order to move on with experimentation (Brosnan et al., 2010).

The experimenter then offered each baboon subject 5 successive pieces of the low-value food to ensure that the subjects were willing to eat several consecutive pieces of this food item. This was important, because each subject would be required to eat several successive pieces of this food item during inequity testing. This step ensured that any negative reaction by a baboon subject after receiving the low-value food reward during inequity tests would be due to an aversion to the reward distribution and not to the dislike of the food item itself.

## Apes

Food preference tests with gorillas, orangutans, and gibbons were similar to those completed with baboons, with the exception of a few procedural changes. To ensure that the ape subjects' preferences would not change, the food preference tests were completed over a two-day period. In initial food preference tests, subjects appeared to maintain side biases, even after implementing the changing of foods from one hand to the other between trials. Therefore, to further avoid side biases, a computerized randomizer was used to determine in which hand the experimenter would hold each food item during each trial (as opposed to a continuous right-then-left pattern).

When testing apes, the experimenter began by holding the two food items approximately 2.5 cm apart for about 1 s and then would separate the two items to approximately 30 cm apart. Each ape subject was exposed to 10 trials of each food preference test (30 trials per day and 60 trials total). All gorilla, orangutan, and gibbon subjects were also required to eat 15 consecutive pieces of the low-value food item, as each subject would be required to eat this amount during inequity testing.

Food items offered to ape subjects during food preference tests varied by species according to previous food preferences documented by the apes' caregivers. Gorillas completed food preference trials with apple vs. carrot, apple vs. grape, and carrot vs. grape. Orangutans were offered apple vs. orange, apple vs. grape, and orange vs. grape during food preference tests. Gibbons completed food preference tests with apple vs. melon, apple vs. grape, and melon vs. grape. All food items for

gorillas and orangutans were approximately 2.5 cm x 2.5 cm x 3 mm in size. All food items for gibbons were approximately 6 mm x 6 mm x 3 mm in size.

### Training

Prior to inequity testing, all nonhuman primate subjects were trained to complete a task. Following task completion during training sessions, the experimenter rewarded baboon subjects with a 2.5 cm x 2.5 cm x 3 mm piece of apple, gorilla subjects with a 2.5 cm x 2.5 cm x 3 mm piece of banana, orangutan subjects with a 2.5 cm x 2.5 cm x 3 mm piece of papaya, and gibbon subjects with a 6 mm x 6 mm x 3 mm piece of banana. These food items were used only during training sessions for each species to ensure that the subjects did not become biased toward the food item used for training (Brosnan et al., 2010). To avoid side biases, the experimenter alternated between trials which hand held the target or token and which hand held the food reward (Brosnan et al., 2010).

### Baboons and Gibbons

Baboons and gibbons were trained to accomplish a targeting task which required each subject to hold a designated target for 1 s and then release the target (Freeman et al., 2013). The target used for baboons was a piece of curved PVC pipe (approximately 7.5 cm long and 3.5 cm wide) with a circular chain running through the opening of the pipe which attached to a clip at the opposite end. This item was approved and provided by SNPRC. The target used for gibbon subjects was a small piece of bamboo

(approximately 7.5 cm long and 6 mm wide), which was approved and provided by NZP.

For baboons, the experimenter stepped up to the subject's cage with the target in one hand and the piece of banana visible to the subject in the other hand. The experimenter then clipped the target onto the middle of the cage at the subject's eye level, and then stepped back. The baboon was given 30 s to approach and hold the target with their hand or foot for 1 s. When the subject removed their hand or foot from the target, the experimenter handed the baboon a piece of apple. The experimenter then moved on to the second subject in the pair and repeated the procedure. The experimenter alternated between individuals in the pair, completing 10 trials with each subject. Each baboon subject was required to complete 8 of 10 targeting tasks before moving on to testing sessions.

For gibbons, the experimenter stepped up to the subject's enclosure, held one end of the bamboo in one hand and the piece of banana visible to the subject in the other hand. The experimenter then placed the opposite end of the bamboo into the enclosure mesh at the subject's waist level (or what would be waist level if the subject was not sitting at the start of the trial). The gibbon was given 30 s to approach and hold the target with their hand or foot for 1 s. When the subject removed their hand or foot from the target, the experimenter handed them a piece of banana. The experimenter then moved on to the second subject in the pair and repeated the procedure. The experimenter alternated between individuals in the pair, completing 15 trials with each subject. Each gibbon subject was required to complete 12 of 15 targeting tasks before moving on to testing sessions.

## Gorillas and Orangutans

Gorilla and orangutan subjects completed a token-exchange task during training sessions, which required each subject to trade a piece of bamboo (approximately 15 cm long and 3.5 cm wide) with an experimenter. The bamboo tokens were approved and provided by NZP. For the token-exchange task, the experimenter stepped up to the subject's enclosure holding one end of the bamboo in one hand and a piece of banana (for gorillas) or papaya (for orangutans) visible to the subject in the other hand. The experimenter then placed the opposite end of the bamboo into the enclosure at the subject's waist level (or what would be waist level if the subject was not sitting at the start of the trial). Each subject was given 30 s to take the piece of bamboo from the experimenter, hold onto it for 1 s, and then give it back to the experimenter through the enclosure mesh. When the subject completed this task, the experimenter handed the ape a piece of banana (for gorillas) or papaya (for orangutans). The experimenter then moved on to the second subject in the pair and repeated the procedure. The experimenter alternated between individuals in the pair, completing 15 trials with each subject. Each gorilla and orangutan subject was required to complete 12 of 15 token-exchange tasks before moving on to testing sessions.

## Testing

Each primate participated in a series of five tests (described below), completing 30 trials (20 trials for baboons) as the role of the subject (Session 1) and 30 trials (20 trials for baboons) as the role of the partner (Session 2) for each test. The subject and



partner were visible to one another through either cage bars (baboons) or enclosure mesh (apes) during all testing sessions, indicating that each subject had the opportunity to see which food reward their partner received. During each test, high and low-value rewards were visible through clear containers to both the subject and partner at all times (Brosnan et al., 2011).

During each trial, the partner completed the task in exchange for a food reward prior to the subject; whether each primate began as the subject or partner was randomized (Brosnan et al., 2010). The first exchange between the *partner* and the experimenter constituted the first trial of the session. The first exchange between the *subject* and the experimenter represented the second trial of the session. This indicates that each individual completed 15 tasks (10 tasks for baboons) per session. For each trial, each primate had 30 seconds to complete the task. If the task was completed within the 30 seconds, the experimenter handed the primate a food reward. If the task was not completed within 30 seconds, the experimenter did not give that primate a food reward and instead moved on to the second individual in the pair. For each pair of primates, all tests described below occurred on separate days, meaning that no individual completed more than one test per day.

Following each trial, each primate's reaction after completing a task for a food reward was marked as either negative or positive. If the primate stopped participating in the task, did not take the reward from the experimenter, or took the reward but did not eat it, the experimenter considered the reaction to be a reward rejection, or a negative response (Brosnan et al., 2010; Brosnan et al., 2011; Brosnan and de Waal, 2003; Freeman et al., 2013; Hooper et al., 2013; Massen et al., 2012; Talbot et al., 2011; van

Wolkenten et al., 2007). If the primate continued to participate in task completion and ate the food reward, the reaction was marked as positive for that trial (Brosnan et al., 2010; Brosnan et al., 2011; Brosnan and de Waal, 2003; Freeman et al., 2013; Hooper et al., 2013; Massen et al., 2012; Talbot et al., 2011; van Wolkenten et al., 2007). Following each trial, the experimenter recorded on data sheets whether the responses of the subjects and partners were negative or positive.

The experimenter also recorded *ad libitum* instances of abnormal and aggressive behavior observed for the subject and partner. Abnormal behaviors included pacing, in which an individual moves back and forth in the enclosure for at least two cycles, self-biting, in which an individual bites a part of their own body (Lutz et al., 2003), and cage-licking, in which an individual licks the sides, ceiling, or floor of the enclosure. Aggressive behaviors included yawning, in which an individual opens their mouth to display their teeth (Maestripieri et al., 1992) and cage-banging, in which an individual uses a body part (usually their hands, feet, or head) to apply excessive force to the walls, ceiling, or floor of the enclosure. After all behaviors were recorded for the trial, the next trial immediately followed.

### Test 1: Testing for Contrast Effects

To test for contrast effects, or individual expectations (Chen and Santos, 2006), each pair of primates completed two sessions consisting of 30 trials each (20 trials each for baboons). For the first session, both the subject and partner were shown a high-value reward prior to task completion but were given a low-value reward following task completion. For the second session, both the subject and partner were shown a

large-quantity reward (three pieces of low-value food) prior to task completion but were given a small-quantity reward (one piece of low-value food) following task completion.

### Test 2: Equitable Reward Quality

Prior to inequitable quality testing, each pair of primates completed two control sessions, in which both the subject and partner received the same reward. In the first control session, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for a low-value food reward (named the low-value control). In the second control session, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for a high-value food reward (named the high-value control). Because the reward quality was increasing across control sessions, individual expectations were not expected to affect the results.

### Test 3: Inequitable Reward Quality

In the inequity-quality test, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for a food reward. However, the partner always received the high-value food reward after task completion, and the subject always received the low-value food reward after task completion. To test for disadvantageous inequity aversion, the subjects' responses to this test were compared to their responses in the low-value control; to test for advantageous inequity aversion, the partner's responses to this test were compared to their responses in the high-value control (Brosnan et al., 2010).

#### Test 4: Equitable Reward Quantity

Prior to inequitable quantity testing, each pair of primates completed two control sessions, in which both the subject and partner received the same amount of rewards. In the first control session, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for one low-value food reward (named the small-quantity control). In the second control session, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for three low-value food rewards (named the large-quantity control). Because, the reward quantity was increasing across control sessions, individual expectations should not have affected the results.

#### Test 5: Inequitable Reward Quantity

In the inequity-quantity test, 30 trials (20 trials for baboons) were completed in which the subject and partner alternated completing a task for a food reward. However, the partner always received the large-quantity food reward (three pieces of low-value food) after task completion, and the subject always received the small-quantity food reward (one piece of low-value food) after task completion. To test for disadvantageous inequity aversion, the subjects' responses to this test were compared to their responses in the small-quantity control. To test for advantageous inequity aversion, the partner's responses to this test were compared to their responses in the large-quantity control.

### Interobserver Reliability

Interobserver reliability scores were calculated to ensure that observations and scoring of animals' behaviors were without bias. 20% of live-time sessions at SNPRC were scored by a second experimenter not involved in the study. All sessions completed at NZP were video-recorded using a Canon EOS Rebel T5 camera, and 20% of experiments were scored from video footage by a person not involved in the study. Each of these people was given identical copies of the primary experimenter's data sheets and was asked to score whether each subject did or did not complete the task and whether each subject did or did not accept the food reward. Following this procedure, the score consistencies between the experimenter and the second scorers were compared. The interobserver reliability score for sessions observed at SNPRC was 1.00, indicating that 100% of baboon observations were consistent between the experimenter and the second scorer. The interobserver reliability score for sessions observed at NZP was .998, indicating that 99.8% of ape observations were consistent between the experimenter and the second scorer.

### Statistical Analysis

Wilcoxon signed-ranked tests for related samples were used to compare test conditions to control conditions (Brosnan et al., 2010). To test for quality contrast effects, the subjects' responses to the quality contrast condition were compared to their responses in the low-value control. The subjects' responses to the disadvantageous

inequitable quality condition were also compared to their responses in the low-value control in order to test for disadvantageous inequity aversion when rewards varied by quality. To test for advantageous inequity aversion when rewards varied by quality, the subjects' responses to the advantageous inequitable quality condition were compared to their responses in the high-value control. To test for quantity contrast effects, the subjects' responses to the quantity contrast condition were compared to their responses in the small-quantity control. The subjects' responses to the disadvantageous inequitable quantity condition were also compared to their responses in the small-quantity control in order to test for disadvantageous inequity aversion when rewards varied by quantity. To test for advantageous inequity aversion when rewards varied by quantity, the subjects' responses to this test were compared to their responses in the large-quantity control.

In order to determine whether there was variation in responses across conditions for each species, Friedman's tests were conducted (Brosnan et al., 2010). Friedman's test was used once for each species to determine whether there was variation across quality conditions. Friedman's tests were also conducted for each species to determine whether responses varied across quantity conditions. Friedman's tests were then conducted a third time for each species to assess variation across all ten conditions (including both quality and quantity conditions).

