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Relationship Formation and Maintenance in Captive Chimpanzees (*Pan troglodytes*)

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Abstract

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Social risk is a unique domain of risk whereby the costs, benefits and uncertainty of an interaction stem from the ability to predict the behavior of another individual. The unique characteristics of social risk cause humans to overvalue the costs of a socially risky decision when compared to that of economic risk. While many studies investigate the cognitive requirements of social decision-making in non-human primates, the purpose of this study was to examine whether uncertainty in the social realm influences relationship formation and maintenance in chimpanzees. We accomplished this through the use of both an economic trust-game and an observational study. The eight subjects in the trust-game preferred to take economic risks to social risks and based their choices on the actions of their partners as opposed to their relationships with them. Similarly, when we observed the social behaviors of chimpanzees in two newly formed groups we found that they did not rely on only one strategy but both maintained old relationships and invested in new ones. These studies demonstrate that, like humans, chimpanzees are averse to social losses and base their social decisions on the costs and benefits of an interaction as opposed to solely on their familiarity with a group mate.

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1. INTRODUCTION

While ecological demands influence overall group organization (Clutton-Brock & Janson, 2012), the foundation of primate social structure is formed by dyadic interactions between individuals that vary in content and quality (Hinde, 1997). In other words, what happened during an interaction and whether it was positive or negative influences the association between two individuals. These repeated interactions within a dyad over time form a predictable pattern that develops into a relationship (Hinde, 1976).

Relationships are long-term associations with another individual and each separate social interaction either adds to the value of the relationship or takes away from it (Kummer, 1978). If a relationship is like a bank account, some interactions are positive while some are negative and each either withdraws from the account or pays into it. The valuable relationship hypothesis illustrates this point as it asserts that individuals invest the most in their highest value associations and will work to keep the relationship quality high when it is damaged (Watts, 2006). When agonism or competition in a relationship promotes negative interactions, affiliative behaviors decrease uncertainty and increase the lost value. Dyads with the most to lose invest highly in reconciliation behaviors.

In an economic sense the positive outcome of a social interaction can be considered a benefit and the negative outcome a cost. Costs take the form of aggression (Mitani & Amsler, 2003), opportunity costs due to partner choice (Kummer, 1978) or energy loss (de Waal & Davis, 2003) and can decrease the value or predictability of a relationship (Cords & Aureli, 2000). Benefits range from an increase in access to resources to the emotional rewards of social interactions (Kummer, 1978; de Waal, 1997;

Wittig et al., 2008). Along with the outcome of social interactions, various intrinsic and extrinsic factors can increase or decrease the overall value of the relationship. These include physical characteristics such as sex or size, how their behavior varies across situations, and how often they are in proximity or engaged with a third party (Kummer, 1978).

Each social relationship has a positive or negative value and the amount invested in a relationship depends directly on the alternatives available, suggesting that individuals choose the most valuable partners accessible to them (Hinde, 1997). Seyfarth (1977; 1980) provides a model of and evidence for this through his observations of vervet monkey affiliation. He argues that females preferentially groom higher ranked individuals because higher rank equates to a higher value association. Lower ranked individuals, though, cannot always access the highest ranking monkeys so must make due with potentially less valuable partnerships (Seyfarth, 1980).

The value of a social partner also determines whether the benefits from a relationship outweigh the risks of negative social interactions (Cords & Aureli, 2000; Fraser, Schino, & Aureli, 2008; van Schaik & Aureli, 2000). Hinde (1997) discusses the interdependence theory in humans which is defined as a discord between someone's satisfaction with a relationship and their dependence on it. This concept could also apply to non-human primate group members. A very subordinate group member, for instance, relies on the group for protection from predators, help finding food and mating opportunities. While this group member may benefit from the general advantages of group living, he or she may not have relationships that provide net positive outcomes in terms of gains and losses.

As the value of a relationship changes, the investment in that relationship should change accordingly. This is because the positive or negative outcome of past interactions as well as the predicted result of future interactions influences the type and frequency of associations (Hinde, 1997). This has been demonstrated in wild vervets (*Chlorocebus pygerythrus)* (Seyfarth & Cheney, 1984) and captive chimpanzees (*Pan troglodytes)* (Melis, Hare, & Tomasello, 2006; Trivers, 1971; de Waal, 1997; de Waal & Luttrell, 1988). Chimpanzees, for example, more often share food with individuals who recently groomed them indicating that affiliative social investments enhance the chances for further positive interactions (de Waal, 1997).

Since the positive or negative outcome of a social interaction depends on the actions of another individual it is characterized by a degree of uncertainty. This factor, plus the potential for costs implies that social interactions have a degree of risk (Bohnet, Greig, Herrmann, & Zeckhauser, 2008) since a risky decision has a potential cost, a magnitude and an uncertain outcome (Yates & Stone, 1992). In the strictest sense though, the economic definition of risk requires a known probability for each result with variable choices of unknown probability considered as ambiguous as opposed to risky (Knight, 2006). This distinction between ambiguity and risk becomes unclear in non-human decision-making, though, as it is difficult to ascertain what a non-human perceives about their chances for success under variable conditions. We assume that as individuals build up experience with the variable outcomes of uncertain decisions and learn their value, their choices switch from ambiguity to risk. In their study examining risk preferences Rosati and Hare (2011) found that chimpanzees and bonobos preferred risky choices to ambiguous ones. The authors, though, did not find a difference between the two in later sessions of the experiment. This suggests that the subjects potentially learned the probabilities of the ambiguous option over the course of the study causing the distinction between the two conditions to disappear.

One common paradigm for investigating how individuals respond to the costs and uncertainty inherent in some social interactions is the use of an economic trust game. In humans, a trust game includes varying numbers of trials between a subject and a partner. The subject begins with a quantity of money and can choose to either keep it or to give it to a partner. If they give it to their partner, the amount of money is tripled and the partner decides how much money they will keep and how much money they will give to the subject. For example, if a subject receives $10 and passes it to their partner their partner decides how to distribute a total of $30 between themselves and the subject. In this way, the subject makes a risky investment in their partner for a potentially larger sum of money than they would have received otherwise.

The results of studies using this paradigm have shown that the norm for humans from western cultures is to default to high levels of social risk-taking, meaning that they tend to invest their money in their partner (Eckel & Wilson, 2004; Engle-Warnick & Slonim, 2006; Glaeser, Laibson, Scheinkman, & Soutter, 2000; Krueger et al., 2007). This is notable because the rational equilibrium for trust game subjects is to assume that their partners are selfish and to behave in a way that mitigates risk against this, mainly keeping their money (Naef & Schupp, 2009). In fact, Eckel and Wilson (2004) found that subjects who invested in a partner only received, on average, the same amount that they gave, suggesting that those who made trusting choices did not profit.

In the only study, to date, using a similar paradigm with non-human primates, Engelmann, Herrmann, & Tomasello (2015) concluded that chimpanzees, like humans, are also prone to taking social risks. The chimpanzees returned this result even with a very low average return from chimpanzee partners. More work on this is subsequently needed to help determine what evolutionary pressures encouraged social risk-taking in the primate lineage and what fitness benefits resulted.

1.1 The Domain of Social Risk

Because primates have specialized mechanisms for processing social information at the neural level, social cognition is often considered a unique domain (Brothers, 2002). Functional magnetic resonance imaging (fMRI) studies and hormonal studies in humans provide evidence for this as the processes used to evaluate socially risky decisions are found to be distinct from those used to evaluate risks that are purely resource based (Rilling et al., 2004; Rilling, King-Casas & Sanfrey, 2008; Kosfeld et al., 2005). This suggests that the domain of social risk is separate from that of non-social risk.

When human subjects played trust games while undergoing fMRI, for example, the ventral medial prefrontal cortex responded to negative outcomes in social conditions but not negative outcomes in non-social conditions (Rilling et al., 2004). Since this area of the brain is central to reward processing, the authors concluded that positive social interactions are rewarding in a way that is distinct from gaining economic rewards. A similar fMRI study to Rilling et al. (2004), focused on the left hippocampus, the right anterior insula and the left anterior insula because of their function in memory, face recognition and aversive social stimuli (Rilling, King-Casas, & Sanfrey, 2008). The authors discovered activity differences between social and non-social conditions in all brain areas targeted. This indicates that human's use of memory, individual identity and emotional reaction when making choices in social games is different from their use of memory and emotion in non-social games.

Along with neural evidence, there is also hormonal evidence for different processes in social versus non-social decision-making under risk. When examining the effects of intranasal oxytocin on the choices made by test subjects in trust games, Kosfeld et al. (2005) found significant differences in the effect of oxytocin in social conditions but not non-social conditions. This suggests that oxytocin regulates aspects of neural decision-making that are unique to social interactions. It is important to note, though, that oxytocin research potentially suffers from high rates of false positive results (Walum et al., in press), flawed methods for administration and a bias against negative findings (Leng & Ludwig, in press).

Behaviorally, two separate paradigms demonstrate differences in social and non-social decision-making under risk. Firstly, studies suggest that humans have a higher tolerance for risk when playing in a non-social condition of a trust game than they do when playing in a social condition of a trust game (Blount, 1995; Bohnet & Zeckhauser, 2004). This indicates that they would rather lose money due to chance than lose the same amount because of the actions of another person. This reaction suggests an aversion to social betrayal, which is defined as an increased emotional response due to the actions of another individual (Bohnet, Greig, Hermann & Zeckhauser, 2008). Bohnet et al. (2008) replicated these results across five cultures suggesting that social betrayal aversion may be widespread among humans.

Secondly, the tools used to measure general risk preferences in humans often do not correlate with behavioral measures of willingness to take social risks (Eckel & Wilson, 2004; Kanagaretnam, Mestelman, Nainar, & Shehata, 2009). Ben-Ner and Halldorsson (2010), for example, used both a survey about attitudes towards non-social risk and choices made while gambling to examine a participant's overall risk aversion. They then compared these measures to the outcome of a social trust game. The amount of money sent to a social partner did not correlate with the survey score or likelihood to take risks. These results indicate that different factors control the assessment of risk in non-social situations than those that control the assessment of risk in social situations, suggesting that the domain of social risk deserves specific investigation.

Because of our close evolutionary relationship, various homologous similarities exist between human brain function and that of non-human primates (Rushworth, Mars, & Summerfield, 2009; Squire, 1992). If social risk-taking has similar neural and behavioral correlates in both humans and non-human primates it would provide evidence that humans and non-human primates evaluate social risks in a similar way. This could indicate that the way humans evaluate social risks evolved in a primitive non-human ancestor in order to combat selection pressures against the costs of social interactions. Studying our closest genetic relatives, the chimpanzees, helps to distinguish between uniquely human traits and those that have a common evolutionary background (Chen & Li, 2001; Steiper & Young, 2006).