## CHAPTER 4

### RESULTS

#### Intraspecific Comparisons

##### Food Preference Tests and Training

Food preference tests showed that baboon subjects chose a mini marshmallow (high-value reward) over a piece of carrot (low-value reward) in 60 out of 60 overall trials (100% of the time). Gorilla subjects preferred a piece of grape (high-value reward) over a piece of carrot (low-value reward) in 68 out of 80 overall trials (85% of the time). Gibbon subjects preferred a piece of grape (high-value reward) over a piece of cantaloupe (low-value reward) in 64 out of 80 overall trials (80% of the time). One pair of orangutan subjects (Kyle and Bonnie) preferred a piece of grape (high-value reward) over a piece of carrot (low-value reward) in 75 out of 80 overall trials (94% of the time). The other pair of orangutan subjects (Kiko and Iris) preferred a piece of grape (high-value reward) over a piece of orange (low-value reward) in 65 out of 80 overall trials (81% of the time). Given that each pair was required to choose the high-value food item over the low-value food item in at least 80% of trials, each pair of subjects moved on to training.

During training sessions, each of the twelve baboon subjects, each of the two gorilla subjects, each of the two gibbon subjects, and each of the four orangutan subjects completed the designated task in exchange for a food reward in at least 80% of trials (the criteria for beginning experimentation). Therefore, all baboon, gorilla, gibbon, and orangutan subjects moved on to testing sessions.

### Notes on Testing Orangutans

One pair of orangutans (Bonnie and Kyle) stopped willingly separating into adjacent enclosures after the second day of testing, and therefore did not complete either of the quality control conditions, either of the inequitable quality conditions, or either of the inequitable quantity conditions. Therefore, this pair of individuals was only included in analyses regarding quantity contrast effects.

### Testing for Quality Contrast Effects

To test for quality contrast effects, subjects' refusal rates during the quality contrast condition (in which the subject was shown a high-value reward prior to task completion but was given a low-value reward following task completion) were compared to the same individuals' refusal rates in the low-value control (in which the subject was shown a low-value reward prior to task completion and was given that same low-value reward following task completion) (Table IV). Results showed that five of the twelve baboon subjects responded with higher refusal rates during the quality contrast condition than during the low-value control (Figure I; Table V). However, a Wilcoxon signed-rank test showed that there was no statistical difference between baboons'



refusal rates during the low-value control and the refusal rates during the quality contrast condition ( $Z = -1.134$ ,  $p = .257$ ) (Table V). Both of the two gorilla subjects responded with higher refusal rates during the quality contrast condition than during the low-value control (Figure I; Table VI); however, a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = -1.414$ ,  $p = .157$ ) (Table VI). Neither of the two gibbon subjects responded with higher refusal rates during the quality contrast condition than during the low-value control (Figure I; Table VII); a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during these conditions ( $Z = -1.000$ ,  $p = .317$ ) (Table VII). Neither of the two orangutan subjects responded with higher refusal rates during the quality contrast condition than during the low-value control (Figure I; Table VIII); a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during these conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VIII).

#### Testing for Quantity Contrast Effects

To test for quantity contrast effects, subjects' refusal rates during the quantity contrast condition (in which the subject was shown three pieces of low-value food prior to task completion but was given only one piece of low-value food following task completion) were compared to the same individuals' refusal rates during the small-quantity control (in which the subject was shown only one piece of low-value food prior to task completion and was given that same piece of low-value food following task completion) (Table IV). Results showed that six of the twelve baboon subjects

responded with higher refusal rates during the quantity contrast condition than during the small-quantity control (Figure II; Table V). A Wilcoxon signed-rank test showed that there was a statistical difference between baboons' refusal rates during the small-quantity control and the refusal rates during the quantity contrast condition ( $Z = -2.449$ ,  $p = .014$ ) (Table V). Both of the gorilla subjects responded with higher refusal rates during the quantity contrast condition than during the small-quantity control (Figure II; Table VI); however, a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = -1.414$ ,  $p = .157$ ) (Table VI). One of the two gibbon subjects responded with higher refusal rates during the quantity contrast condition than during the small-quantity control (Figure II; Table VII); a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during the small-quantity control and the refusal rates during the quantity contrast condition ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VII). Two of the four orangutan subjects responded with higher refusal rates during the quantity contrast condition than during the small-quantity control (Figure II; Table VIII); however, a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during these conditions ( $Z = -1.414$ ,  $p = .157$ ) (Table VIII).

#### Disadvantageous Inequitable Reward Quality

To test for disadvantageous inequity aversion when the reward qualities differed, subjects' refusal rates from the disadvantageous inequitable quality condition (in which the subject was given a low-value reward after task completion and the partner was given a high-value reward after task completion) were compared to the same

individuals' refusal rates during the low-value control (in which both the subject and partner were each given a low-value reward following task completion) (Table IV). Five of the twelve baboon subjects responded with higher refusal rates during the disadvantageous inequitable quality condition than during the low-value control (Figure III; Table V). However, a Wilcoxon signed-rank test showed no statistical difference between baboons' refusal rates during the low-value control and the refusal rates during the disadvantageous inequitable quality condition ( $Z = -1.134$ ,  $p = .257$ ) (Table V). One of the two gorilla subjects responded with higher refusal rates during the disadvantageous inequitable quality condition than during the low-value control (Figure III; Table VI), although a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = -1.000$ ,  $p = .317$ ) (Table VI). One of the two gibbon subjects responded with higher refusal rates during the disadvantageous inequitable quality condition than during the low-value control (Figure III; Table VII); however, a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during the low-value control and the refusal rates during the disadvantageous inequitable quality condition ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VII). Neither of the two orangutan subjects responded with higher refusal rates during the disadvantageous inequitable quality condition than during the low-value control (Figure III; Table VIII), and a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VIII).

### Disadvantageous Inequitable Reward Quantity

To test for disadvantageous inequity aversion when reward quantities differed, subjects' refusal rates from the disadvantageous inequitable quantity condition (in which the subject was given one piece of low-value food after task completion and the partner was given three pieces of low-value food after task completion) were compared to the same individuals' refusal rates from the small-quantity control (in which both the subject and partner were each given one piece of low-value food following task completion) (Table IV). Four of the twelve baboon subjects responded with higher refusal rates during the disadvantageous inequitable quantity condition than during the small-quantity control (Figure IV; Table V). However, a Wilcoxon signed-rank test showed that there was no statistical difference between baboons' refusal rates during the small-quantity control and the same individual's refusal rates during the disadvantageous inequitable quantity condition ( $Z = -.816$ ,  $p = .414$ ) (Table V). Only one of the two gorilla subjects responded with higher refusal rates during the disadvantageous inequitable quantity condition than during the small-quantity control (Figure IV; Table VI); however, a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VI). Only one of the two gibbon subjects responded with higher refusal rates during the disadvantageous inequitable quantity condition than during the small-quantity control (Figure IV; Table VII), and a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during the small-quantity control and the refusal rates during the disadvantageous inequitable quantity condition ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VII). Neither of the two orangutan subjects responded with

higher refusal rates during the disadvantageous inequitable quantity condition than during the small-quantity control (Figure IV; Table VIII), and a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VIII).

#### Advantageous Inequitable Reward Quality

To test for advantageous inequity aversion when reward qualities differed, subjects' refusal rates from the advantageous inequitable quality condition (in which the subject was given a high-value reward after task completion and the partner was given a low-value reward after task completion) were compared to the same individuals' refusal rates from the high-value control (in which both the subject and partner were each given a high-value reward following task completion) (Table IV). Three of the twelve baboon subjects responded with higher refusal rates during the advantageous inequitable quality condition than during the high-value control (Figure V; Table V). A Wilcoxon signed-rank test showed that there was no statistical difference between baboons' refusal rates during the high-value control and the same individual's refusal rates during the advantageous inequitable quality condition ( $Z = -1.732$ ,  $p = .083$ ) (Table V). Neither of the two gorilla subjects responded with higher refusal rates during the advantageous inequitable quality condition than during the high-value control (Figure V; Table VI), and a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VI). Neither of the two gibbon subjects responded with higher refusal rates during the advantageous inequitable quality condition than during the high-

value control (Figure V; Table VII), and a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VII). Similarly, neither of the two orangutan subjects responded with higher refusal rates during the advantageous inequitable quality condition than during the high-value control (Figure V; Table VIII), and a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during the high-value control and the refusal rates during the advantageous inequitable quality condition ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VIII).

#### Advantageous Inequitable Reward Quantity

To test for advantageous inequity aversion when reward quantities differed, subjects' refusal rates from the advantageous inequitable quantity condition (in which the subject was given three pieces of low-value food after task completion and the partner was given one piece of low-value food after task completion) were compared to the same individuals' refusal rates from the large-quantity control (in which both the subject and partner were each given three pieces of low-value food following task completion) (Table IV). One of the twelve baboon subjects responded with higher refusal rates during the advantageous inequitable quantity condition than during the large-quantity control (Figure VI; Table V). A Wilcoxon signed-rank test showed that there was no statistical difference between baboons' refusal rates during the large-quantity control and the same individual's refusal rates during the advantageous inequitable quantity condition ( $Z = -1.000$ ,  $p = .317$ ) (Table V). Only one of the two gorilla subjects responded with higher refusal rates during the advantageous

inequitable quantity condition than during the large-quantity control (Figure VI; Table VI), a Wilcoxon signed-rank test showed that there was no statistical difference between gorillas' refusal rates during these two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VI). Only one of the two gibbon subjects responded with higher refusal rates during the advantageous inequitable quantity condition than during the large-quantity control (Figure VI; Table VII); however, a Wilcoxon signed-rank test showed that there was no statistical difference between gibbons' refusal rates during the large-quantity control and the refusal rates during the advantageous inequitable quantity condition ( $Z = -1.000$ ,  $p = .317$ ) (Table VII). Neither of the two orangutan subjects responded with higher refusal rates during the advantageous inequitable quantity condition than during the large-quantity control (Figure VI; Table VIII), and a Wilcoxon signed-rank test showed that there was no statistical difference between orangutans' refusal rates during the two conditions ( $Z = 0.000$ ,  $p = 1.000$ ) (Table VIII).

### Overall Results

To determine whether subjects' refusal rates varied across conditions for each species, Friedman's tests were conducted. Friedman's tests indicated that baboon subjects' refusal rates did not significantly vary across the five different conditions related to reward quality ( $X^2 = 7.447$ ,  $p = .114$ ) (Table IX). Friedman's tests indicated that baboon subjects' refusal rates did significantly vary across the five different conditions related to reward quantity ( $X^2 = 13.491$ ,  $p = .009$ ) (Table IX), and the ten total conditions overall ( $X^2 = 20.810$ ,  $p = .014$ ) (Table IX). However the statistically significant results found for baboons in the quantity contrast effects condition (Table V) may have

caused the statistically significant variation across the five different conditions related to reward quantity and the ten total conditions overall. Friedman's tests indicated that gorilla subjects' refusal rates did not significantly vary across the five different conditions related to reward quality ( $X^2 = 6.400$ ,  $p = .171$ ) (Table IX), across the five different conditions related to reward quantity ( $X^2 = 4.000$ ,  $p = .406$ ) (Table IX), or across the ten total conditions overall ( $X^2 = 11.824$ ,  $p = .223$ ) (Table IX). Similarly, Friedman's tests indicated that gibbon subjects' refusal rates did not significantly vary across the five different conditions related to reward quality ( $X^2 = 4.000$ ,  $p = .406$ ) (Table IX), across the five different conditions related to reward quantity ( $X^2 = 1.857$ ,  $p = .762$ ) (Table IX), or across the ten total conditions overall ( $X^2 = 6.581$ ,  $p = .681$ ) (Table IX).

Because only two orangutan subjects completed all of the ten conditions, only these two subjects were considered for analyses regarding variation across conditions. These two orangutan subjects showed 0% refusal rates for each of the ten conditions (Figures I-VI); therefore, no Friedman's tests were needed to indicate variation across conditions. It is clear to see that orangutan subjects' refusal rates did not vary across the five different conditions related to reward quality, across the five different conditions related to reward quantity, or across the ten total conditions overall.

### Interspecific Comparisons

Because most of the intraspecific results were not statistically significant, any interspecific comparisons using this data must be interpreted with caution. Similarly, the



small sample size of individuals within each species, as well as the small number of species tested here, renders interpreting species differences more difficult.

Nonetheless, qualitatively comparing the trends observed for contrast effects and inequity aversion in each species can provide insight into possible evolutionary pressures that may have contributed to the emergence of inequity aversion in primates.

### Contrast Effects

When testing for quality contrast effects, it was found that five (almost half of) baboon subjects, both (all of) gorilla subjects, zero gibbon subjects, and zero orangutan subjects responded negatively more often during the quality contrast condition than during the low-value control (Tables V-VIII). Notably, these baboon subjects' refusal rates ranged from 10% to 40%, whereas these gorilla subjects' refusal rates ranged from 6.7% to only 13.3% (Figure I). When testing for quantity contrast effects, it was found that six (half of) baboon subjects, both (all of) gorilla subjects, one (half of) gibbon subject, and two (half of) orangutan subjects responded negatively more often during the quantity contrast condition than during the small-quantity control (Tables V-VIII). First, it is important to note that these results were only statistically significant for baboons (Table V). Second, it is important to consider that these baboon subjects' refusal rates ranged from 10% to 50%, whereas these gorilla subjects' refusal rates ranged from 6.7% to 40%, and these gibbon and orangutan subjects' refusal rates were all only 13.3% (Figure II).

### Disadvantageous Inequity Aversion

None of the four species tested (olive baboons, western-lowland gorillas, white-cheeked gibbons, or orangutans) showed significant differences in their refusal rates during the disadvantageous inequitable quality condition as compared to the low-value control. However, five of the twelve (nearly half of) baboon subjects, one of the two (half of) gorilla subjects, and one of the two (half of) gibbon subjects responded negatively more often in the disadvantageous inequitable quality condition than in the low-value control (Tables V-VII). Notably, however, these baboon subjects' refusal rates ranged from 10% to 100%, whereas the gorilla and gibbon subjects' refusal rates were both only 13.3% (Figure III). Orangutan subjects' refusal rates remained at 0% (Figure III).

A similar pattern was found when subjects were tested for disadvantageous inequity aversion when reward quantities differed. Four of the twelve baboon subjects, one of the two gorilla subjects, and one of the two gibbon subjects responded negatively more often during the disadvantageous inequitable quantity condition than during the small-quantity control (Tables V-VII). Again, it is important to note that these baboon subjects' refusal rates ranged from 10% to 80%, whereas these gorilla and gibbon subjects' refusal rates were both only 13.3% (Figure IV). Orangutan subjects' refusal rates remained at 0% (Figure IV).

### Advantageous Inequity Aversion

When testing for advantageous inequity aversion when reward qualities differed, it was found that only three baboon subjects and zero ape subjects responded negatively more often during the advantageous inequitable quality condition than during

the high-value control (Tables V-VIII). When testing for advantageous inequity aversion when reward quantities differed, it was found that only one baboon subject, one gorilla subject, and one gibbon subject responded negatively more often during the advantageous inequitable quantity condition than during the large-quantity control (Tables V-VII). No orangutan subjects refused the reward or refused to participate when given a greater amount of rewards than were given to a social partner (Table VIII).

### Individual Trends

Although no statistically significant differences were found between any of the conditions for gorillas (Table VI), individual trends did exist for this species. For example, one gorilla individual (Kojo) responded negatively more often in both contrast conditions and both disadvantageous inequity conditions than they did during the control conditions (Figures I-IV). Similarly, the other gorilla subject (Kwame) responded negatively more often in both contrast conditions than they did during the control conditions but did not show disadvantageous inequity aversion (Figures I-IV).

Similar trends were found for gibbon subjects, although no statistically significant differences were found between conditions for this species (Table VII). For instance, one gibbon subject (Tuyen) responded negatively more often in both disadvantageous inequity conditions, the quantity contrast condition, and the advantageous inequitable quantity condition than they did during the control conditions (Figures II, III, IV, and VI). On the other hand, the other gibbon subject (Sydney) did not respond negatively to any of the conditions presented (Figures I-VI).

Unlike gorillas and gibbons, baboon individuals' responses were much more variable. However, some trends among individuals were apparent. For instance, eleven of the twelve baboon subjects responded negatively to at least one test condition, and five of the twelve baboon subjects responded negatively to at least three test conditions (Figures I-VI). This result was dichotomous in that an individual either responded negatively to only one condition, or the individual responded negatively to at least half of the conditions presented. This could indicate that some individuals are more sensitive to inequity than others. Also, one baboon subject (27885) responded negatively in all of the quality test conditions, but none of the quantity test conditions (Figures I-VI), which may indicate that this individual was sensitive to differences in reward quality but not differences in reward quantity.

While some individual trends seem apparent in orangutans, these results should be interpreted with caution. For instance, one orangutan subject (Bonnie) responded to both contrast conditions (Figures I and II). However, this individual was not tested during the other conditions, so no conclusions can be made about whether this individual always responds negatively during test conditions. One interesting trend, however, is that two individuals (Kiko and Iris) did not respond to any of the conditions presented (Figures I-VI).

### Behavioral Observations

After recording *ad libitum* instances of behavior for each primate subject, the number of instances of each behavior was determined for each experimental condition.

It was found that none of the ape subjects exhibited instances of abnormal or aggressive behavior (pacing, self-biting, cage-licking, yawning, or cage-banging) during any of the control or test conditions. Similarly, no instances of abnormal or aggressive behavior were observed for any of the baboon subjects during control conditions, and none of the baboon subjects were observed pacing or self-biting during any of the test conditions.

However, some of the baboon subjects did exhibit abnormal and aggressive behaviors during some of the test conditions. During the quality contrast condition, one baboon (27885) showed three instances of cage-banging, and another baboon (26058) showed yawning behavior once and cage-banging behavior once. During the disadvantageous inequitable quality condition, one baboon (13228) showed nine instances of yawning, another baboon (16486) showed two instances of cage-licking, and a third baboon (15225) showed nine instances of cage-licking. During the disadvantageous inequitable quantity condition, one baboon (13228) showed seven instances of yawning. During the advantageous inequitable quality condition, one baboon (13246) showed one instance of yawning, and another baboon (16486) showed one instance of cage-licking. During the advantageous inequitable quantity condition, one baboon (26058) showed two instances of yawning. These results could indicate that stress levels may have been elevated in some of the individual baboon subjects when the individuals were given an unequal reward. However, instances of abnormal and aggressive behavior were not assessed for these individuals prior to experimentation, and therefore, this correlation should be further explored.

## CHAPTER 5

### DISCUSSION

#### Contrast Effects

Chen and Santos (2006) hypothesized that a negative response to unequal outcomes is a reply to a violation of previous expectations, or contrast effects, rather than a reply to a violation of social expectations. However, in this study, it was hypothesized that none of the four nonhuman primate species tested would exhibit contrast effects. This is because the primate subjects in this study were accustomed to receiving food items that were less or more preferred than food items once shown or given to them, and therefore, should not form expectations regarding the value or quantity of their provisions. It was predicted that baboons, gorillas, gibbons, and orangutans would not respond negatively after receiving a lesser reward following task completion than the reward that was shown to them prior to task completion.

Results indicated that this prediction was supported statistically for gorillas, gibbons, and orangutans when rewards varied by quality and when rewards varied by quantity. The prediction was also supported statistically for baboons when rewards varied by quality. However, the prediction was not supported statistically for baboons

when rewards varied by quantity. There was a statistically significant difference between baboons' refusal rates during the quantity contrast effects condition -- in which the subjects were shown three pieces of low-value reward prior to task completion but were only given one piece of low-value reward following task completion—and baboons' refusal rates during the low-value control – in which the subjects were shown one piece of low-value reward prior to task completion and were given one piece of low-value reward following task completion. This suggests that baboons may have individual expectations about the amount of rewards they receive following the completion of a task, but they may not have individual expectations about the quality of rewards they receive following task completion.

While the baboon subjects in this study have, in the past, often received food items that are less or more preferred than food items once shown or given to them, the baboons may not be accustomed to a change in reward value following the completion of a task. It is possible that requiring the monkeys to put in effort by completing a task causes their individual expectations about rewards to change, because they may expect similar rewards each time a task is completed. This would be consistent with prior studies that showed that subjects' reward refusal rates were lower when food provisions were given in the absence of a task than when the subjects were required to “work” for their food rewards (Brosnan et al., 2010; Talbot et al., 2011). However, this does not explain why baboons react negatively to receiving a lesser amount of rewards than previously shown to them but do not react negatively to receiving a lower quality reward than previously shown to them.

Although the results from this study suggest that the expectations about quality and quantity are decoupled, it would still be expected that individual expectations following task completion would be consistent regardless of whether the individual was expecting a certain quality or quantity of rewards. From an ecological perspective, it would make sense that individuals would wish to maximize the amount of food available to them, perhaps leading to enhanced individual expectations about food quantity. One explanation for the differences seen between quality contrast effects and quantity contrast effects in olive baboons may be related to within-group food competition and dominance rank. For instance, one study showed that dominance rank in olive baboons was significantly correlated with the amount of food intake but not with food quality (Barton and Whiten, 1993), suggesting that food competition was enhanced when the amount of food was reduced but not when the food available varied by quality. This may suggest that increased within-group food competition led to an increase in the selective pressure to form expectations about the amount of food an individual should receive; this may also explain why baboons respond negatively to quantity contrast effects but not quality contrast effects.

Although food competition may not be as pronounced for western-lowland gorillas, white-cheeked gibbons, and orangutans, the possibility that these species exhibit quantity contrast effects cannot be ruled out at this time. Because only a small number of gorillas, gibbons, and orangutans were tested in this study, it is possible that these species also respond negatively to receiving a lesser amount of rewards than previously shown to them, and the small sample size is the cause of the statistically



nonsignificant result. Therefore, quantity contrast effects should be further explored in these species.

### Disadvantageous Inequity Aversion

In opposition to Chen and Santos (2006), Brosnan and de Waal (2003) hypothesized that a negative response to unequal outcomes is a reaction to a violation of social expectations, as opposed to a violation of previous expectations. This suggests that inequity aversion evolved in tandem with an increase in cooperative relationships with non-kin group members in species living in large, complex social groups (Brosnan and de Waal, 2003). This hypothesis has thus far been supported considering only chimpanzees (*Pan troglodytes*), capuchin monkeys (*Cebus apella*), and macaques (*Macaca mulatta* and *Macaca fascicularis*) have been shown to be inequity averse, while orangutans (*Pongo pygmaeus*), squirrel monkeys (*Saimiri sciureus* and *Saimiri boliviensis*), owl monkeys (*Aotus*), marmosets (*Callithrix jacchus*), and tamarins (*Saguinus oedipus*) did not respond to inequitable outcomes (Brosnan and de Waal, 2014).

In the current study, it was therefore hypothesized that primate species which typically cooperate with non-kin and non-pair-bonded group members would show aversive reactions to disadvantageous inequitable outcomes. Because olive baboons and western-lowland gorillas are species which typically live in large social groups (greater than four individuals) and show cooperation among non-kin, non-pair-bonded group members, these species were expected to respond negatively after receiving a

lesser reward than their social partner. It was also predicted that gibbons and orangutans would not respond negatively after receiving a lesser reward than their social partner, because gibbons and orangutans do not live in large social groups and do not typically cooperate with non-kin, non-pair-bonded conspecifics.

The predictions were supported statistically for gibbons and orangutans but not for baboons and gorillas. Although no statistically significant differences in refusal rates between the disadvantageous inequity conditions and the control conditions were found for any of the four species in the current study, there was a similar trend in results for baboons, gorillas, gibbons, and orangutans. This was true when rewards varied by quality and when rewards varied by quantity. None of the orangutan subjects tested responded negatively to disadvantageous inequity in the quality or quantity conditions. However, nearly half of the baboon subjects and exactly half of the gorilla and gibbon individuals tested had higher refusal rates during disadvantageous inequity conditions than during control conditions. This suggests that a tendency for baboons, gorillas, and gibbons to recognize and respond negatively to unequal reward distributions should not yet be rejected. Based on the small sample size of individuals tested for each species in this study, it is possible that future studies could find statistically significant differences in response rates for baboons, gorillas, and gibbons.

Importantly, the results found for orangutans in this study match the results found in a previous study that examined inequity aversion in orangutans (Brosnan et al., 2011). In this and a previous study, orangutans were tested for inequity aversion using a method which required the subjects to alternate exchanging a token for a food reward with a social partner. It was found that the seven orangutan subjects tested in the

previous study (Brosnan et al., 2011) and the two orangutans tested here did not have higher refusal rates during the disadvantageous inequity conditions as compared to the control conditions. Considering orangutans were the only species tested in the current study that have been previously tested in inequity experiments, this similarity in results across studies could be considered validation for the current study's methodology.

While the predictions made about disadvantageous inequity aversion for baboons, gorillas, and gibbons were not supported statistically, a few important points should be taken into consideration. It is imperative to note that an absence of performance in an individual does not equate to an absence of ability to respond. While an individual's negative reaction can be interpreted as an ability to recognize differences in reward distribution, the absence of a negative reaction does not indicate the absence of an ability to recognize unequal reward allocations.