1.2 Factors that Influence Socially Risky Decisions

Hinde (1976) discusses that exposure learning, classical conditioning and operant conditioning are employed in the formation and maintenance of relationships in similar ways to non-social situations. If social risk is indeed a distinct domain from that of non-social risk then how might decision-making between the two domains differ? The most parsimonious explanation is for the utilization of the same types of simple learning mechanisms between each domain with additional factors, such as emotions and individual disposition, contributing to the processing of social information. In some cases the characteristics of social relationships may provide unique heuristics for decision-making.

1.2.1 Emotions

Emotion is one important influence on both social and non-social decision-making. Emotions in humans such as fear and anxiety either directly influence or mediate choices made in risky economic situations and act as an important heuristic for uncertain decisions (Finucane, Alhakami, Slovic, & Johnson, 2000; Loewenstein, Weber, Hsee, & Welch, 2001). Humans, for instance, often make irrational economic decisions that diverge from predictions based on the purely cognitive evaluation of the costs and benefits of a choice (Kahneman & Tversky, 1979). Likewise, chimpanzees and bonobos display emotional reactions to negative outcomes in risky decision-making tasks, indicating that emotions are an important element of risk assessment and response in apes as well as humans (Rosati & Hare, 2013).

Emotions are also important for social decision-making in both humans and non-human primates. Kagan & Snidman (2004) recognized that highly emotional children tended to be socially inhibited whereas less emotional children had more socially outgoing personalities. In response to this study, Hare and Tomasello's emotional reactivity hypothesis (2005) applied Kagan & Snidman's theory to chimpanzees, hypothesizing that the emotions arising from social interactions inhibit the abilities of chimpanzees to work together. According to Hare (2007), while humans are capable of overcoming a majority of the influence of emotion during social interactions it still greatly affects non-human primates. If emotions are an important influence in both risky economic decision-making and social decision making, it is likely that they are an essential factor in whether an individual initiates a social interaction with an uncertain result as well as how they respond to the outcome.

Aureli & Schaffner (2002), for example, argue that non-human primates rely heavily on emotions during risky social interactions in order to bridge the costs and benefits of a social interaction with the appropriate behavior. The outcome of an interaction influences learning through the development of either a positive or negative affect and this response drives subsequent behavior. One example is the increased anxiety, in some monkey species, that is characteristic of close proximity to a higher ranked animal. This negative affect functions to keep lower ranking individuals at a safe distance (Aureli & Schaffner, 2002).

Another example of an emotion that could be an important heuristic for mediating social interactions is the feeling of trust. In humans, the positive product of social risk assessment is thought to result in an affective state that is termed trust. The most complete definition is by Rousseau et al. who define trust as "a psychological state comprising the intention to accept vulnerability based upon positive expectations of the intentions or behavior of another"(1998, p.395). A state such as trust can help to reduce the cognitive demands that come from assessing the risks of social interactions. It can help to quickly bridge the evaluation of social risks and rewards with the manifestation of social behavior without the use of complex cognitive processes such as scorekeeping (Colquitt, Scott, & LePine, 2007; Dirks & Ferrin, 2001).

What then are the emotional characteristics of social interactions that contribute to increased responses relative to non-social situations? One characteristic may be that social interactions have an *additional* emotional component that causes negative outcomes to be overvalued during risky decision-making (Aureli, 1997; Hopper, Schapiro, Lambeth, & Brosnan, 2011). Bohnet et al. (2008) discuss that humans have an emotional aversion to negative social situations because they not only respond to the outcome of a social interaction but also to how the outcome was produced. This suggests that one person attributes their negative result to the intentions of another other person. Therefore a negative outcome not only results in an economic loss but also an additional emotional reaction due to the actions of a partner. Whether or not non-human primates are capable of this type of response is unknown. An increased aversion to a loss caused by a partner over one that is the result of chance in a trust game would provide evidence to suggest that they have similar biases to humans.

Evidence that chimpanzees and capuchins aid a human needing help (Call, Hare, Carpenter, & Tomasello, 2004; Hare & Tomasello, 2004; Phillips et al., 2009), and give more rewards to partners that signal the desire for food (Horner, Carter, Suchak & de

Waal, 2011) indicates that they do indeed assign intentions to the actions of another individual. Experimental findings have suggested, though, that these intentions are interpreted differently depending on the circumstances. Melis, Hare and Tomasello (2008), for example, examined whether manipulating how a partner behaved towards a test subject would influence that subject's choices. They did this by framing one chimpanzee partner as a "nice stooge," by training it to cooperate with a test subject as a partner. They framed a different chimpanzee as a "mean stooge," by training it not to pick a test subject as a partner. The authors hypothesized that the chimpanzee subject would reciprocate cooperation by choosing to work with the "nice stooge" when given the choice. In general, the manipulations did not influence which partner the chimpanzee subject picked, indicating that the subjects did not directly attribute their own success or failure to the actions of their partner. These findings call into question whether non-human primates are capable of perceiving that their social partner did something unfair but could also have arisen due to the already held relationships of the chimpanzee subjects and partners.

In humans, researchers have suggested additional reasons for a negative emotional response to social betrayal that might also function in non-human primates. These are the negative reactions to a partner gaining rewards at the expense of the subject (Rilling, King-Casas & Sanfey, 2008) and a perceived decrease in control of the outcome of a social interaction relative to one that does not involve a partner (Bohnet & Zeckhauser, 2004). Inequity aversion is documented in both monkeys (Brosnan & de Waal, 2003; van Wolkenten, Brosnan & de Waal, 2007) and apes (Brosnan, Schiff, & de Waal, 2005) and is a feasible explanation for an increased aversion to social losses, but it is unknown whether perceived control over a situation influences social behavior in non-human primates.

If a subject blames their partner for a negative outcome during a social interaction, a loss of confidence in the relationship with their partner could result. Therefore, changes in the security and value of social bonds may increase uncertainty about a relationship as well as add an emotional element to social risk-taking (Cords & Aureli, 2000). This would in turn increase the perceived risk of interacting with this individual and decrease their tendency to interact with them.

Similarly to increasing uncertainty, a decrease in the security and value of social bonds can increase the net loss of an interaction. If a subject plays a trust game and looses a reward because of the actions of their partner, they are not only losing the economic reward but are also losing security and value in their relationship. This suggests that a subject loses less during the non-social condition of a trust game than they do during the social condition and provides an explanation for why individuals are more averse to social losses than they are to purely economic ones. All of these examples indicate that at least some animals rely on emotions more heavily than other cognitive processes during social interactions. Overall, the emotional aspect of social risk decreases the tendency for social risk-taking when compared with non-social risk-taking in humans (Fehr, 2009) and is still open to study in non-human primates.

1.2.2 Relationship

Along with emotion, an individual's already established relationship with a partner could influence whether the costs and benefits of a social interaction influence future interactions. This occurs because the social characteristics of a relationship, such as affiliation levels, can influence how an individual interprets the behavior of another (Eckle & Wilson, 2004; Hwang & Burgers, 1997). A human, for example, will interpret the actions of a friend as less threatening than he or she will interpret the same actions from a stranger (Dirks & Ferrin, 2001). Robinson (1996) examined this through a survey of employers and their employees. He concluded that a person's attitude towards another determines the recognition and the reaction to social behaviors. This would mean that under conditions of already high affiliation, ambiguous actions are more likely interpreted in a positive manner but under conditions of previously low affiliation, the same actions are likely to be interpreted negatively.

Relationship quality could also influence how the costs and benefits of short-term interactions affect subsequent behaviors because the balance of costs and benefits in an affiliative relationship are not as important to the value of the relationship (Clark & Mills, 1979). Therefore, even if an expectation about the outcome of an interaction is violated, it does not cause enough damage to the relationship to influence future interactions (Schino & Aureli, 2009). When Melis et al. (2008) concluded that chimpanzee subjects did not respond to the level of cooperation from their partners, the authors suggested that the experimental manipulations of the test subjects towards the partners could not overcome their already established perceptions of those individuals. Because they had never interacted with these individuals on this specific task, direct past experience did not influence the choices of the test subject but relationship likely played a role. This suggests that because of their affiliative relationships the test subjects did not interpret a negative social outcome as weakening their social bond.

Brosnan and de Waal (2009) found a similar connection between relationship and how a test subject interpreted social outcomes. The authors used a trading paradigm to examine whether capuchin subjects trade with a predictable human who always gave a food reward, or an unpredictable human who only occasionally gave a food reward. The subjects did not choose to trade more with the predictable humans over the unpredictable ones. In some cases Brosnan and de Waal used familiar experimenters possibly causing the monkeys to bring their beliefs about the humans into the experiment, which "predisposed the monkeys to believe that the experimenters were basically reliable, and that the events in (the) study were an anomaly" (2009 p. 10). In this experiment, though, the capuchins did have direct past experience trading with the experimenters so could have called on past experience with the task as well as relationship.

When a relationship is not affiliative or established, non-human primates may behave in ways that help them to quickly gain knowledge about another individual in order to assess the risks of interacting in a social way. These relationship building or testing behaviors are characterized by actions that make them prone to injury in controlled ways such as presenting sensitive areas to each other or sticking fingers in one another's mouths (Perry, 2011). By initiating a controlled situation in which they are vulnerable, individuals build up positive expectations that are based on interactions that are risky, but deliberately so. In this way, non-human primates build something akin to trust and reduce the need to continuously monitor the potential costs and benefits of a relationship.

One situation where this type of behavior might be particularly important is for interactions between individuals that do not commonly interact. Humans are often considered unique in the degree to which they interact with strangers (Fehr & Fischbacher, 2003; Gächter & Falk, 2002) but the fission-fusion dynamics of many social primate groups, as well as natural immigration from one group to another, can introduce uncertainty into primate social relationships as well. Evidence from captive introductions in primates provides most of the data for behavioral strategies used during interactions between unfamiliar individuals. Chimpanzees, for example, tend to mitigate interactions with unknown individuals through submissive and ritualized behaviors (Baker & Aureli, 2000; Brent, Kessel, & Barrera, 1997). Although Baker & Aureli (2000) discuss that the basis for this premise is provided both experimentally and by game theory, the mechanisms behind relationship development are not well understood and are open for further investigation.

Even individuals that interact repeatedly often make themselves vulnerable in controlled ways that function to reinforce social bonds and maintain social knowledge. Chimpanzee greeting behaviors are one example of this type of behavior as they often put their mouths around areas that could be easily damaged from a bite such as fingers and anogenital swellings in a way similar to that of the capuchins mentioned above (Okamoto, Agetsuma, & Kojima, 2001). Grooming could also be viewed as important for making oneself vulnerable in a controlled way as individuals being groomed often have sensitive body parts exposed.