One possibility for the lack of consistency among baboon, gorilla, and gibbon responses to inequity could be attributed to individual differences within the trait. For instance, in one study of chimpanzees by Brosnan and colleagues (2015), no differences were found between some chimpanzees' refusal rates during the inequity condition and the individuals' refusal rates during the control condition (Brosnan et al., 2015). These results were unexpectedly contradictory to those found in another study of chimpanzee inequity aversion led by some of the same researchers, in which chimpanzee's refusal rates statistically differed across conditions (Brosnan et al., 2010). Additionally, a study of bonobo inequity aversion found that some subjects responded negatively to receiving unequal rewards, but the results were not statistically significant

(Brauer et al., 2009); this is similar to the results found for baboons, gorillas, and gibbons in this study.

Importantly, observing individual differences in a behavioral trait is not unique to inequity aversion; individual variation both within and across nonhuman primate species has been recorded in several additional cognitive and behavioral traits in primates. For example, one study showed that only one out of eleven chimpanzees tested for mirror self-recognition actually exhibited the behavior (Swartz and Evans, 1991), whereas another study showed that all four chimpanzees tested were able to recognize themselves in mirrors (Gallup, 1970). Similarly, individual variation in mirror self-recognition was found for both gibbons and gorillas. For instance, several studies showed no evidence of the behavior in gibbons (Hyatt, 1998; Inoue-Nakamura, 1997; Suddendorf and Collier-Baker, 2009), but one study did show that hylobatids are capable of mirror self-recognition (Ujhelyi et al, 2000). In gorillas, some evidence of mark-directed behaviors in the presence of mirrors has been found (Matsuzawa, 2001) while one study did not show evidence of the behavior in this species (Suarez and Gallup, 1981). These results pertaining to gibbons and gorillas are especially important when considering the results of the current study of inequity aversion; the previous mirror self-recognition studies show that individual variation within a behavioral trait is not unusual for these two nonhuman primate groups.

In an attempt to explain why only some baboons, gorillas, and gibbons responded with higher refusal rates during the inequity condition, the data were qualitatively examined for correlations between refusal rates and demographic variables, such as age, sex, dominance rank, social group size, and rearing history.

However, no pattern was found that would correlate inequity aversion with any of these characteristics. Primate subjects which responded negatively to inequity varied across sex, age, dominance rank, social group size, and rearing history both within and between species (Tables 1-3).

Similarly, responses to inequity do not appear to be related to the strength of the pair's social relationship. This is assumed because all baboon subjects were introduced to their partner at the start of experimentation, and the strength of relationship was presumed to be similar for all pairs in this species. This would be consistent with a recent study of chimpanzee inequity aversion, in which no correlation was found between inequity aversion and the length of time chimpanzee subjects had lived with their experimental partner (Brosnan et al., 2015). However, the results from the current study should be interpreted with caution, as the strength of relationship between individuals in each pair was not quantified. Future studies may benefit from using an established sociality index (Silk and Alberts, 2006) to assess bonds between individuals in each pair prior to testing pairs for inequity aversion.

It is possible that inequity aversion varies among individuals for reasons other than those that can be explained by demographic characteristics. For example, individual variation in inequity aversion has been observed in humans, in which responses appear to be context-dependent. Human inequity responses vary by culture (Paulus, 2015; Shaw and Olson, 2012), the subjects' goals (Skitka, 2012) and whether inequity is related to productivity (Konrad and Pfeffer, 1990) or cooperation (Leung, 1986). This may suggest that several species, including baboons, gorillas, and gibbons,

exhibit individual variation in inequity responses that is unrelated to demographic characteristics.

One recent study exposed the individual variation in inequity aversion that can result from using different methodological paradigms within the same species, even when both paradigms require a task. The first study of inequity aversion in nonhuman primates showed that capuchin monkeys were inequity averse when required to complete a token-exchange task, in which the subject would receive either a lesser or greater reward than a social partner after task completion (Brosnan and de Waal, 2003). However, Sheskin and colleagues (2014) used a different experimental procedure and found contradictory results. In this study, capuchin monkeys were required to choose between experimenters, who each gave the subject the same reward; however, one experimenter gave the subject's partner a lesser reward, and the other experimenter gave the subject's partner a greater reward (Sheskin et al., 2014). The results showed that capuchin monkeys did not respond differently to equal and unequal reward distributions (Sheskin et al., 2014), which contradicted the results previously found for capuchin monkeys (Brosnan and de Waal, 2003).

While several researchers have highlighted the importance of a task for eliciting inequity aversion (Brosnan, 2013; Brosnan and de Waal, 2012; Brosnan et al., 2010; Hopper et al., 2013; Talbot et al., 2011; van Wolkenten et al., 2007), the study by Sheskin and colleagues (2014) was the first to show that even when a task is used, other procedural differences may lead to differing responses in inequity. The variation in inequity responses found for capuchin monkeys suggests that inequity aversion may be context-dependent for nonhuman primates. However, the tasks used in this study were

identical to those used in previous studies that indicated the presence of inequity aversion in nonhuman primates (Brosnan and de Waal, 2004; Talbot et al., 2011). Most importantly, the procedure used for each subject was identical to that used for the subject's partner. For this reason, it could be assumed that the experimental procedure used here is not the cause of the intraspecific individual variation observed in this study. However, nonhuman primates may be sensitive to subtle variation in procedures that were not apparent to the experimenter. In this case, potential subtle variation in methodology cannot, at this point, be excluded as a cause of individual differences in inequity responses.

Another recent study suggested that variation within inequity responses may be related to variation within personality traits. This study showed that certain personality variables characterized to the chimpanzee subjects (determined by caretaker questionnaires; see Freeman et al., 2013) significantly affected individual refusal rates during inequity testing (Brosnan et al., 2015). Chimpanzees which were rated more highly on the "extraversion" variable were more likely to stop participating in the task or refuse food rewards; individuals which scored more highly on the "openness," "agreeableness," "reactivity," and "dominance" variables, however, had lower overall refusal rates (Brosnan et al., 2015:83). It is possible that the individual variation in inequity aversion found for baboons, gorillas, and gibbons, similar to that found in chimpanzees, is also due to differences in personality traits of the subjects. However, personality data for the individuals tested in this study are not currently available, and therefore, this correlation must be further explored.

In addition to differences in personality and subtle procedural differences, other possible explanations for the individual variation in inequity responses observed for gibbons in particular cannot be ignored. One explanation for the variation in responses between the two gibbon subjects may be related to vigilance toward the subject's partner. The gibbon subject who had higher refusal rates during inequity conditions than control conditions was observed not to be consistently vigilant toward their social partner during testing. Therefore, it was not fully clear that this individual was continuously aware of rewards shown to and received by their partner. In contrast, the second gibbon subject appeared to be consistently vigilant toward their partner during inequity testing. It is possible that the results found for gibbons do not indicate the presence of inequity aversion in the subject which responded to unequal reward distributions and may not accurately reflect this species' tendency toward inequity aversion. Instead, the refusal to participate in the task may have been due to a lack of vigilance toward their social partner, due to factors such as distractions in the subject's environment or a general disinterest in their partner.

A second possible explanation for why one gibbon subject reacted negatively to inequity, but the other did not, may be due to the short relationship duration for the pair. It is known that adult gibbons typically form strong social bonds with an opposite-sex conspecific (Reichard and Boesch, 2003; Palombit, 1996), and it was predicted that gibbons would not be inequity averse given their small group size and lack of cooperation with non-kin, non-pair-bonded conspecifics. However, it has been suggested that pair-living partners with a newly formed relationship are more likely to respond negatively to unequal outcomes than partners with a longer relationship



history, because replacing a social partner is less costly for the former individuals (DeAngelo and Brosnan, 2013). Notably, the gibbon subject which responded negatively to unequal reward allocations in this study had been recently moved to the National Zoological Park and was introduced to their partner only 9 months prior to inequity testing. The fact that this gibbon subject recently formed a new relationship with their social partner could explain why this subject responded negatively to disadvantageous inequity, although the relatively new partnership was likewise true for the individual who did not show inequity aversion tendencies. It is possible that the change in location in addition to the newly formed relationship caused the apparently inequity averse gibbon subject to respond in a possibly anomalous manner. Future studies of inequity aversion in gibbons would benefit from studying pairs which have lived together for longer durations in order to determine whether the results found here are anomalous for this species.

### Advantageous Inequity Aversion

It was hypothesized that species which are group-living and which cooperate with non-kin and non-pair-bonded group mates would be inequity averse. It was also hypothesized that individuals within these species and which have a strong relationship with their social partner will show aversive reactions to advantageous inequitable outcomes. It was predicted that the gorilla subjects tested would respond negatively after receiving a greater reward than their social partner, because the gorilla subjects met these criteria; gorillas typically live in large groups and cooperate with non-kin

conspecifics, and the gorilla subjects tested were full-siblings that have lived together for thirteen years (indicating that they presumably had a strong social relationship). It was also predicted that baboons, gibbons, and orangutans would not respond negatively after receiving a greater reward than their social partner. This was because gibbons and orangutans are not large-group living species which cooperate with non-kin, non-pair-bonded conspecifics, and the baboon subjects tested had no prior exposure to their social partners; therefore, the baboon subjects were not presumed to have strong social relationships.

The prediction was supported statistically for baboons, gibbons, and orangutans but was not supported statistically for gorillas. The results indicated that there was no significant difference in refusal rates during the advantageous inequity conditions as compared to the control conditions for any of the four species tested. This was true when rewards varied by quality as well as when rewards varied by quantity. Only one of the two gorillas had a higher refusal rate when they were given a greater amount of rewards than their social partner as compared to their refusal rate during the large-quantity control. Furthermore, neither of the two gorillas had higher refusal rates when they were given a greater value reward than their social partner as compared to their refusal rates during the high-value control.

Notably, one baboon subject had a higher refusal rate when they were given a greater amount of rewards than their social partner as compared to their refusal rate during the large-quantity control. Similarly, three baboon subjects had higher refusal rates when they were given a greater value reward than their social partner as compared to their refusal rates during the high-value control. This result was especially

surprising considering none of the baboon subjects had a prior relationship with their conspecific partner.

One possible reason why no significant differences were found between gorillas' responses during advantageous inequity conditions and their responses during control conditions is that the sample size was too small to detect statistically significant differences. It is also possible that the social relationship of the gorilla pair did not differ substantially from the relationships of the other species. No direct measure of social relationship strength was conducted, and social relationship strength was assumed *a priori* as an outcome of social structure. However, such an assumption may be inadequate to reveal subtle differences in the response to inequitable rewards.

Another plausible explanation is that advantageous inequity aversion is not related to the strength of the relationship between subject and partner. This would be consistent with recent results found in a study of chimpanzee inequity aversion, in which no correlation was found between inequity aversion and the length of time chimpanzee subjects had lived with their experimental partner (Brosnan et al., 2015). Although humans respond negatively to inequity more often when they have a stronger relationship with their social partner and when partners have spent more time together, this may not be true for nonhuman primates. However, little data has been collected to test this in nonhuman primates, and therefore, this idea should be further explored.

## Addressing the Evolution of Inequity Aversion

Although some olive baboons, western-lowland gorillas, and white-cheeked gibbons showed negative responses to inequitable outcomes, these observations must be considered preliminary as they were not statistically significant. Because of the mixed nature of the results, i.e. some baboons, gorillas, and gibbons did not show inequity aversion while other members of these species did, it is difficult to label these species as inequity averse. Therefore, using this data to make assumptions about whether the trait is homologous or homoplastic for primate lineages becomes even more complicated.

In contrast to the mixed results found for baboons, gorillas, and gibbons, none of the orangutan subjects in this study responded negatively to unequal reward distributions. This confirmed the results from a prior study of orangutan inequity aversion (Brosnan et al., 2011) and suggests that inequity aversion is unlikely to be present in orangutans. With regard to orangutans, this data can more easily be used to address the question of whether inequity aversion is a homology or homoplasy in apes.

If future tests of larger samples of western-lowland gorillas and white-cheeked gibbons show that these species are inequity averse, a few hypotheses could be made about the evolution of inequity aversion in the superfamily Hominoidea. The presence of inequity aversion in humans, chimpanzees, bonobos, gorillas, and gibbons would mean that orangutans are the only ape species that is not averse to inequitable outcomes. This may suggest that inequity aversion is homologous, that it may have already been present in the last common ancestor of all apes, and that it was

secondarily lost only in orangutans. In this case, evolutionary pressures that would have led to the loss of inequity aversion in orangutans would have to be further explored.

If gorillas and gibbons were suggested to be inequity averse, it would also be possible for inequity aversion to have been absent in the last common ancestor of all apes. This would suggest that present-day inequity aversion in apes is a homoplastic trait that evolved independently in all ape lineages except *Pongo*, although this is the least parsimonious explanation. In this case, it would be necessary to explore the possible socioecological pressures that would have caused inequity aversion to evolve in gibbons, gorillas, chimpanzees, bonobos, and humans.

If future tests of western-lowland gorillas and white-cheeked gibbons show that these species are not averse to inequitable outcomes, it is likely that inequity aversion is homoplastic for the superfamily Hominoidea. Because it is rare for a trait to be lost in several species in one lineage, it is unlikely that inequity aversion was present in the last common ancestors of apes, but secondarily lost in orangutans, gorillas, and gibbons. Nonetheless, it would be necessary to explore evolutionary pressures that could lead to the loss of inequity aversion in these three species of the Hominoidea lineage.

If future tests of a larger sample of olive baboons can confirm that this species is inequity averse, a few additional hypotheses about the evolution of inequity aversion could be made. Considering rhesus macaques and long-tailed macaques have been suggested to respond negatively to inequitable outcomes (Hopper et al., 2013; Massen et al., 2012), inequity aversion could be a homologous trait in the subfamily Cercopithecinae and in the superfamily Cercopithecoidea. As only three Old World

monkeys have now been tested for inequity aversion, even if all three species were considered inequity averse, it is still possible that the trait is homoplastic for Old World monkey lineages. For instance, olive baboons, rhesus macaques, and long-tailed macaques may have evolved inequity aversion in response to similar socioecological pressures, such as increased cooperation among non-kin group members. Additional members of the subfamily Cercopithecinae, such as vervet monkeys, and additional members of the superfamily Cercopithecoidea, such as colobus monkeys of the subfamily Colobinae, would need to be tested for inequity aversion to better understand the evolution of the trait in these lineages and to come to a better conclusion of the trait's existence at higher taxonomic nodes, including all Old World monkeys.

If future tests of olive baboons suggest that this species is not averse to inequitable outcomes, there could be more than one evolutionary explanation for the trait's absence in this species. It is possible that inequity aversion could be a homologous trait in the subfamily Cercopithecinae and in the superfamily Cercopithecoidea, but the trait was secondarily lost in olive baboons. It is also possible that inequity aversion is a homoplasy for Old World monkeys; it would then follow that perhaps only macaques or only some macaque species were exposed to evolutionary pressures that led to the emergence of the trait, whereas olive baboons were not subjected to these evolutionary pressures. Studying additional Old World monkey species is a necessary requirement to advance the question of the evolution of inequity aversion and would help to better understand this distinction.

Given that humans and four species of nonhuman primates have been shown to be inequity averse, while several other species did not respond to inequitable outcomes

(Brosnan and de Waal, 2014), it may be argued that it is unlikely that inequity aversion is homologous for the order Primates. However, individual variation in the trait was found even in species that do show inequity aversion, such as humans (Paulus, 2015; Pruitt, 1985; Skitka, 2012), chimpanzees (Brosnan et al., 2015) and bonobos (Brauer et al., 2009), and now this study extends this list to include olive baboons, western-lowland gorillas, and white-cheeked gibbons. Considering only a small number of individuals from each nonhuman primate species have been tested for inequity aversion, it seems possible that the samples may have contained some individuals from each species that may respond differently from their conspecifics. Therefore, it is too soon to rule out the possibility that all primates are capable of responding negatively to unequal reward distributions. In conclusion, a homology of inequity aversion for the order Primates is still a possibility, suggesting that inequity aversion could have been present in the last common ancestor of primates.

More species within the class Mammalia need to be investigated if future studies of primate inequity aversion show that the trait may be homologous in the order Primates. A few studies already suggest that inequity aversion may be present in non-primate mammals, such as domestic dogs (Range et al., 2009), which have been shown to respond negatively to inequitable outcomes. Researchers have interpreted these results to suggest that inequity aversion evolved in domestic dogs in response to an increase in cooperative relationships in this species (Brosnan and de Waal, 2014). Testing for inequity aversion in mammalian species which do not live in large groups or cooperate with non-kin conspecifics, such as gray foxes (Lord, 1961), could highlight whether the trait may have evolved in response to increased cooperation and could

also lead to inferences about whether the trait may be homologous for the class Mammalia.

## Conclusions

There are several possibilities as to why no statistically significant results were found to support the overall hypothesis that there is a positive relationship between inequity aversion and species sociality. One explanation is that the sample size in this study was too small to detect statistically significant differences between conditions. While a sample size of twenty nonhuman primate subjects is relatively large compared to previous studies of inequity aversion (Brosnan et al., 2010; Brosnan et al., 2011), incorporating only two western-lowland gorillas, two white-cheeked gibbons, four orangutans, and twelve olive baboons may not have been adequate to detect within-species responses to unequal resource distributions. Similarly, including only four species in a study of inequity aversion may not have given an accurate account of between-species differences in inequity aversion. Therefore, future studies of nonhuman primate inequity aversion should attempt to maximize both the number of individuals within a species as well as the number of species tested in a given study.

A second explanation for a lack of statistical support for nonhuman primate inequity aversion in this study is the possibility that sociality was inadequately assessed. For example, this study considered both orangutans and gibbons to be “semi-social” (i.e. they do not live in large groups or cooperate with non-kin, non-pair-bonded conspecifics). Additionally, gorillas and baboons were both considered to be “social”



(i.e. they live in large social groups and cooperate with non-kin, non-pair-bonded group members). However, this “social”/“semi-social” dichotomy greatly simplifies each species’ social relations with conspecifics and omits important differences between the four species’ social organizations.

For example, it is important to recognize the differences between orangutan and gibbon social organizations. Orangutans, for instance, are considered solitary foragers which have only brief social interactions with non-kin conspecifics (Mitani et al., 1991; te Boekhorst et al., 1990). Gibbons, on the other hand, form strong pair-bonds with a non-relative conspecific and spend a large amount of time interacting and cooperating with that individual (Reichard and Boesch, 2003; Palombit, 1996). While white-cheeked gibbons, like orangutans, do not typically cooperate with multiple individuals of their species, it may not be appropriate to consider gibbons as equally “semi-social” as orangutans.

Likewise, western-lowland gorillas and olive baboons have very different social structures. For example, western-lowland gorillas often live in family groups averaging nine individuals (Yamagiwa et al., 2003) and consisting of one or two males and multiple females or in bachelor groups of all adult males (Doran and McNeilage, 1998). Olive baboons, on the other hand, typically live in multi-male, multi-female, fission-fusion societies, averaging between 15 and 150 individuals (Barton et al, 1996; Dunbar and Dunbar, 1974; Ray and Sapolsky, 1992; Rowel, 1966). Considering western-lowland gorillas and olive baboons to be equally “social” greatly reduces the important variation between the social organizations of these two species.

Given the vast variation in social structure among all nonhuman primate species, future studies examining the relationship between primate inequity aversion and species sociality may benefit from reassessing the definition of sociality. Specifically, it may be favorable to consider sociality as a continuous variable, as opposed to a dichotomous characteristic. If sociality was assessed as a continuous variable, it may better explain why the most social species tested in this study, olive baboons, had the highest refusal rates during most of the test conditions, why the intermediately social species, gorillas and gibbons, had intermediate refusal rates, and why the least social species, the orangutans, had the lowest refusal rates (Figures I-VI). Although it is feasible that inequity aversion evolved in tandem with increased cooperation among individuals living in large groups of conspecifics, more meaningful variation in inequity aversion between different cooperative, group-living species may be found by treating sociality as a continuous variable.

## TABLES

**TABLE I.** Baboon Demographic Characteristics

Pair #	Subject ID	Relationship w/ Partner	Age	Sex	Group Size	Group Composition
1	27666	None	9	Male	8	All 9-10 y.o. adult males
1	27885	None	9	Male	4	All 8-10 y.o. adult males
2	13228	None	19	Female	12	One adult male, eleven 11-21 y.o. females
2	26058	None	10	Female	13	One adult male, twelve 11 y.o. females
3	13246	None	19	Female	11	One adult male, nine 13-20 y.o. females, one infant
3	16486	None	14	Female	14	One adult male, thirteen 10-13 y.o. females
4	15225	None	16	Male	8	All 11-18 y.o. adult males
4	14068	None	17	Male	6	All 11-15 y.o. adult males
5	28420	None	9	Male	4	All 9 y.o. adult males
5	14528	None	17	Male	9	One adult male, eight 12-17 y.o. females
6	14800	None	22	Female	9	All 18-22 y.o. adult females
6	11284	None	17	Female	11	One adult male, nine 13-20 y.o. females, one infant

**TABLE II.** Additional Baboon Characteristics

Pair #	Subject ID	Rearing History	Days in Clinic	Cage Size	Reason for Clinic Stay
1	27666	Mother-reared until 10 months	5	1 x 1.2 m	Left rear foot injury
1	27885	Mother-reared until 10 months	13	1 x 1.2 m	Lacerated left hand
2	13228	Nursery-reared	8	1 x 1.2 m	Lacerated tail
2	26058	Mother-reared	7	1 x 1.2 m	Multiple body lacerations
3	13246	Mother-reared	85	1 x 1.2 m	Fractured left arm
3	16486	Mother-reared until 9 months	78	1 x 1.2 m	Fractured left arm
4	15225	Mother-reared until 11 months	15	1 x 1.2 m	Lacerated left cheek
4	14068	Mother-reared until 9 months	13	1 x 1.2 m	Weight loss
5	28420	Mother-reared until 12 months	31	1.5 x 1.8 m	Lacerated right hand
5	14528	Mother-reared until 10 months	3	1 x 1.2 m	Cheek abscess
6	14800	Mother-reared until 10 months	5	1 x 1.2 m	Hair growth
6	11284	Mother-reared until 6 months	4	1 x 1.2 m	Sedation recovery

**TABLE III.** Ape Demographic Characteristics

Pair #	Subject ID	Species	Relationship w/ Partner	Age	Sex	Group Size	Group Composition
7	Kwame	Gorilla	Full siblings	15	Male	2	Two adult males
7	Kojo	Gorilla	Full siblings	13	Male	2	Two adult males
8	Sydney	Gibbon	Bonded pair	15	Male	2	One adult male, one adult female
8	Tuyen	Gibbon	Bonded pair	8	Female	2	One adult male, one adult female
9	Kiko	Orangutan	Bonded pair	27	Male	2	One adult male, one adult female
9	Iris	Orangutan	Bonded pair	28	Female	2	One adult male, one adult female
10	Kyle	Orangutan	Bonded pair	18	Male	2	One adult male, one adult female
10	Bonnie	Orangutan	Bonded pair	38	Female	2	One adult male, one adult female

**TABLE IV.** Conditions and Rewards for all Primate Subjects

<u>Test Condition</u>	<u>Control Condition</u>	<u>Reward Shown to Subject</u>	<u>Reward Given to Subject</u>	<u>Reward Shown to Partner</u>	<u>Reward Given to Partner</u>
Quality Contrast	Low-value Control	High-value	Low-value	High-value	Low-value
Quantity Contrast	Small-quantity Control	3 pieces low-value	1 piece low-value	3 pieces low-value	1 piece low-value
Disadvantageous Inequity-Quality	Low-value Control	Low-value	Low-value	High-value	High-value
Disadvantageous Inequity-Quantity	Small-quantity Control	1 piece low-value	1 piece low-value	3 pieces low-value	3 pieces low-value
Advantageous Inequity-Quality	High-value Control	High-value	High-value	Low-value	Low-value
Advantageous Inequity-Quantity	Large-quantity Control	3 pieces low-value	3 pieces low-value	1 piece low-value	1 piece low-value

**TABLE V.** Test Results for Baboons

<u>Test</u>	<u>Ratio of Individuals which Responded</u>	<u>Z value</u>	<u>p value</u>
Quality Contrast Effects	5 out of 12	-1.134	0.257
Quantity Contrast Effects	6 out of 12	-2.449	0.014
Disadvantageous Inequity Aversion-Quality	7 out of 12	-1.134	0.257
Disadvantageous Inequity Aversion-Quantity	6 out of 12	-0.816	0.414
Advantageous Inequity Aversion-Quality	3 out of 12	-1.732	0.083
Advantageous Inequity Aversion-Quantity	2 out of 12	-1.000	0.317

**TABLE VI.** Test Results for Gorillas

<u>Test</u>	<u>Ratio of Individuals which Responded</u>	<u>Z value</u>	<u>p value</u>
Quality Contrast Effects	2 out of 2	-1.414	0.157
Quantity Contrast Effects	2 out of 2	-1.414	0.157
Disadvantageous Inequity Aversion-Quality	1 out of 2	-1.000	0.317
Disadvantageous Inequity Aversion-Quantity	1 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quality	0 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quantity	0 out of 2	0.000	1.000