1.2.3 Disposition

There is evidence that species specific ecology and individual bias influences an individual's general predisposition towards risk (Dammhahn & Almeling, 2012; Heilbronner et al., 2008; Huntingford, 1976). This suggests that disposition toward social interactions is also one of the factors that can influence the propensity to take social risks. These differences could be from extrinsic factors such as culture (Bohnet, Greig, Herrmann & Zeckhauser, 2008; Buchan, Johnson, & Croson, 2006; Levitt & List, 2007) or a situational influence enhancing vulnerability such as an injury or newborn infant. They could also be due to intrinsic characteristics such as genetic variation (Cesarini et al., 2008). Differences between individuals in the propensity towards social risk-taking are most likely due, though, to a combination of all of these.

The theory that individuals have different propensities towards social risk-taking is discussed in detail throughout the trust literature in humans (see for example: Kee & Knox, 1970; Mayer, Davis, & Schoorman, 1995; Rotter, 1967). Experimental evidence suggests that subjects have individual differences in their tendency to trust others. Cesarini et al. (2008) used monozygotic and dizygotic twins as test subjects in a trust game in an effort to separate the influence of genetic and environmental factors on these individual differences. There were more similarities between monozygotic twins than dizygotic twins, leading them to conclude that social risk-taking has a genetic component influencing individual decision-making. In addition, Naef & Schupp (2009) concluded that those who volunteered to participate in both an experiment and a survey had more trusting dispositions than those who would only participate in a survey. The evidence for individual consistency between various situations led them to conclude that people's choices for social risk are influenced by a unique disposition towards or against it.

The theory that individuals have a predisposition towards or against social risk-taking is open to further exploration in humans, as well as an initial investigation in non-human primates. Given that great apes are our closest genetic relatives, initial experiments would provide a starting point for an investigation into what influences disposition and how disposition mediates one's propensity to take social risks. Answering these questions could lead to investigations of how an individual's unique propensity towards social risk influences other social aspects such as rank, levels of affiliation and ability to cooperate.

1.3 Objective

We have discussed that relationships in primates are investments influenced by the costs and benefits of social interactions. We have also provided evidence that the processes that influence socially risky decisions are different from those that do not have a social component. Factors such as emotions, relationship and disposition all contribute to the propensity to take social risks as well as the response to their outcome. There is little information, though, regarding how each of these factors influences social risk assessment and which has the strongest effect. One of the central elements of this thesis is whether the risks inherent to social interactions influence levels of affiliation and choice of social behavior in non-human primates.

In this thesis I report on two projects that help to illuminate the role of uncertainty and potential for costly outcomes in predicting social interactions and relationship development in chimpanzees. The first project is an experiment that uses a trust game paradigm to ask whether chimpanzees are more averse to decisions involving social risk than they are to decisions involving economic risk. Here we also investigate the role of relationships in making social investments. The second project is an observational study where we ask whether uncertainty influences relationship formation and maintenance in a newly formed group of captive chimpanzees. These projects together will help to answer whether social risk influence how chimpanzees interact and whom they interact with.

Chimpanzees diverged from the human lineage around 6 million years ago and share most of our genetic code (Chen & Li, 2001; Steiper & Young, 2006). Because of this, using chimpanzees in this study serves to provide a genetic comparison with humans as well as a glimpse into the social capabilities of primates. If chimpanzees react to social risk in a way that is similar to that of humans, then we can conclude that certain behaviors and responses to social risk are not unique to the human lineage. However if we do find differences, understanding where in our evolutionary history these behaviors developed helps to determine what selection pressures led to them and whether human traits have precursors that are present in more distant relatives.

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2. SOCIAL RISK IN CHIMPANZEES

In the animal kingdom, risky decisions involving resources, also considered economic risk, often encompass how far to travel for food or water (Smallwood, 1996). Social risk, in contrast, is a unique category of risk where the costs, benefits and source of uncertainty of an interaction derive from a known individual or group mate (Bohnet, Greig, Herrmann, & Zeckhauser, 2008). Because the outcome of a social interaction depends on the reactions of independent individuals, with distinct motivations, assesing the level of risk in social interactions differs from risk assessment in the physcial realm.

Social risk may be especially prominent in non-human primates (NHP) with several unique factors of their social ecology contributing to the uncertainty of whether an interaction will result in a cost or benefit. Examples of these factors are the large number of different individuals with which many NHP interact, the wide variation of social behaviors in the NHP repertoire and the fact that NHP often behave differently towards group-mates depending on relationship characteristics such as kinship and dominance status (Kummer, Daston, Gigerenzer, & Silk, 1997; Silk, 2007; Whiten & Byrne, 1988). This suggests that non-human primates must have effective heuristics and social conventions in order to reduce the cognitive demand of assessing with whom to interact and what social behaviors to employ.

Because of our close evolutionary relationship, there are strong similarities between human brain function and that of non-human primates (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Squire, 1992). Given the importance of social group living in most monkey and ape societies, there is a likely homology with the mechanisms for social decision-making in humans. If both humans and non-human primates assess social risk in similar ways, this provides evidence that the relationship factors and individual characteristics to which humans attend, may be similar in non-human primates.

Primates benefit from repeated social interactions through longer lives (Kummer, 1978; Silk et al., 2010) through enhanced offspring survival (Silk et al., 2010; Silk, Alberts, & Altmann, 2003), stress reduction (Cheney & Seyfarth, 2009; Crockford et al., 2008), coalitionary support (Schino, 2007) and increased access to mating and resources (Henzi et al., 1999). The potential costs of risky social interactions stem from injury due to aggression (Mitani & Amsler, 2003; Newton-Fisher, 1999), opportunity costs from choosing one individual over another and the loss of security and value in a relationship (Cords & Aureli 2000). Little is known, though, about how these costs and benefits encourage different decision-making in the social realm compared to the physical realm, influence social behaviors or dictate partner choice.

Due to their phylogenetically close link with humans chimpanzees are an especially good species for investigating questions about social decision-making (Chen & Li, 2001; Steiper & Young, 2006). Experimental and observational studies of chimpanzee responses to positive and negative social interactions have repeatedly produced negative results as they have frequently been studied through the lens of reciprocity as opposed to social risk-taking (Clutton-Brock, 2009; Pele et al., 2009; Silk et al. 2005). Chimpanzees for example did not take advantage of an opportunity to provide no-cost rewards to a partner (Silk et al. 2005) and Brosnan et al. (2009) concluded that, even with no risk involved, chimpanzees did not provide rewards to partners who had previously rewarded them. This indicates that the subjects of the study did not respond to the benefits afforded them by a partner from a social interaction, at least not in a tit-for-tat manner.

Using the assurance game, which does investigate social risk, Brosnan and colleagues (2011) analyzed their results for differences between individuals depending on partner choice and the results were inconsistent. Some chimpanzee subjects varied their tendency to invest in different individuals but others reacted to all individuals in the same way. This either indicates that chimpanzees do not use relationship characteristics to evaluate whether to take social risks or they do not distinguish between risky and non-risky social interactions. Bullinger and colleagues (2011) also tested chimpanzees in an assurance game paradigm and found that most of their chimpanzee subjects chose the cooperative and highest-risk option. Their subjects, like the subjects in the Brosnan et al. 2011 study, though, did not alter their behavior based on that of their partners. This outcome may have been due to the fact the partners could see each other when choosing whether to take social risks, which allowed them to use the low risk strategy of reacting to the choice of the first test subject to choose.

In contrast, other experimental studies conducted with chimpanzees produced more positive effects. When de Waal (1997) provided chimpanzees with the opportunity to share food he found that they preferentially shared with individuals who had recently groomed them. In two studies investigating partner choice chimpanzees adjusted their levels of cooperation according to the way a partner behaved and, in a separate study, chose to work with a partner who had provided past benefits to them (Melis, Hare & Tomasello 2006; Melis, Hare & Tomasello, 2008). Here chimpanzees appear to assess the potential benefits that a partner can provide and respond accordingly. Contrary to those mentioned above, these studies suggest that the costs and benefits of a social interaction have the potential to influence with whom a chimpanzee interacts as well as what behaviors are employed.

One common limitation in controlled studies that investigate social decision-making in chimpanzees is that researchers often select only tolerant and affiliative dyads to work together as partners or do not report relationship (Bullinger, Wyman, Melis, & Tomasello, 2010; Hirata & Fuwa, 2007; Melis et al., 2006, 2008). Although how closely they must work together during a task often enables chimpanzees to dictate what partners they will tolerate, limiting dyads to positive relationships may hide subtle effects of relationship on social behaviors, especially those that may arise between rivals. Recently, Engelmann and Hermann (2016) played a trust game with chimpanzee subjects and assigned them multiple partners with whom they had both positive and negative relationships. As expected, subjects were more willing to invest in friends than in non-friends but their level of social risk-taking was not influenced by the amount of rewards that they received from their partner.

In NHP experiments, attitude towards non-social risk is determined by whether or not a constant medium reward is chosen over a variable one with potential high and low payoffs (Haun, Nawroth, & Call, 2011; Hayden, Heilbronner, Nair, & Platt, 2008; Heilbronner et al., 2008; McCoy & Platt, 2005; Rosati & Hare, 2011). According to Yamagishi (2011), one controlled way to measure social risk, while ruling out confounds, is to play an economic "faith" game as, with this paradigm, a test subject must assess their confidence in a partner. In order to operationalize social risk the variable choice is contingent on the behavior of a social partner and a non-social option pays out a guaranteed small reward. Often a non-social gambling condition is added in order to compare how an individual responds to social uncertainty versus uncertain rewards that do not originate from the choices of another individual (Blount 1995; Bohnet & Zeckhauser 2004).

The results of these behavioral studies in humans suggest that participants are more averse to taking risks when the outcome relies on the choices of a social partner than they are to taking risks when the outcome is due to chance (Blount 1995; Bohnet & Zeckhauser 2004). Various explanations could account for the discrepancy between social and non-social risk preferences, many of which have not been experimentally studied. Inequity in reward distribution, the inherent value of social relationships and the emotional salience of interacting with another individual may all play a role (a discussion of which is outlined in the Introduction).

Conducting a trust game experiment with non-human primates will add to the existing literature on whether the costs and benefits of social interactions do indeed influence with whom an individual will interact and what types of decisions they make. Using a modified trust game with randomly partnered chimpanzees, Engelmann et al. (2015) argue that chimpanzees establish behaviors indiciative of trust since on 83% of trials subjects chose to invest in a social partner. Before making claims, though regarding chimpanzee's tendencies for or against social risk-taking, or trust, it is important to establish whether they behave differently when presented with non-social choices with similar rewards. This type of trust-game paradigm allows for a comparison between social risk and non-social risk in order to investigate whether social decision-making in NHP differs from decision-making about economic risk. Only then can we conclude that chimpanzees make decisions based on social information and not purely the presence or absence of rewards.