**TABLE VII.** Test Results for Gibbons

<u>Test</u>	<u>Ratio of Individuals which Responded</u>	<u>Z value</u>	<u>p value</u>
Quality Contrast Effects	0 out of 2	-1.000	0.317
Quantity Contrast Effects	1 out of 2	0.000	1.000
Disadvantageous Inequity Aversion-Quality	1 out of 2	0.000	1.000
Disadvantageous Inequity Aversion-Quantity	1 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quality	0 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quantity	1 out of 2	-1.000	0.317

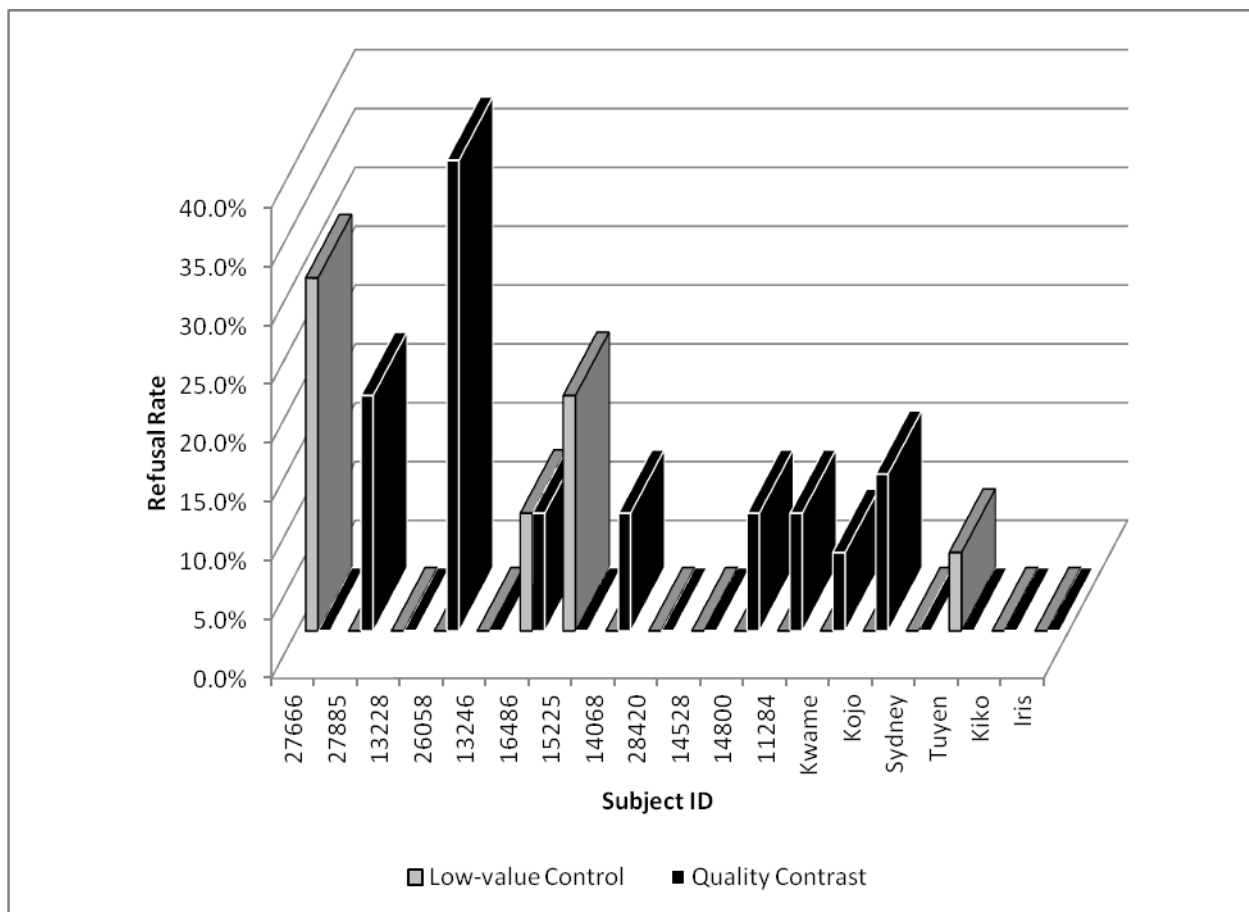
**TABLE VIII.** Test Results for Orangutans

<u>Test</u>	<u>Ratio of Individuals which Responded</u>	<u>Z value</u>	<u>p value</u>
Quality Contrast Effects	0 out of 2	0.000	1.000
Quantity Contrast Effects	2 out of 4	-1.414	0.157
Disadvantageous Inequity Aversion-Quality	0 out of 2	0.000	1.000
Disadvantageous Inequity Aversion-Quantity	0 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quality	0 out of 2	0.000	1.000
Advantageous Inequity Aversion-Quantity	0 out of 2	0.000	1.000

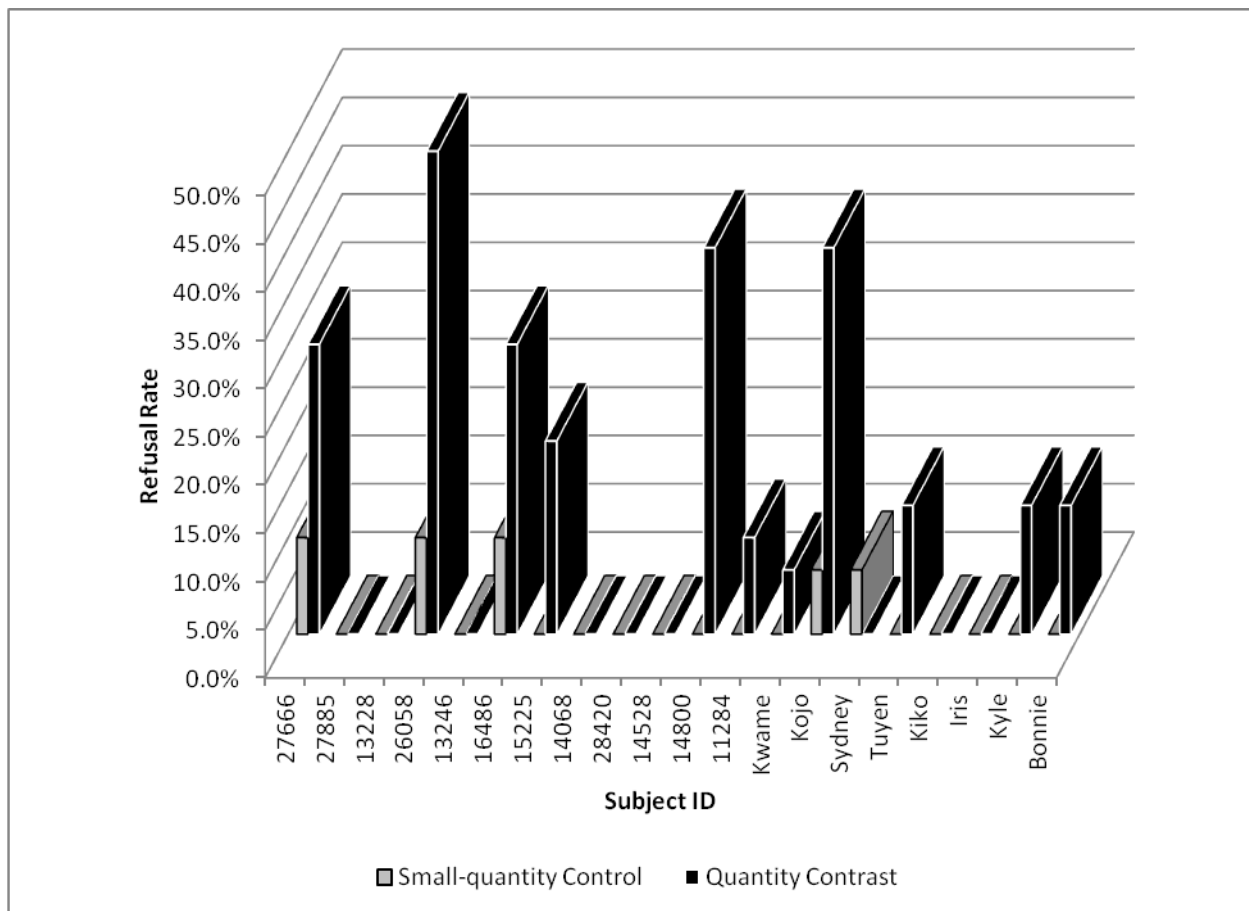
**TABLE IX.** Results of Friedman's Tests

<b><u>Species</u></b>	<b><u>5 Quality Conditions</u></b>	<b><u>5 Quantity Conditions</u></b>	<b><u>All 10 Conditions</u></b>
Baboons	$X^2 = 7.447, p = .114$	$X^2 = 13.491, p = .009$	$X^2 = 20.810, p = .014$
Gorillas	$X^2 = 6.400, p = .171$	$X^2 = 4.000, p = .406$	$X^2 = 11.824, p = .223$
Gibbons	$X^2 = 4.000, p = .406$	$X^2 = 1.857, p = .762$	$X^2 = 6.581, p = .681$
Orangutans	N/A	N/A	N/A

## FIGURES

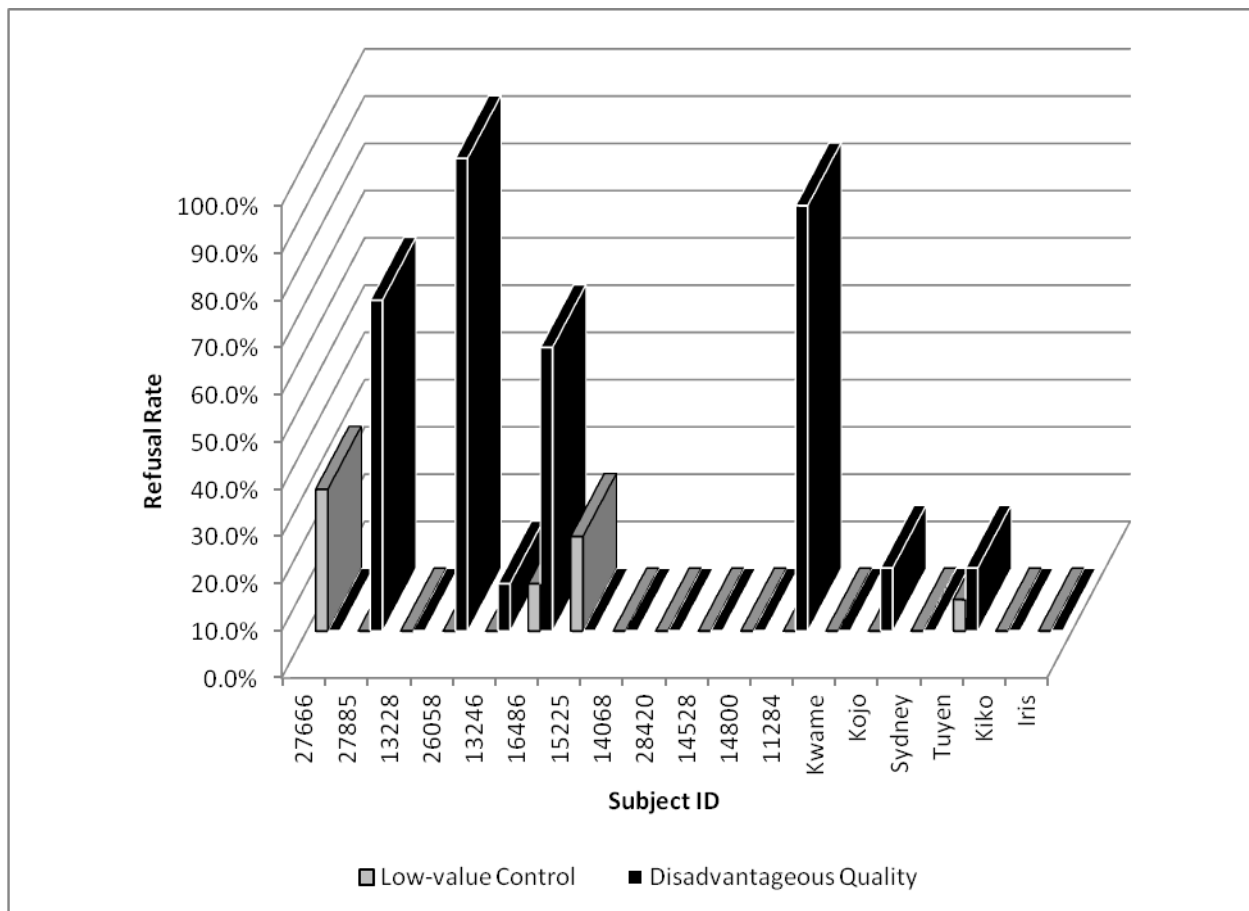


**FIGURE I.** Contrast effects when rewards varied by quality. Refusal rates of each nonhuman primate subject during the quality contrast condition compared to refusal rates during the low-value control.

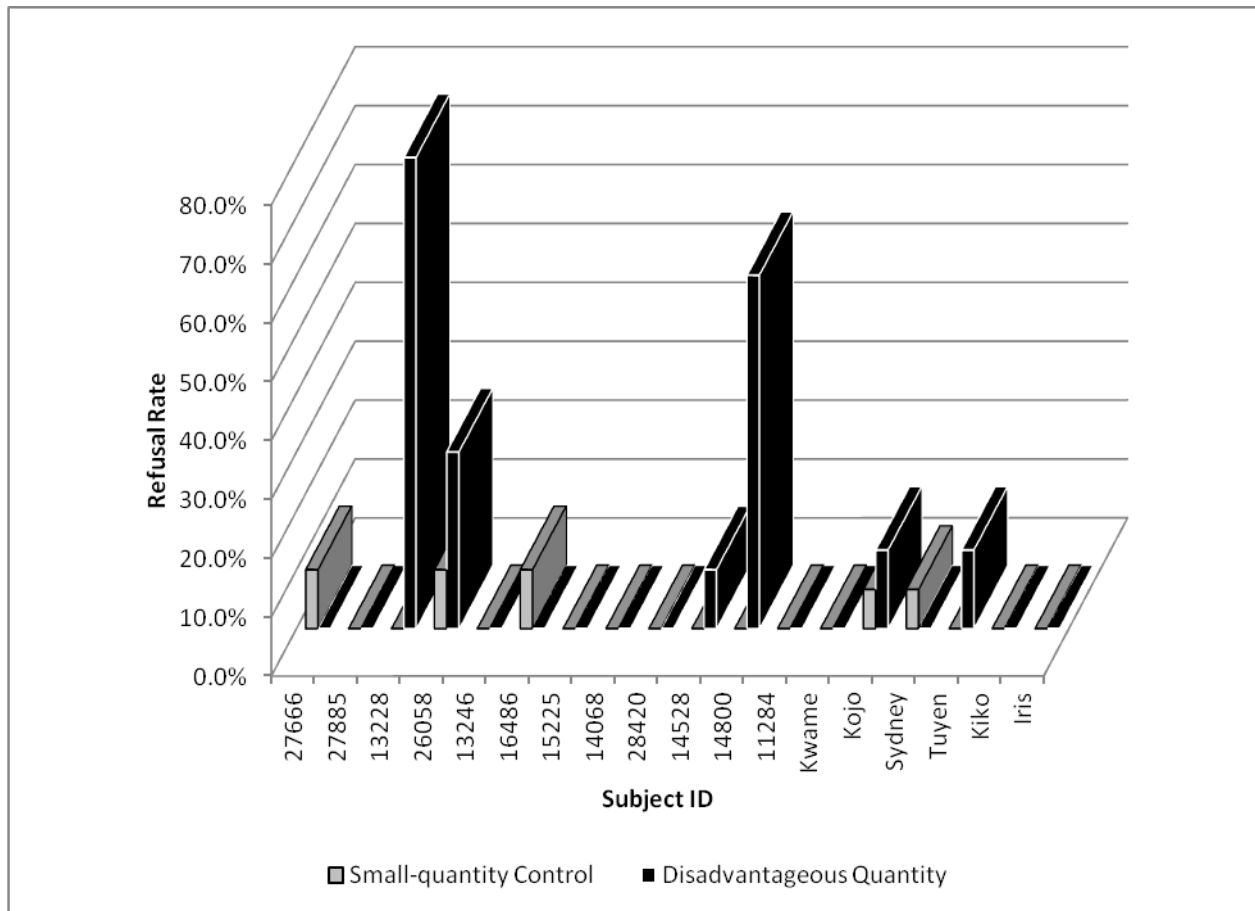


**FIGURE II.** Contrast effects when rewards varied by quantity. Refusal rates of each nonhuman primate subject during the quantity contrast condition compared to refusal rates during the small-quantity control.

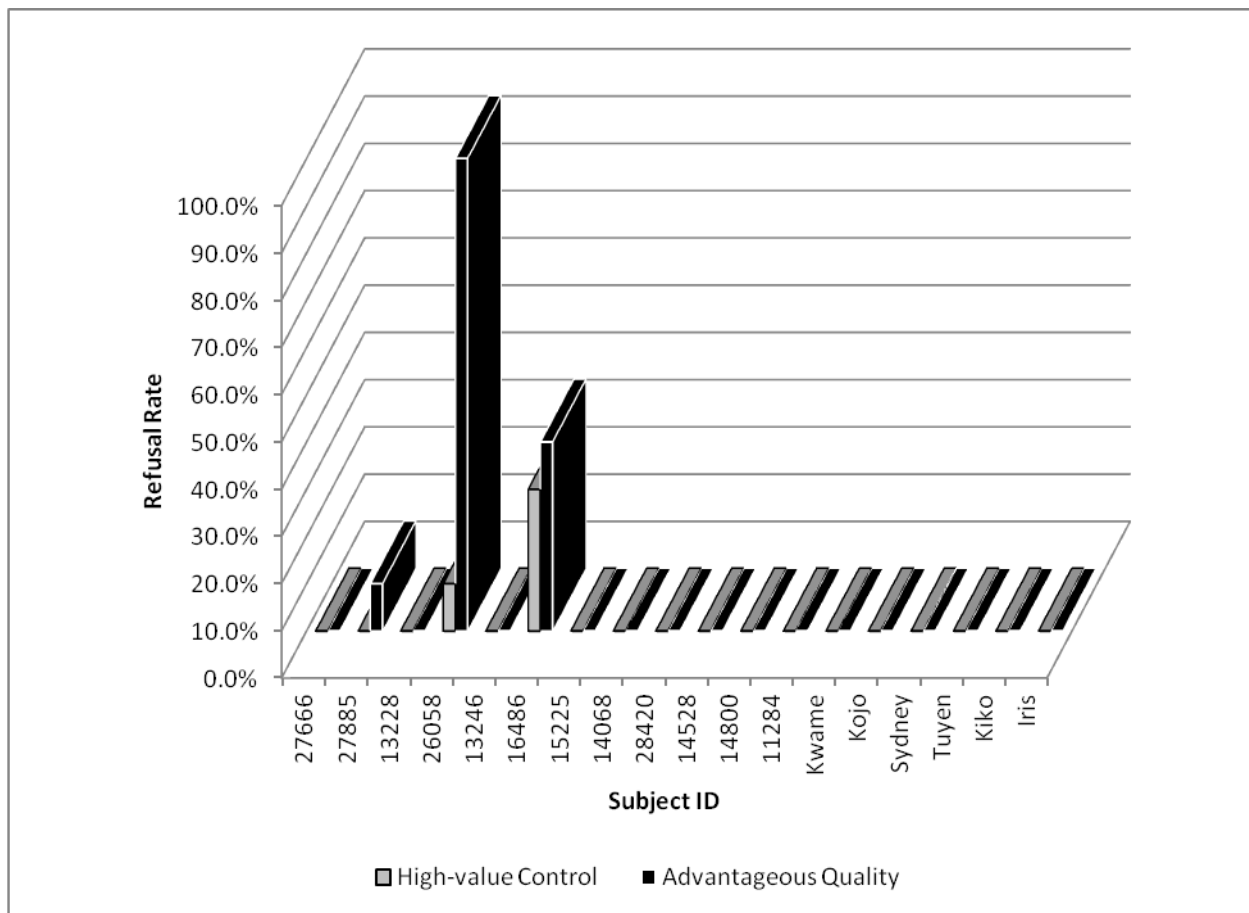




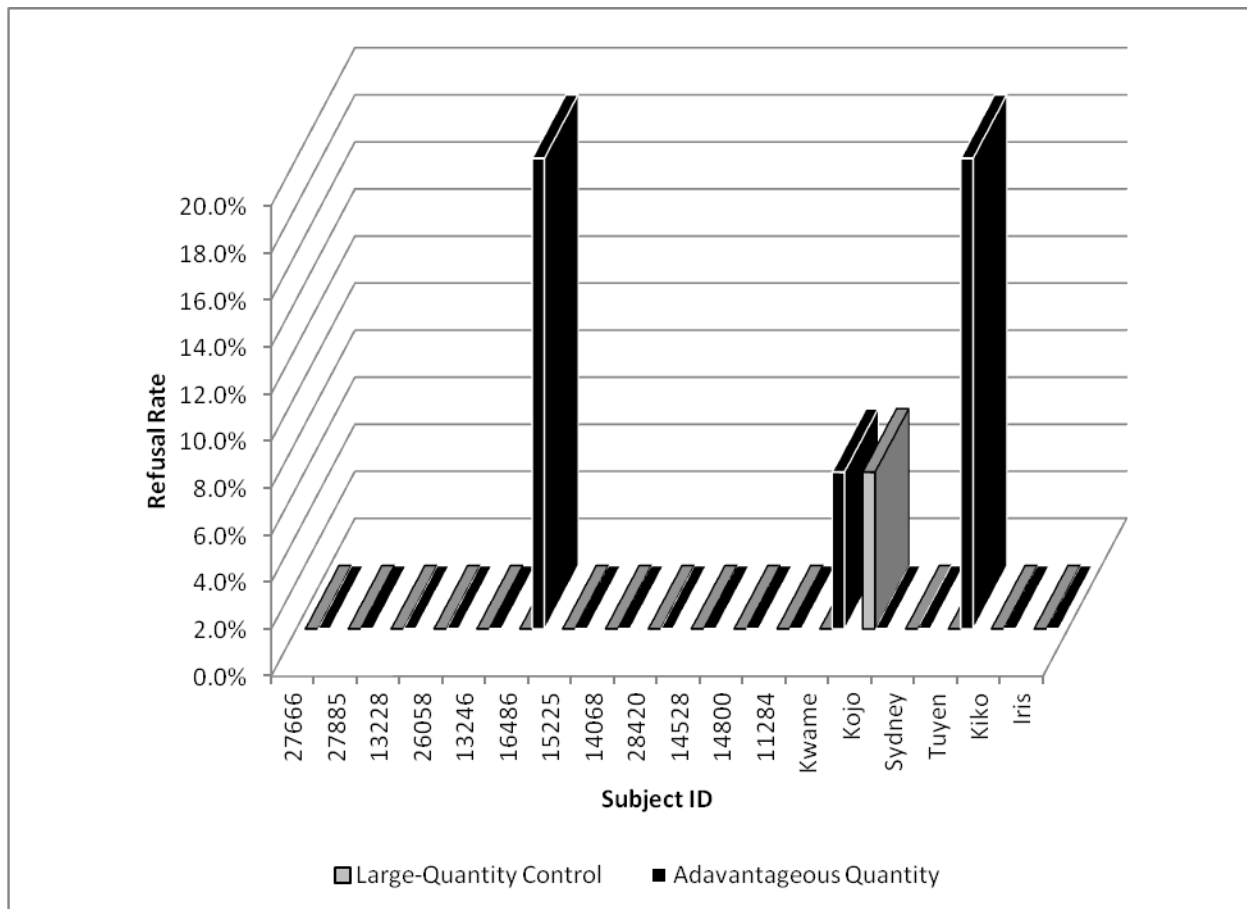
**FIGURE III.** Disadvantageous inequity aversion when rewards varied by quality. Refusal rates of each nonhuman primate subject during the disadvantageous inequitable quality condition compared to refusal rates during the low-value control.



**FIGURE IV.** Disadvantageous inequity aversion when rewards varied by quantity. Refusal rates of each nonhuman primate subject during the disadvantageous inequitable quantity condition compared to refusal rates during the small-quantity control.



**FIGURE V.** Advantageous inequity aversion when rewards varied by quality. Refusal rates of each nonhuman primate subject during the advantageous inequitable quality condition compared to refusal rates during the high-value control.



**FIGURE VI.** Advantageous inequity aversion when rewards varied by quantity. Refusal rates of each nonhuman primate subject during the advantageous inequitable quantity condition compared to refusal rates during the large-quantity control.

## BIBLIOGRAPHY

- Barnard AM, Hughes KD, Gerhardt RR, DiVincenti Jr, L, Bovee JM, Cantlon JF. 2013. Inherently analog quantity representations in olive baboons (*Papio anubis*). *Number without language: comparative psychology and the evolution of numerical cognition*: 76.
- Barton RA, Byrne RW, Whiten A. 1996. Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology* 38(5):321-329.
- Barton RA, Whiten A. 1993. Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour* 46(4):777-789.
- Beran MJ. 2007. Rhesus monkeys (*Macaca mulatta*) enumerate large and small sequentially presented sets of items using analog numerical representations. *Journal of Experimental Psychology: Animal Behavior Processes* 33(1):42.
- Beran MJ. 2001. Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 115(2):181.
- Beran MJ, Evans, T.A. and Harris, E.H., 2008. Perception of food amounts by chimpanzees based on the number, size, contour length and visibility of items. *Animal Behaviour* 75(5): 1793-1802.