Our experimental paradigm was a human economic trust game with both a social and a non-social condition that we modified for use with chimpanzees (Berg, Dickhaut & McCabe 1995). Using this paradigm we operationalize social risk as the willingness to invest the opportunity for a reward in the decision of a social partner. We ran two experiments in order to ask three research questions: (1) Are chimpanzees more averse to a loss resulting from the choices of a conspecific than a loss incurred through non-social means? (2) Do individual differences in social risk preferences correlate with independent measures of social behavior? (3) Does quality of social relationship outside the experimental setting influence decisions made during a social investment game?

2.1 Methods

2.1.1 Subjects and housing

Our test subjects were eight socially housed female chimpanzees living in a social group at the Field Station of the Yerkes National Primate Research Center in Lawrenceville, Georgia. The group consisted of 11 individuals including two males and one additional female that were not subjects. All group members had access to $711\mathrm{m}^2$ of outdoor space containing a large wooden climbing structure and various enrichment devices such as barrels and tubes. Additionally, an indoor space consisting of five interconnected runs with sleeping platforms, hammocks and nesting material was accessible to the animals. All chimpanzees received primate chow and water *ad libitum* as well as two daily meals of mixed fresh fruit and vegetables. Any rewards given for testing were supplemental to the animals' daily diet.

In order to participate in testing we called each individual into a five-run testing facility connected to the enclosure. The chimpanzees voluntarily participated in all testing and as soon as each individual was positioned correctly we rewarded them. Both the subject and their partner entered into adjacent runs that were separated by 2" square mesh. This allowed the subject and partner full visual access to each other's choices as well as limited physical contact. They then took part in either one session of the trust game or a control condition. If either chimpanzee signaled that they wanted to leave the testing facility, we aborted the test session and released the individual outside.

2.1.2 Experiment I: Chimpanzee trust game

2.1.2.1 Social condition

In the social condition of our modified paradigm, chimpanzee subjects used a 3" Polyvinylchloride (PVC) token to indicate one of two possible choices by either placing the token in a box or giving it to a partner. The first option was a box that always rewarded one slice of banana, measuring approximately 1/4", to the subject only (Constant Box). We considered this the safe choice (Social Safe). For the second option the subject could hand a token directly to their conspecific partner by passing it through the mesh into the adjacent run. We consider this the risky option (Social Risk).

If the partner obtained the token she then had two possible options; a Prosocial Box (Prosocial Choice) and a Selfish Box (Selfish Choice). If the partner chose the Prosocial Box both she and the subject received two slices of banana. If the partner placed the token in the Selfish Box she received two banana slices but the subject did not receive any reward. By giving the token to her partner, the subject gave up a certain small reward for the possibility of a reward that had twice the value, but was not guaranteed. This arrangement is pictured in Figure 2.1.

To control for potential bias in the partner's choices due to the position of the boxes, we mounted both the Selfish Box and Prosocial Box on a spinning apparatus enabling each to be positioned in one of four possible places, a photograph of which is in Figure 2.2. We then randomized their position and rotated them for each trial. Additionally, we were concerned that if the partner did not immediately make a choice when she obtained the token, the increased latency to reward might influence the subject's choices. We controlled for this by measuring the amount of time it took for the partner to choose a box and the next time that the subject chose Social Safe, we waited the same amount of time before rewarding the subject. This ensured that the subject waited approximately the same amount of time for both Social Risk and Social Safe choices.

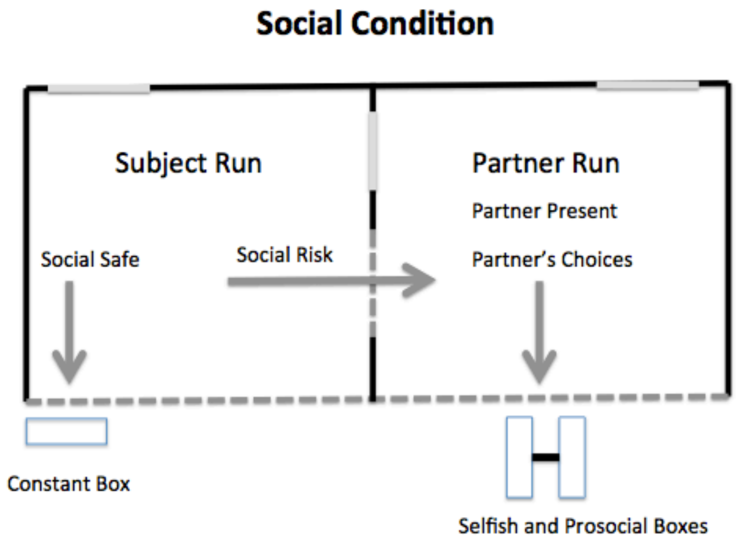

Figure 2.1 A schematic drawing of the social condition. The Social Safe choice rewarded the subject with one slice of banana. For Social Risk, the subject passed a token to her partner and either received two slices of banana (Prosocial Box) or no reward (Selfish Box) depending on which box the partner chose.

Figure 2.2 A photograph of the apparatus holding the Selfish Box and Prosocial Box. It was positioned at the mesh where the partner used a token to make a choice between the boxes. The apparatus rotated in order to place the boxes in a different position for each trial.

2.1.2.2 Non-social condition

In the non-social condition, the Constant Box that always rewarded one slice of banana was still an available choice (Non-Social Safe). Here the variable option for the test subject was to insert the token into an apparatus that had the Prosocial Box and Selfish Box positioned beneath it (Non-Social Risk). We designed the apparatus so that the surreptitious twist of a key by the researcher directed the token into one of the two boxes. The test subject could not see the key and did not have any knowledge as to whether she would be rewarded or not for her choice. Since this condition had no social component, the outcome was hopefully perceived by the chimpanzees as a result of chance.

In order to compare the social and non-social conditions, we manipulated the apparatus so that the average number of wins and losses in the non-social condition were the same as the partners' choices in the social condition. Occasionally a subject did not ever choose Social Risk during the social condition but did choose Non-Social Risk during the non-social condition. In this case we set her average at 50% so that she received equal numbers of wins and losses. If she did choose Social Risk in subsequent sessions we then adjusted the non-social condition accordingly.

In order to control for the presence of another individual the partner still sat in the same run during the non-social condition. If the token fell into the Prosocial Box, both the subject and partner received two slices of banana. If the token fell into the Selfish Box, only the partner received two slices of banana. To maintain consistency we used the same boxes for both the social and non-social conditions. In both conditions we indicated both possible options to the subject using square plastic targets attached to the mesh with token-sized holes drilled into the center. Figure 2.3 shows the set-up of the non-social condition while Figure 2.4 shows a photo of the non-social apparatus. Table 2.1 outlines all possible choices by the subject and the partner as well as what they rewarded each.

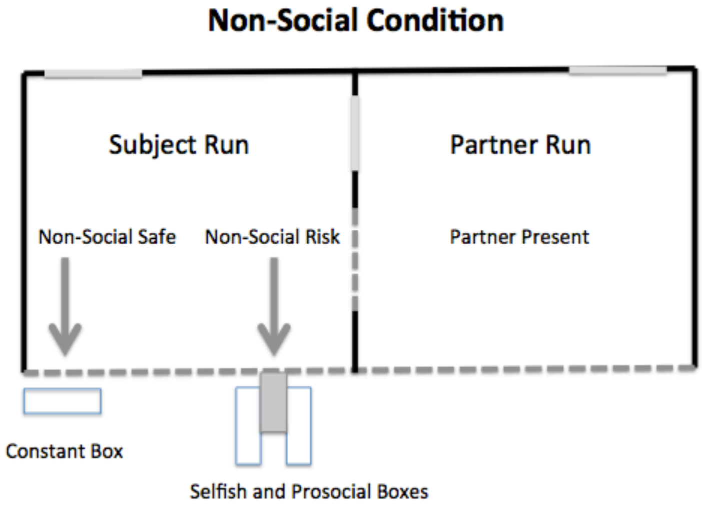

Figure 2.3 A schematic drawing of the non-social condition. In this condition the Non-Social Safe choice rewarded the subject with one banana slice. The Selfish Box and Prosocial Box were underneath an apparatus that obscured where they were going to land.

Figure 2.4 A photograph of the apparatus used in the non-social condition. The subject inserted a token into the tube and a flap inside directed it into either the Selfish Box or Prosocial Box.

Table 2.1 Each choice in the social and non-social conditions.

Choice	**Role**	**Action**	**Reward Structure**
Social Risk	Subject	Pass token to partner	Subject: Reward based on partner's choice. Either 2 banana slices (Prosocial Box) or 0 banana slices (Selfish Box). Partner: 2 banana slices
Social Safe	Subject	Put token in Constant Box	1 banana slice to subject only
Non-Social Risk	Subject	Put token in apparatus	Subject: Based on average of partner's choices from social condition. Either 2 banana slices (Prosocial Box) or 0 banana slices (Selfish Box). Partner: 2 banana slices
Non-Social Safe	Subject	Put token in Constant Box	1 banana slice to subject only
Selfish Choice	Partner	Put token in Selfish Box	Partner: 2 banana slices Subject: 0 banana slices
Prosocial Choice	Partner	Put token in Prosocial Box	Partner: 2 banana slices Subject: 2 banana slices

2.1.2.3 Test sessions

Both the social and non-social conditions consisted of three 60-trial sessions. We divided each 60-trial session into two days of testing with the chimpanzees completing up to 30 trials per day. If the subject did not complete all 60-trials in two days we added more test sessions until all trials were completed. Once a subject completed 60-trials of one condition they then completed 60-trials of the next condition and then moved back to the first condition. We repeated this process until they finished 3 sessions of each condition.

To control for the effect of the order of each condition, we randomized which subjects began with a social condition and which began with a non-social condition. Since we manipulated the outcomes in the non-social conditions to pay out the same mean as the previous social condition, we gave subjects who started on a non-social condition an extra non-social session at the end of the experiment in order to have a social condition with which to compare it. Subjects who began with a non-social condition were rewarded 50% of the time and we did not include the data from the first non-social condition in our comparative analysis.

Each test session began with forced choice trials that functioned to remind the subject of all possible options and to ensure that the subject was willing to pass to the partner when no other alternatives were available. These trails entailed the subject passing the token to the partner two times, once in which the partner could only choose the Prosocial Box and again where the partner could only choose the Selfish Box. The subject then put the token in the Constant Box twice in order to counterbalance the number of times she received rewards for each choice. We randomized the order of these forced choice trials and if a subject refused to pass the token to the partner at least twice we aborted the session. If the subject consistently refused to pass the token during forced choice trials then that subject/partner pair was not tested together. During the first phase of the experiment we never interchanged subject-partner pairs.

Horner et al. (2011) did not find that a difference in relationship outside of the testing context had an influence on whether chimpanzee subjects chose a social or prosocial option in their experiment. In Engelmann and Hermann's (2016) trust study on chimpanzees, though, subjects chose to invest more in affiliative partners over non-affiliative ones. Because of this, it was important to control for the role of relationship on subject's choices. Therefore, for this phase of the experiment, we assigned subject/partner pairs who's relationship at the time measured as neutral according to behavioral observations from which we calculated adjusted standardized Pearson's residuals. Although in a subsequent experiment we did explore the role of relationship on the subject's choices.

To calculate this measure we obtained the expected frequency of affiliation for each dyad based on the number of individuals in the group and then calculated the actual frequency of affiliation based on our behavioral observations. The adjusted standardized Pearson's residuals produced a z score based on what we would expect their relationship to be due to chance. Table 2.2 lists all subjects in Experiment I along with their relationship index with their partners. Occasionally, partners and subjects became aggressive with each other either before or during testing. When this happened they were given the opportunity to calm down and continue with the experiment or, if they indicated it, to stop the session.

Table 2.2 Subject/partner pairs in Experiment I.

Subject	Partner	Relationship Index
Azalea	Dara	-2.27^
Barbi	Katie	-0.40
Dara	Barbi	-1.13
Fiona	Barbi	-1.32
Katie	Rowena	-1.40
Liza	Katie	0.08
Rita	Liza	-0.56

*An arrow indicates a dyad that measured as significantly avoidant according to an adjusted standardized Pearson's residual.

2.1.2.4 Behavioral observations

In order to select partners according to their dyadic relationship outside of the experimental paradigm, as well as correlate subject choices with independent measures of behavior, we used data from weekly systematic behavioral observations. de Waal and Van Hooff created the ethogram that we used for behavioral coding (de Waal & van Hooff 1981) and it had been in use in its current form since 1989 (de Waal, 1989). Each observation lasted 90-minutes and consisted of 10 scan samples recorded every 10-minutes. For each sample we recorded which dyads were in proximity as defined by individuals who sat within an arms reach of each other. We also recorded directional grooming as well as which individuals had moved out of view. Because all chimpanzees had indoor and outdoor access during observation times, each was visible for a different number of scans. To adjust for these differences, we divided all behavioral frequencies by the number of observation hours unique to each individual to obtain a mean rate per hour for each individual across each behavior.

In order to determine each subject and partner's position within a linear dominance hierarchy we recorded dyadic pant-grunts. Three researchers (SC, JW and MS) recorded every instance heard, both during systematic observations and *ad libitum*. We chose this behavior because, in chimpanzees, pant-grunts are considered the formal dominance signal and, in most cases, represent a 100% unidirectional sign of submission (Noë, de Waal, & van Hooff, 1980).

2.1.2.5 Training and criteria

In order to participate as a test subject all individuals had to pass a preference test, where, according to a binomial test, they picked two slices of banana significantly more often than one slice of banana when presented with 20 trials for two subsequent days. They also had to pass a token to a non-partner chimpanzee for a reward to ensure that they were amenable to passing a token through the mesh and giving it to another individual. The only group members that that we did not test were the males as they would not reliably lock into the testing enclosure as well as one female that was added to the group during the study. Before testing started, we exposed all subjects to the meaning of all choices in both the subject and the partner role using a human as the subject/partner and either passing the token to them, having them pass the token to us or placing the token in the Constant Box. We exposed the subjects to each role for 20 trials per day for two consecutive days.

Before each subject began testing we trained her to significantly choose the Prosocial Box over the Selfish Box so that when the partner made choices during the experiment the subject recognized the meaning of both boxes. This served to help with the subject's concept that her rewards originated from her partner's choices. Because of this, once a subject completed the experiment with two boxes, they did not use the same two boxes when they acted as a partner. This meant that we trained most of the subjects and partners on several sets of boxes, as distinguished by various colors and patterns, through the course of the experiment. The partner never had any training or previous experience with the meaning of the unique boxes for their condition before the start of the experiment. Thus, we expected partners to chose randomly, at least during the initial trials of the experiment.

2.1.3 Experiment II: Dyadic variation trust game

In order to answer Question 3, we repeatedly ran the social condition of the trust game with multiple subject/partner combinations. Each subject-partner combination completed four 30-trial sessions of the social condition. Each subject played the game with a maximum of three new partners. Due to management reasons and time constraints, some subjects completed fewer sessions. Table 2.3 lists subject-partner pairs as well as their relationship index. For this experiment, we wanted as much variability in relationship as possible so chose partners that measured as affiliative according to the adjusted Pearson's residual as well as pairs that were neutral and avoidant.

Table 2.3 Subject/partner pairs in Experiment II.

Subject	Partner	Relationship Index
Azalea	Fiona	-2.54^
Azalea	Liza	6.57*
Dara	Katie	-1.87
Dara	Rowena	6.10*
Fiona	Azalea	-2.53^
Fiona	Dara	7.17*
Katie	Barbi	-0.40
Katie	Liza	0.08
Katie	Rita	2.30*
Liza	Azalea	6.57*
Liza	Barbi	-1.68
Liza	Rowena	0.12
Rita	Katie	2.20*
Rita	Rowena	-1.52
Rowena	Dara	6.10*
Rowena	Fiona	3.68*
Rowena	Katie	-1.39

*An asterisk indicates dyads that were significantly affilative while an arrow indicates those that were significantly avoidant.

2.1.4 Control conditions

In order to ascertain what aspects of the experiment were driving subject's choices, we ran two control conditions and eventually added a third control condition. We began running control conditions after the subject finished all sessions from Experiment I, and continued while Experiment II was ongoing. The first control condition was an open-door condition, with the partner absent, where the subject had access to the Constant Box as well as the partner's Prosocial Box and Selfish Box. This is outlined in Figure 2.5. The choice that paid the most rewards was the Prosocial Box in the run adjacent to the subject, where the partner was positioned during the experiments.

If the subject put the token in this box she received four banana slices, two in the partner's run and two in her run. If she placed the token in the Selfish Box she received two slices of banana in the partner's run and if she placed the token in the Constant Box in her run she received one slice of banana.

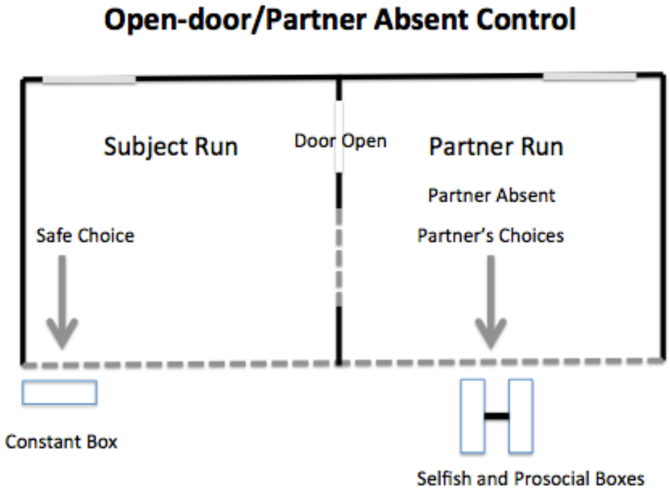

Figure 2.5 A schematic drawing of the open-door/ no partner control. In this control the subject could either choose the Constant Box for one slice of banana or could walk into the run that the partner was previously in and choose between the Prosocial Box and Selfish Box.

The second control condition was a closed-door, partner absent condition where the test subject had access to the Constant Box and could also pass the token into the empty run in a similar manner to when the partner was present. Figure 2.6 shows the set-up for this condition. If they passed the token through the mesh there was no one on the other side to take it, and they did not receive a reward. Both control conditions consisted of two 20-trial sessions.

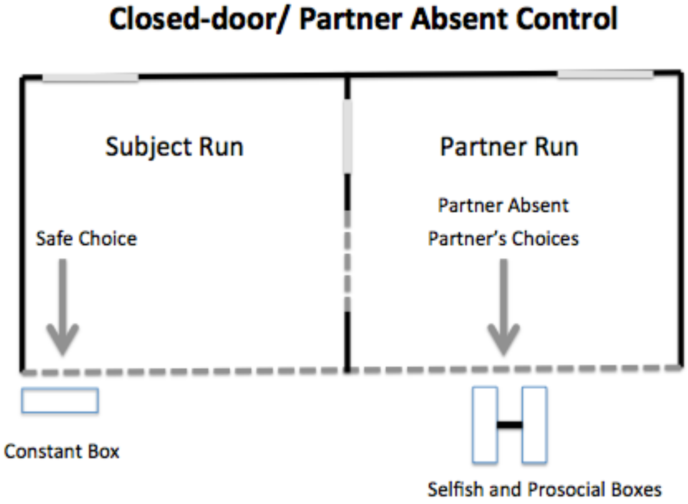

Figure 2.6. A schematic drawing of the closed door/ partner absent control. The subject had access to the Constant Box but not to the Selfish Box or Prosocial Box in the partner's run.

2.2 Predictions, Analyses and Results

2.2.1 Question 1: Are chimpanzees more averse to a loss resulting from the choices of a conspecific than a loss incurred through non-social means?

Cognitive processes that lead to irrational outcomes drive economic decisions in both humans and NHPs (Lakshminarayanan, Chen, & Santos, 2011; Tversky & Kahneman, 1981). One reason for this is that subjective factors such as emotions interfere with rational decision-making and this is especially true in the social realm (Brosnan & de Waal 2003). Therefore, we predict that chimpanzees will consider a loss due to the actions of a conspecific to be more aversive than a loss that is purely economic.

Because chimpanzees ascribe intentionality to another's actions (Call, Hare, Carpenter, & Tomasello, 2004), they may be capable of linking the positive or negative outcome of the trial to the actions of their partner whereas they will not ascribe the same intentions to an inanimate apparatus. If chimpanzees do attribute the outcome of the trial to their partner's actions this could impact the perception of their relationship or violate their already held expectations. This could happen, in part, because social relationships in chimpanzees hold value (Cords & Aureli, 2000; Fraser, Schino, & Aureli, 2008; Koski, de Vries, van de Kraats, & Sterck, 2012) and chimpanzees respond as if prosocial interactions are rewarding in and of themselves (Horner et al. 2011), although several studies have found that chimpanzees are not spontaneously prosocial (Brosnan et al. 2009; Jensen et al. 2006; Silk et al. 2005).

If chimpanzees do respond more aversively to social risk than non-social risk it implies that when a chimpanzee loses a reward due to the actions of a social partner they are losing more than the economic value of the prize. They are also losing confidence in the relationship as well as the emotional reward that a partner provides. We could obtain the predicted results even if the threat of losing a reward due to the actions of a social partner is driving the subjects choices regardless of whether or not that threat is realized in the partner's actions or in the subject's understanding of the game. In other words, it is the added risk in the social condition that might motivate the subject's response, not necessarily the outcome of the game.