- Bercovitch FB. 2006. Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour* 36(4):1198-1209.
- Boesch C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48: 653-667.
- Boysen, S.T. and Berntson, G.G., 1995. Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes* 21(1):82.
- Brannon EM, Terrace HS. 1998. Ordering of the numerosities 1 to 9 by monkeys. *Science* 282(5389):746-749.
- Brauer J, Call J, Tomasello M. 2006. Are apes really inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology* 71(2):175-181.
- Brauer J, Call J, Tomasello M. 2009. Are apes really inequity averse? *Proceedings of the Royal Society: Biological Sciences* 273(1605):3123-3128.
- Brosnan SF. 2013. Justice and fairness related behaviors in non-human primates. *Proceedings of the National Academy of Sciences* 110:10416-10423.
- Brosnan SF. 2011. A hypothesis of coevolution between cooperation and responses to inequity. *Frontiers in Neuroscienc*e [Hypothesis and Theory] 5(43):1-12.
- Brosnan SF, de Waal FB. 2014. Evolution of responses to (un)fairness. *Science* 346(6207):1251776-1 - 1251776-7.
- Brosnan SF, de Waal FB. 2012. Fairness in Animals: Where to from Here? *Social Justice Research* 25:336-351.
- Brosnan SF, de Waal FB. 2005. A simple response to barter in chimpanzees (*Pan troglodytes*). *Primates* 46:173-182.

- Brosnan SF, de Waal FBM. 2004a. A concept of value during experimental exchange in brown capuchin monkeys. *Folia Primatologica* 75:317–330.
- Brosnan SF, de Waal FB. 2004b. Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey (*Cebus apella*). *J Comp Psychol* 118:133-139.
- Brosnan SF and de Waal FB. 2003. Monkeys reject unequal pay. *Nature* 425:297-299.
- Brosnan SF, Flemming T, Talbot CF, Mayo L, Stoinski T. 2011. Orangutans (*Pongo pygmaeus*) Do Not Form Expectations Based on Their Partner's Outcomes. *Folia Primatologica* 82(1):56-70.
- Brosnan SF, Hopper LM, Richey S, Freeman HD, Talbot CF, Gosling SD, Lambeth SP, Schapiro SJ. 2015. Personality influences responses to inequity and contrast in chimpanzees. *Animal behaviour* 101:75-87.
- Brosnan SF, Schiff HC, de Waal FB. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society of London Series B* 1560:253-258.
- Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Shapiro SJ. 2010. Mechanisms underlying responses to inequitable outcomes in chimpanzees (*Pan troglodytes*). *Animal Behaviour* 79:1229-1327.
- Chen KM, Santos LR. 2006. Some Thoughts on the Adaptive Function of Inequity Aversion: An Alternative to Brosnan's Social Hypothesis. *Social Justice Research* 19(2):201-207.
- Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM. 2010. Contingent cooperation between wild female baboons. *PNAS* 107(21):9562–9566.

- Corning P. 2011. *The Fair Society: The Science of Human Nature and the Pursuit of Social Justice*. The University of Chicago Press.
- Cronin KA. 2012. Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour* 84:1085-1093.
- DeAngelo G, Brosnan SF. 2013. The importance of risk tolerance and knowledge when considering the evolution of inequity responses across the primates. *Journal of Economic and Behavioral Organization* 90:105-112.
- Doran DM, Mcneilage A. 1998. Gorilla ecology and behavior. *Evolutionary anthropology: Issues, news, and reviews* 6(4):120-131.
- Dreber A, Fudenberg D, Rand DG. 2014. Who cooperates in repeated games: The role of altruism, inequity aversion, and demographics. *Journal of Economic Behavior and Organization* 98:41-55.
- Dunbar RIM, Dunbar EP. 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia . *Folia Primatol* 21:36-60.
- Englmaier F, Wambach A. 2010. Optimal incentive contracts under inequity aversion. *Games and Economic Behavior* 69(2):312-328.
- Fehr E, Schmidt KM. 1999. A Theory of Fairness, Cooperation, and Competition. *The Quarterly Journal of Economics* 114(3):817-868.
- Freeman HD, Brosnan SF, Hopper LM, Lambeth SP, Schapiro SJ, Gosling SD. 2013. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous topdown/bottomup design: chimpanzee personality. *American Journal of Primatology*:75.



- Freeman HJ, Sullivan J, Hooper LM, Talbot CF, Holmes AN, Schultz-Darken N, Williams LE, Brosnan SF. 2013. Different Responses to Reward Comparisons by Three Primate Species. *PLoS ONE* 8: e76297.
- Gallup GG. 1970. Chimpanzees: self-recognition. *Science* 167(3914):86-87.
- Hanus D, Call J. 2007. Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology* 121(3):241.
- Higham JP and Maestriperi D. 2010. Revolutionary coalitions in male rhesus macaques. *Behaviour* 147:1889-1908.
- Hopper LM, Lambeth SP, Schapiro SJ, Bernacky BJ, Brosnan SF. 2013. The ontogeny of social comparisons in rhesus macaques (*Macaca mulatta*). *Journal of Primatology* 2:109.
- Hyatt CW. 1998. Responses of gibbons (*Hylobates lar*) to their mirror images. *American Journal of Primatology* 45(3): 307-311.
- Inoue-Nakamura N. 1997. Mirror Self-recognition in Nonhuman Primates: A Phylogenetic Approach. *Japanese Psychological Research* 39(3):266-275.
- Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour* 67(1):125-139.
- Kogut T. 2012. Knowing what I should, doing what I want: From selfishness to inequity aversion in young children's sharing behavior. *Journal of Economic Psychology* 33(1):226-236.

- Konrad AM and Pfeffer J. 1990. Do You Get What You Deserve? Factors Affecting the Relationship between Productivity and Pay. *Administrative Science Quarterly* 35:258-286.
- Leung K. 1986. Effects of interactional goal on choice of allocation rule: A cross-national study. *Organizational Behavior and Human Decision Process* 37(1):111-120.
- Loewenstein GF, Thompson L, Bazerman MH. 1989. Social Utility and Decision Making in Interpersonal Contexts. *Journal of Personality and Social Psychology* 57(3):426-441.
- Lord Jr RD. 1961. A population study of the gray fox. *American Midland Naturalist* 87-109.
- Lutz C, Well A, Novak M. 2003. Stereotypic and self-injurious behavior in rhesus macaques: a survey and retrospective analysis of environment and early experience. *American Journal of Primatology* 60(1):1-15.
- Maestriperi D, Schino G, Aureli F, Troisi A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour* 44:967-979.
- Massen JJ, Van Den Berg LM, Spruijt BM, Sterck EH. 2012. Inequity aversion in relation to effort and relationship quality in long-tailed Macaques (*Macaca fascicularis*). *American Journal of Primatology* 74(2):145-156.
- Matsuzawa T. 2001. *Primate Origins of Human Cognition and Behavior*. Tokyo; New York: Springer.
- McAuliffe KJ, Blake PR, Kim G, Wrangham RW, Warneken F. 2013. Social influences on inequity aversion in children. *PLoS ONE* 8(12):1-11.

- Mitani JC, Grether GF, Rodman PS, Priatna D. 1991. Associations among wild orang-utans: sociality, passive aggregations or chance? *Animal Behaviour* 42(1):33-46.
- Mitani JC, Watts DP. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* 61:915–924.
- Mitchell R. 2015. A critique of Stephane Savanah's 'mirror self-recognition and symbol-mindedness'. *Biology & Philosophy* 30(1):137-144.
- Neiwirth JJ, Johnson ET, Whillock K, Greenberg J, Brown V. 2009. Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology* 123(1):10.
- Nishida T. 1983. Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24(3):318-336.
- Palombit RA. 1996. Pair bonds in monogamous apes: a comparison of the siamang *Hylobates syndactylus* and the white-handed gibbon *Hylobates lar*. *Behaviour* 133(5):321-356.
- Paulus M. 2015. Children's inequity aversion depends on culture: a cross-cultural comparison. *Journal of Experimental Child Psychology* 132:240-246.
- Perry S. 1996. Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology* 17(3):309-330.
- Perry S, Rose L. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capuchinus*. *Primates* 35:409–415.
- Pruitt DG, Carnevale PJD, Forcey B, Van Slyck M. 1986. Gender Effects in Negotiation: Constituent Surveillance and Contentious Behavior. *Journal of Experimental Social Psychology* 22: 264-275.

- Range F, Horn L, Viranyi Z, Huber L. 2009. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences* 106(1):340-345.
- Ray JC, Sapolsky RM. 1992. Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *Am J Primatol* 28(4):231-50.
- Reichard U, Boesch C. 2003. *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. New York: Cambridge University Press.
- Reichard U. 1995. Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology* 100(2):99-112.
- Roma PG, Silberberg A, Ruggiero AM, Suomi SJ. 2006. Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of Comparative Psychology* 120(1):67-73.
- Rose LM. 1997. Vertebrate predation and food-sharing in Cebus and Pan. *International Journal of Primatology* 18:727–765.
- Rowell TE. 1966. Forest living baboons in Uganda . *J Zool* 149:344-65.
- Shaw A, Olson KR. 2012. Children discard a resource to avoid inequity. *Journal of Experimental Psychology: General* 141(2):382.
- Sheskin M, Ashayeri K, Skerry A, Santos LR. 2014. Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation. *Evolution and Human Behavior*, 35(2):80-88.
- Silberberg A, Roma PG, Ruggiero AM, Suomi SJ. On inequity aversion in nonhuman primates. *Journal of Comparative Psychology* 120(1):76.

- Silk J, Altmann J, Alberts S. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol Sociobiol* (2006) 61:183-195.
- Skitka LJ. 2012. Cross-Disciplinary Conversations: A Psychological Perspective on Justice Research with Non-human Animals. *Social Justice Research* 25(3):327-335.
- Smith BR, Piel AK, Candland DK. 2003. Numerity of a socially housed hamadryas baboon (*Papio hamadryas*) and a socially housed squirrel monkey (*Saimiri sciureus*). *Journal of Comparative Psychology* 117(2):217.
- Smuts BB, Watanabe JM. 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *International Journal of Primatology* 11(2):147-172.
- Suárez SD, Gallup GG. 1981. Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution* 10(2):175-188.
- Suddendorf T, Collier-Baker E. 2009. The evolution of primate visual self-recognition: evidence of absence in lesser apes. *Proceedings: Biological Sciences* 276(1662):1671-1677.
- Swartz KB, Evans S. 1991. Not all chimpanzees (*Pan troglodytes*) show self-recognition. *Primates* 32(4):483-496.
- Talbot CF, Freeman HJ, Williams LE, Brosnan SF. 2011. Squirrel monkeys' response to inequitable outcomes indicates a behavioral convergence within the primates. *Biological Letters* 7(5):680-682.

- te Boekhorst IJA, Schürmann CL, Sugardjito J. 1990. Residential status and seasonal movements of wild orang-utans in the Gunung Leuser Reserve (Sumatera, Indonesia). *Animal Behaviour* 39(6):1098-1109.
- Ujhelyi M, Merker B, Buk P, Geissmann T. 2000. Observations on the behavior of gibbons (*Hylobates leucogenys*, *H. gabriellae*, and *H. lar*) in the presence of mirrors. *Journal of Comparative Psychology* 114(3):253-262.
- Van Leeuwen E, Zimmermann M, Davila R. 2011. Responding to inequities: gorillas try to maintain their competitive advantage during play fights. *Biology Letters* 7(1):39-42.
- van Noordwijk MA, van Schaik CP 1987. Competition among adult female long-tailed macaques. *Animal Behaviour* 35:577–589.
- van Wolkenten M, Brosnan SF, de Waal FB. 2007. Inequity responses of monkeys modified by effort. *Proceedings of the National Academy of Sciences* 104:18854-18859.
- van 't Wout M, Sanfey AG. 2011. Interactive decision-making in people with schizotypal traits: A game theory approach. *Psychiatry Research* 185(1-2):92-96.
- Watts DP. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 44(1):43-55.
- Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees. *Animal Behaviour* 61(6):1203-1216.
- Yocum AM. 2010. *Physical and Social Cognition in the White-handed Gibbon (Hylobates lar)* (Dissertation). The Ohio State University, Columbus, OH.

Yamagiwa J, Kahekwa J, Kanyunyi Basabose A. 2003. Intra-specific variation in social organization of gorillas: implications for their social evolution. *Primates* 44:359-69.

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Reward Distributions

Major Professor: Dr. Ulrich H. Reichard