2.2.1.1 Analysis

In order to determine whether or not individuals differentially chose Non-Social Risk over Social Risk, we directly compared the frequency data from the social and non-social conditions via a Wilcoxon Signed Ranks test. We used this test because the data were not normally distributed according to a Kolmogorov-Smirnov test. All significance values are two tailed.

2.2.1.2 Results

In the social condition of Experiment I chimpanzee chose Social Risk an average of 39% of the time (*M*= 69.50; *SD*= 26.55) and their partners chose the Prosocial Box an average of 64% of all of the times that they received the token (*M*= 40.87; *SD*= 45.26). The chimpanzees completed a mean number of 28.91 (*SD*= 4.00) trials per session. In the non-social condition of Experiment I chimpanzees chose Non-Social Risk an average of 64% of the time (*M*=115.38; *SD*= 60.83) and were rewarded an average of 53% of the time (*M*= 63.75; *SD*= 33.70). In this condition they completed a mean number of 26.76

(*SD*= 6.81) trials per session. A binomial test revealed that subjects chose Social Risk less than Social Safe in the social condition (p=0.004) and chose Non-Social Risk more than Non-Social Safe in the non-social condition (p<0.001).

When comparing the social and non-social conditions a Wilcoxon Signed Ranks test revealed that chimpanzees selected Non-Social Risk significantly more often than Social Risk (Z= -1.960, p= 0.049). According to binomial tests four subjects were significantly averse to social risk over non-social risk (Azalea p< 0.001; Rowena p< 0.001; Barbi p< 0.001; Fiona p< 0.001), one individual was significantly averse to non-social risk (Liza p= 0.034) and the remaining subjects showed no significant preference (Katie p= 0.523; Dara p= 0.832; Rita p= 0.472). Figure 2.7 displays the combined average frequency of risky choices for the social condition while Figure 2.8 indicates the frequency of each subjects' risky choices in both conditions. There was a correlation between Social Risk choices and Non-Social Risk choices indicating that individuals' preferences for non-social risk are similar to their preferences for social risk (Spearman r_s= 0.714, p= 0.047, N=8). See Figure 2.9. Taken together, these results indicate that overall chimpanzees are more averse to social risk than to non-social risk but that individuals who are prone to risky choices make them in both social and non-social conditions.

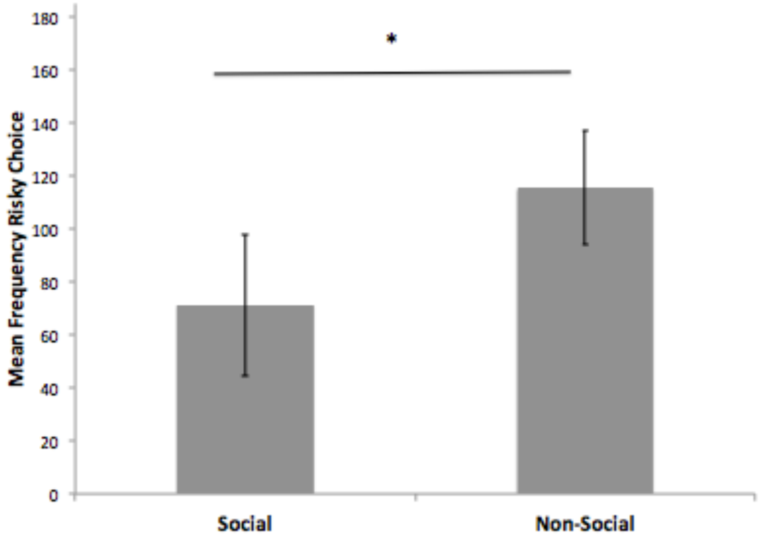

Figure 2.7 The combined mean risky choices in the social and non-social conditions. A Wilcoxon Signed Ranks test revealed a significant difference between the two (*p= .049) and the lines indicate standard error bars.

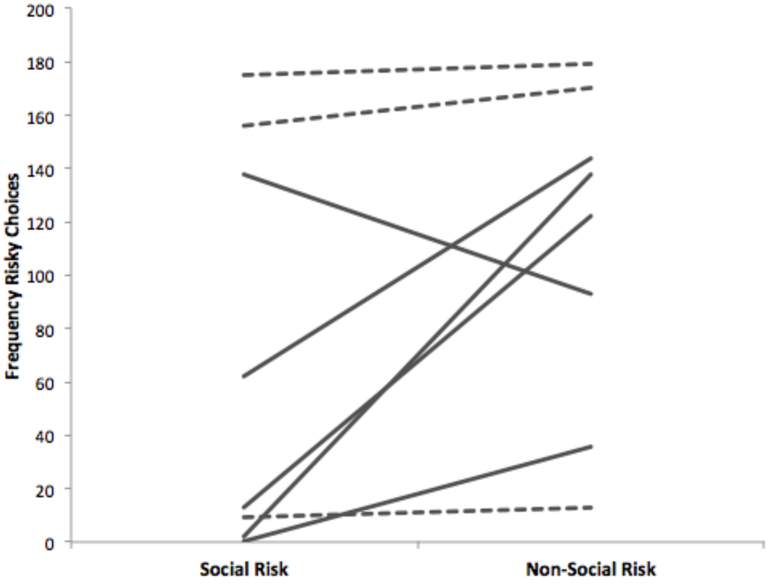

Figure 2.8. The frequency of risky choices by subject in the social and non-social conditions. A solid line signifies a significant difference between social and non-social conditions via a binomial test.

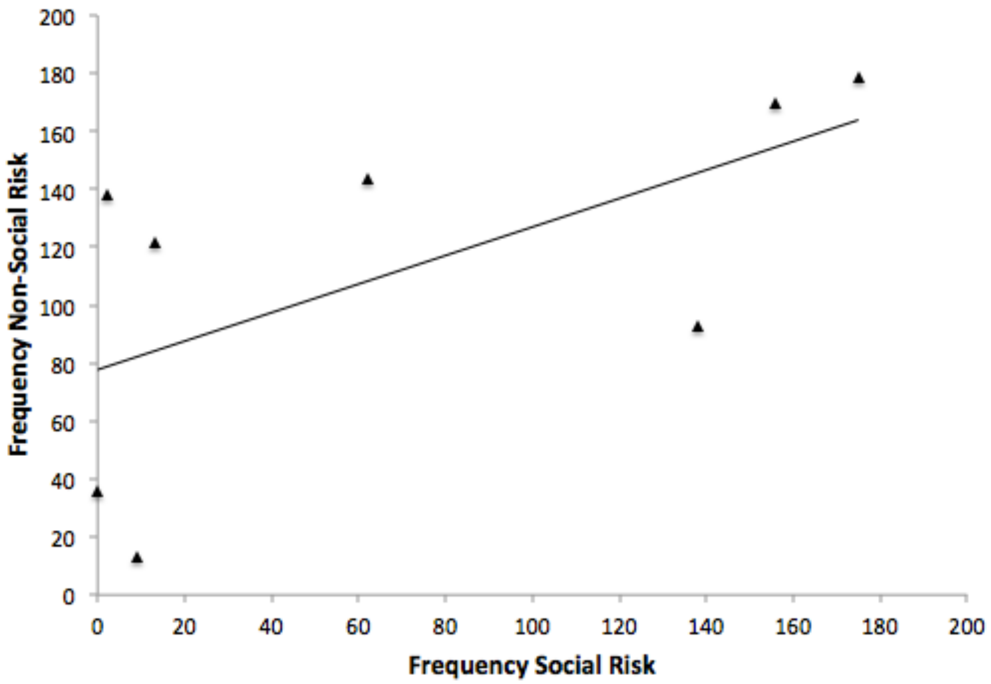

Figure 2.9. The relationship between an individual's frequency of choosing Social Risk and Non-Social Risk. A Spearman analysis indicates a significant correlation (p= .047).

2.2.2 Question 2: Do individual differences in social risk preferences correlate with independent measures of social behavior?

One of the first researchers to use real money in an investment game to determine what personality characteristics help predict trusting and trustworthy behavior in humans concluded that people who are trusting are also trustworthy (Wrightsman, 1966), a finding replicated by Glaeser et al. (2000). In humans this finding most likely relates to individuals projecting their own motives and beliefs onto other people. In our subjects we investigate whether individuals who take more social risks are also more prosocial, as partners. We expect, though, that a positive relationship between the two factors may instead be due to individual variation in levels of prosocial behavior or aversion to inequity as opposed to motives and beliefs.

In humans, individuals who have high ‘social capital’ as measured through number of friends and amount of money are trusted more than those who are perceived to have low social capital (Glaeser et al. 2000). In our study we predict that these findings may translate to chimpanzee subjects choosing a social option more often when their partner has a higher overall rank in the group. This paradigm also allows us to examine other ways in which rank influences the choices of subjects and partners. Horner et al. (2011) found, for example, that higher ranked individuals behaved more prosocially than lower ranked ones. Given these results, we predicted that our higher ranked partners would choose the prosocial box more frequently than lower ranked partners.

2.2.2.1 Analyses

We correlated data collected from Experiments I and II with data from behavioral observations, as well as the linear dominance rank for each individual, using Spearman's rank-order correlations.

2.2.2.2 Results

We conducted 57 hours of observation between 2/24/14 and 1/10/15. Overall group rank and individual characteristics did not have a relationship with choices made in the trust game. Partners did not choose the Prosocial Box more often when a subject had a higher group rank ($r_s = 0.046$, N=21, $p = 0.842$), partners with a higher rank in the group did not choose the Prosocial Box more often than those with a lower rank in the group ($r_s = 0.384$, N=21, $p = 0.085$) and subjects who chose Social Risk more were not more prosocial when they were a partner ($r_s = - 0.286$, N=7, $p = 0.535$).

2.2.3 Question 3. Does quality of social relationship outside of the experimental setting influence decisions made during a social investment game?

The results of several studies indicate the potential for an effect of outside relationship on the choices made between partners during experimental tests. A chimpanzee group with more stable relationships was less averse to inequity presented within a testing paradigm (Brosnan, Schiff, & de Waal, 2005) and chimpanzees participating in a modified trust game with two partners of differing relationship quality invested most readily in those with whom they were more socially affiliative (Engelmann & Hermann 2016). Horner et al. (2011) found no correlation, though, between the strength of a subject and partner relationship outside of the context of a social choice experiment and the number of prosocial choices the subject made. Brosnan et al. (2015) did find that relationship outside of an experimental context predicted what chimpanzees would enter a testing facility together but did not predict inequity aversion once they were inside. Given the similarities between our study and Engelmann and Hermann (2016), we predict that our subjects will also make a distinction between affiliative and avoidant partners when choosing whether or not to take social risks. Since Engelmann et al. (2015) found trial-by-trial contingencies between partner's prosocial choices and the amount of risk that their subjects took we also predict similar findings.

2.2.3.1 Analyses

We referred to data on grooming and proximity taken from behavioral observations to calculate the strength of each dyadic relationship based on adjusted, standardized Pearson's residuals. We then calculated a multiple linear regression to ascertain whether dyadic relationship index or the percentage of time the partner chose the Prosocial Box predicted Social Risk in Experiment II. We also calculated whether each subjects' choices depended on partner choice in the previous trial by obtaining the frequency of partner choice/subject choice outcomes and creating a 2x2 contingency table analyzed using a Chi Square test with Yates correction.

2.2.3.2 Results

We conducted Experiment II with an additional 18 dyadic combinations. Combining these with the pairs in Experiment I produced a total of N=26 dyadic combinations for our analysis in Experiment II. The chimpanzees in this experiment completed a mean of 29.01 (*SD*= 4.06) trials per session. We calculated a multiple linear regression to ascertain first whether percent Prosocial choice by the partner predicted percent Social Risk by the subject and then added relationship index into the regression to ascertain whether it added predictive power to the model. The regression equation in the first model was not significant. When we added the relationship index into the equation the second model also failed to predict a change in subject's risky choices. Table 2.4 outlines the results of the regression.

Table 2.4 The results of a multiple regression for Experiment II

Social Condition	*B*	*S.E.B*	β	R^2	R^2 change	Partial Correlation	*F*	*p*
Prosocial Choice	.042	.345	.028	.000		.028	.000	.985
Relationship Index	.019	.029	.155	.024	.024	.154	.459	.506

In order to further elucidate whether subjects made risky choices based on past rewards or based on relationship with their partner, we analyzed the choices of each dyad by session in Experiment II using a multiple regression. Our findings indicate that the percentage of Prosocial choices significantly predicted Social Risk by the subject in Session 1 and 4. The regression equation was non-significant in Sessions 2 and 3 (See Table 2.5 for statistics). Relationship never predicted risky choice.

For comparison we also analyzed the choices of each subject by session for the non-social condition using a linear regression. Here, the percent Prosocial Box significantly predicted Non-Social Risk in Session 2 and 4 but not Sessions 1 or 3. The permutation procedure, though, indicates non-significance. Table 2.6 outlines the results of the regression.

Table 2.5 Multiple linear regression results by social session

Social Condition	*B*	*S.E.B.*	β	R^2	R^2 change	Partial Correlation	*F*	*p*
Session 1								
Prosocial Choice	.785	.278	.596	.287		.602	6.03	**.027***
Relationship Index	.030	.019	.334	.394	.108	.389	2.49	.137
Session 2								
Prosocial Choice	-.065	.346	-.048	.004		-.048	0.06	.810
Relationship Index	.009	.027	.087	.011	.007	.087	0.11	.741
Session 3								
Prosocial Choice	-.068	.330	-.054	.003		-.055	0.04	.848
Relationship Index	-.013	.029	-.121	.017	.015	-.121	0.21	.655
Session 4								
Prosocial Choice	.755	.252	.600	.363		.600	9.71	**.006***
Relationship Index	-.003	.020	-.032	.364	.001	-.040	0.02	.874

*The permutation procedures for Sessions 1 and 4 indicate significance at p= .008.

Table 2.6 Multiple linear regression results by non-social session

	B	*S.E.B.*	β	R^2	Partial Correlation	*F*	*p*
Session 1	-.857	1.202	-.304	.093	-.304	0.51	.507
Session 2	1.479	.569	.758	.575	.758	6.75	**.048***
Session 3	-.148	1.729	-.038	.001	-.038	0.01	.935
Session 4	-1.259	.354	-.846	.716	-.846	12.61	**.016***

* The permutation procedure for Session 2 and 4 indicates non-significance at p= .063 and p=.105.

The mean frequency of Social Risk by the subject following a Selfish Choice by the partner was 63.14 (*SD*= 32.28) while the mean frequency of Social Risk by the subject following a Prosocial Choice by the partner was 99.43 (*SD*= 86.18). The mean frequency of Social Safe choices by the subject following a Selfish Choice by the partner was 6.00 (*SD*= 6.11) while the mean frequency of Social Safe choices by the subject following a Prosocial Choice by the partner was 5.86 (*SD*= 5.15). Figure 2.10 shows the mean frequency of each subject choice/ partner choice combination.

A 2x2 contingency table using the frequencies for all dyads produced a significant result (χ^2= 9.48, N= 24, *p*=.002) with a large effect size (*r*= .63). When divided by session a contingency table revealed significance in Session 1 but not in Session 2, Session 3 or Session 4 (Session 1: χ^2= 6.70, N=24, *p*=.009; Session 2: χ^2= .012, N=24, *p*= .914; Session 3: χ^2= 2.99, N=24, *p*=.084; Session 4: χ^2= 2.73, N=24, *p*= .099). This indicates that overall the choices of the subject are not independent from the choices of the partner and this is especially true of Session 1, which also had a large effect size (*r*= .53). All frequencies are shown in tables 2.7-2.12.

Tables 2.7- 2.12. The frequencies of subject choice at n and partner choice at n-1.

All Sessions		Subject Choice	
		Risk	Constant
Partner Choice	Prosocial	919	38
	Selfish	506	43

Session 1		Subject Choice	
		Risk	Constant
Partner Choice	Prosocial	205	9
	Selfish	115	15

Session 2		Subject Choice	
		Risk	Constant
Partner Choice	Prosocial	217	13
	Selfish	8	43

Session 3		Subject Choice	
		Risk	Constant
Partner Choice	Prosocial	250	6
	Selfish	133	9

Session 4		Subject Choice	
		Risk	Constant
Partner Choice	Prosocial	247	10
	Selfish	131	11

2.2.4 Control Conditions

In order to test whether subjects understood that they needed a partner present to receive a reward we ran a closed-door/ no partner control condition. In this condition they could either choose to drop the token into an empty run, and not earn a reward, or put the token in the Constant Box, for a small reward. If the subjects placed the token into an empty run, this may indicate that they did not realize the need for a partner in gaining a reward. If they predominantly put the token into the Constant Box, this suggested they understood that they would not be rewarded for this action unless a partner was present.

In order to test whether the subjects understood that their partner dictated whether or not they were rewarded we ran an open-door condition. Here subjects had three choices that each rewarded a different number of banana slices. Choosing the Constant Box rewarded one slice of banana, the Selfish Box two slices of banana and the Prosocial Box four slices of banana (two slices each to the subject and partner positions). To gain access to the Prosocial and Selfish Boxes the subjects had to walk through a door into the adjacent run that their partner had occupied during the experiment.

In this condition, the most effective response was for the subject to move into the adjacent run, put the token into the Prosocial Box, eat the reward presented in that run and move back into their original run to gain the two extra rewards. This implied that they knew what actions of the partners led to their own rewards as well as indicated that they remembered the meaning of each box.

2.2.4.2 Analyses

In the control conditions we measured significance using binomial tests based on the dichotomous choices made by each subject.

2.2.4.3 Results

2.2.4.3.1 Closed-door/ no partner

All test subjects (100%) significantly chose the Constant Box in this condition (*M*= 39.63; *SD*= 0.52) as opposed to placing the token into the empty adjacent run that they could not access. Three subjects pushed the token through once out of forty trials and one subject pushed the token through three times out of forty trials.

2.2.4.3.2 Open-door/ no partner

In this condition only 25% of subjects significantly chose to place the token in the prosocial box. Overall, the mean number of 'risky' choices, meaning the subject moved into the partner's run, was 25.50 out of 40 (*SD*= 13.67). Of those that did chose 'risk' 76% also chose the Prosocial Box (*SD*= 16.13). One subject significantly avoided the Constant Box but both failed to significantly use the Prosocial Box as well as failed to retrieve the rewards in the subject run when she did. One subject failed to significantly avoid the Constant Box but when she did choose between the Prosocial Box and Selfish Box, she significantly chose the Prosocial Box. Four of eight subjects (50%) both failed to avoid the Constant Box and failed to significantly place the token in the Prosocial Box when they did choose to enter into the adjacent run.

During this condition we presented the subjects with the token in their original run. They had to move to the adjacent run and then had to return to their original run both to retrieve the two extra slices of banana as well as to obtain the token for their next trial. This control condition required much more effort than the original experiment and often the chimpanzees seemed reluctant to make so many moves. Many of them waited for the token in the partner run once they had moved there or positioned themselves in front of the Constant Box and stayed there. Because of this, we could not ascertain whether the subjects truly did not recognize the role of their partner during the experiment or if they were unmotivated to switch runs two times per trial for 20 trials. It is important to note, though, that regardless of why, the subjects did not respond as predicted to the open-door/ no partner control condition.

To resolve the potential motivation issue, we set up all three options in one run. This was meant to give subjects the same choices as the open-door/no partner condition and make the level of effort more similar to the experimental condition. When the subjects participated in the control with this arrangement 87.5% of individuals significantly avoided the Constant Box (*M*= 33.50 out of 40; *SD*= 7.15) but only 25% of individuals significantly chose the Prosocial Box (*M*= 64.01; *SD*= 15.70). Because we ran this control after the chimpanzees participated in the open-door/ no partner control these results may show evidence for learning the optimal choices during the control conditions as opposed to understanding the task during the experiment. Since we had already trained the subjects to use the Prosocial Box, the choice that revealed whether they understood that their partner determined their rewards was between the constant and ‘risky’ option and not whether they chose the Prosocial Box or the Selfish Box.

2.3 Discussion

Here, we add the domain of social risk to those experiments in which emotional reactions impact rational decision-making (Lakshminarayanan, Chen, & Santos, 2011; Tversky & Kahneman, 1981). Like humans, chimpanzees are more averse to social risk than to non-social risk, implying that they perceive a loss as greater when engaging with another chimpanzee than they do when playing a gambling condition of a game. This indicates that there is an influence on social interactions that is not based on food rewards. This could suggest that socially risky interactions have an added emotional element that does not exist with economic risk. In humans, this response comes from an aversion to social betrayal, which as defined in Chapter 1 is thought to be a psychological loss due to the actions of another person that outweighs pure economic losses (Bohnet, Greig, Herrmann, & Zeckhauser, 2008). It is less clear as to what specific social aspect the subjects responded to.

The reactions of the chimpanzees might stem from the negative intentions that they ascribe to the actions of a conspecific when they lose a trial; meaning they blame their partner for their loss. This would suggest that they are interpreting the loss during the social condition as an economic loss as well as a loss to security in the actions of their partner. Given that the relationship with their partner did not influence risky choices the chimpanzees may, instead, perceive initiating a social interaction as having a higher level of uncertainty than initiating an economic interaction. This implies that it is more difficult for a chimpanzee to overcome social uncertainty than economic uncertainty.

Because one potential reason for our findings may be inequity aversion (i.e., the partner gaining more rewards than the subject), we aimed to control for this possibility.

We did this by pairing the average outcome for the social and non-social conditions so that one condition could not provide more rewards to the subject than another. Since subjects did not always complete the same number of trials for each session our average reward for the social condition was actually higher than the average reward for the non-social condition. Since this distribution favors the opposing hypothesis, it helps to strengthen our findings because the subjects turned out more averse to the social condition that paid them more. This indicates that they did not base their decisions on reward quantities alone.

While relationship did not ever predict risky choices by the subject in Experiment II, partner behavior did predict them. More specifically, Prosocial choices by the partner significantly predicted Social Risk in the first and fourth sessions of the experiment. In addition, the partner's previous Prosocial Choice or Selfish Choice influenced the subjects' risky choices, especially in the first session. This implies that individuals may build up an expectation for gains or losses from their partner based on their early experiences with the task and then do not consistently attend to further cues. This outcome illuminates some of the decision-making processes that may be taking place during relationship formation and trust building, most notably that once a social expectation is founded it is not easily altered. This complements the work of Berg and Clark (1986) and Clark (1988), who discuss that the most important time in relationship development is at the beginning as those interactions weigh more heavily than later ones.

Although reward helped to predict social risk, individuals' preferences for Non-Social Risk were related to their preferences for Social Risk. We observed that some subjects were almost completely averse to both social and non-social risk and some subjects prone to both. This implies that individual variation in risk preference influenced their choices and that each subject brought a specific risk attitude into the testing situation that was not easily altered based on reward outcome or relationship with their partner. In this way chimpanzees show similarities with humans, whose individual risk preferences are thought to have genetic influences (Cesarini et al., 2008; Naef & Schupp, 2009).

In our study, the social relationship with the partner did not appear to influence risky choices. This finding implies that chimpanzees in this testing situation invest in each other based on the actions of their partner and not based on the quality of their interactions outside of the testing facility. One limitation to this finding is that we had some partners that would not work together. In order to be paired together, all subjects had to pass to their partner at least twice during each session to remind both the subject and the partner of the meaning of each choice. When subjects failed this requirement multiple times we changed their partners. We also had some subject/partner combinations repeatedly fight through the mesh that separated the runs meaning that they could not complete a session. These factors contributed to seven dyadic combinations being unable to work together and as a result we had only three avoidant pairs, while we had nine affiliative and thirteen neutral pairs. This finding is similar to that of Brosnan et al. (2015). The Engelmann and Hermann (2016) study did not have the same requirement as our study so was able to test a wider range of pairs, possibly contributing to the result of an effect of relationship on the risky choices of their subjects. The difference between both studies may therefore be one of methodology rather than actual social effects.

One important difference between the human repeated interaction studies and the chimpanzee studies is that in the human studies relationship is held constant by either using an anonymous individual or, most often, a computer program as the partner. This also serves to remove all social context within the experiment. In chimpanzees we are able to assign and run partners based on a relationship index. This enables us to explore social decision-making under more naturalistic circumstances as well as investigate how individual decisions differ based on relationship with their partner. This is a methodology that has not been run with humans, although it is research that should be undertaken.

The trust game paradigm has rarely been used to investigate chimpanzee social decision-making, although Engelmann et al. (2015) used a similar paradigm to ask related questions. One of the most important differences between our study and that of Engelmann et al. is that our subjects could physically give their tokens to a partner in a similar way to that of Proctor et al. (2013). In the Engelmann study, in contrast, the chimpanzees were positioned in enclosures across from each other and separated by a hallway. They employed a cart that the chimpanzees could send back and forth in order to indicate their choices. Our set-up encouraged true social interactions as opposed to simply promoting a joint task. Because our subjects occupied runs that were next to each other and could engage in physical contact, they were able to communicate either through gestures, spitting water or simply positioning themselves near or far from each other. This could be another reason that the Engelmann study found an effect of relationship on subjects' choices. Since the subjects in the Engelmann study sat far away from their partners, their only cue for whether or not to make socially risky decisions was the identity of their partner whereas our subjects could have relied more heavily on their partner's behavior since they were sitting in close proximity. The positioning of our subjects and partners also meant that our experimental set-up consisted simply of tokens and buckets as opposed to the carts and ropes in the Engelmann study. Because of this our experiment may have been easier for our chimpanzees to understand.

Another difference between our two studies is that in Engelmann et al. the partner did not have an ‘untrustworthy’ choice. Instead the authors relied on a time limit, which implied that the partner did not want to reciprocate the food that was sent as opposed to making the choice explicit. This creates two problems. The first is that it implies a negative decision on the part of the partner as opposed to actually counting a negative choice. It also lengthens the amount of time for risky trials creating a delay to reward for the subject. The subject may have begun choosing the constant option simply in response to the ability to maximize rewards since that choice took less time (Genty, Karpel & Silberberg, 2012) In our study the partners made one of two choices and in this way indicated their decision to reward their partner or not as well as minimized the amount of time that it took for them to make a decision.

Contrary to Engelmann et al. 2015, our study used quantitative differences in rewards for each choice as opposed to qualitative. The subject must balance expectation and potential reward and if the reward is too high it shifts the balance towards the value of the reward instead of whether or not a reward is expected. When utilizing qualitative rewards, it is not possible to measure the value of the highest value reward and the degree to which it influences the decision. Because we used one slice of banana for the constant and two banana slices or none for our risky option, we knew that if a partner chose randomly between prosocial and selfish the subject’s average rewards were equal for constant and risk. In this way we could investigate the effects of both reward frequency and relationship on the subject’s choices.

We did not find any relationship between independent characteristics outside of the testing environment and the subject or partner's decisions made during the trust game. This implies that aspects of rank and prosocial decision-making may encompass more factors than simply the expectation of a positive or negative outcome. Many times social interactions within a group are not simply dyadic but encompass multiple individuals. The nature of the paradigm that we used may have oversimplified social decision-making in relation to characteristics such as dominance and prosocial tendencies.

One limitation to our findings is the results of the control conditions. Because few of the subjects readily moved into the partner's run in order to gain the maximum number of banana slices, we cannot assume that they understood the contingencies of the game. The results of our contingency analysis, including the large effect size, suggest that the subjects' choices were not independent of whether the partner chose the Prosocial Box or Selfish Box as do the findings that rewards predicted risky choices in early sessions with a partner. These factors taken together lead us to believe that the subjects were at least able to learn about the task through reinforcement. Additionally, since the chimpanzees did indicate an understanding of the need for a partner, via a control condition, we can conclude that they did perceive the social condition as social in nature. Even if the subjects did not understand that their rewards were a result of their partner's choices, and their actions were purely the result of reinforcement, the social act of handing the token to a partner set the social condition apart from the non-social condition.

In conclusion we found that the social nature of risk-taking causes chimpanzees to overvalue losses when compared to non-social risk, but that some individuals have an individual preference for overall risk that encompasses both domains. Our findings also suggest that chimpanzees make decisions about social risk that are contingent more on the behavior of their partner in a testing situation than on their relationship in general. This is because they use earlier outcomes to develop an expectation of their partner's actions that they continue to rely on in later interactions as well as base their decisions off of their partner's previous choices. Taken together these results helped to elucidate how chimpanzees make social decisions under conditions of uncertainty and gave us clues into the mechanisms and heuristics that chimpanzees use to assess social risk.

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3. NEW GROUP FORMATION IN CHIMPANZEES

Social interactions afford benefits (Kummer, 1978) but can also result in costs due to aggression (Mitani & Amsler, 2003), energy loss (de Waal & Davis, 2003) or a decrease in relationship value (Cords & Aureli, 2000). Cords and Aureli (2000) suggest that repeatedly balancing these costs and benefits imparts an ingrained value, compatibility and security to each relationship that together make up the overall positive or negative quality of the association. The authors define value as what can be gained by each individual such as through grooming or support. Compatibility is defined by low aggression, high tolerance and coalitionary support. Security is defined as the predictability of each interaction. These components have been verified in chimpanzee observational studies as well as in ravens (Fraser & Bugnyar, 2010; Fraser, Schino, & Aureli, 2008; Koski, de Vries, van de Kraats & Sterck, 2012).

Associations with high value, security and compatibility potentially increase an individual’s life span as well as that of offspring and primates may maintain these relationships through reciprocal exchanges (Silk, 2003; Silk et al., 2009; 2010). Thus an investment of social effort can potentially benefit the initiator as is indicated in the grooming for aid and food for grooming hypotheses (Seyfarth & Cheney, 1984; de Waal, 1997ab). Evidence is lacking, though, regarding how positive expectations or attitudes are initially established within a dyad.

In order to minimize the costs of social interactions, non-human primates have evolved various behavioral and communicative systems that ensure these exchanges are predictable. Affiliative intentions, for example, are often announced via stereotyped signals and are directed towards kin or already established relationships (Silk, 2002;

Watanabe & Smuts, 1999). Dominance hierarchies also function to help anticipate the potential costs of a social interaction, making them more predictable. After a dominance hierarchy is established individuals can anticipate the outcome of a dyadic interaction without the need for aggression during competition over resources (Drews, 1993).

Because it is typical for only one sex to leave the natal group in most non-human primate social systems, many relationships are established at a young age along kinship lines and dyads remain familiar with each other throughout their lives (Clutton-Brock, 1989; Fredrickson & Sackett, 1984). These types of social systems imply that relationships develop early in life, are maintained through symmetry-based reciprocity, are limited to a small number of social partners and are directed towards kin (Brosnan & de Waal, 2002).

Langergraber et al. (2007) argue, though, that many closely bonded chimpanzees are not related and de Waal (1984; 2007) cites instances of coalitionary support between unrelated dyads. Furthermore, Silk et al. (1981) suggest that although kinship is central to relationship formation in bonnet macaques, evidence of grooming between unrelated dyads indicates that it is not the only important factor driving interactions. This implies that in non-human primates, and chimpanzees especially, factors additional to kinship and familiarity can be critical determinants of who associates with whom. Although monkeys and apes most often interact with well-known kin in predictable ways, the benefits of less familiar associations and relationship development may outweigh the costs in some cases.

Affiliative primate relationships change over time and expand to encompass individuals with whom one was previously neutral or avoidant. In baboons, for example, the abundance of food helps to determine association patterns with relationship quality changing from year to year (Henzi et al., 2009). When a baboon female loses a close affiliate she expands her grooming network and strengthens social ties (Engh et al., 2006). Chimpanzee male bonds form and dissolve over one to several years, with kinship, rank and equitable grooming predicting the longest lasting associations (Mitani, 2009).

Although symmetry based reciprocity is most likely the primary mechanism for maintaining familiar kinship-based relationships, the ability to keep track of newly affiliative relationships may require additional cognitive skill and flexible social behaviors. This would occur because less familiar dyads have a smaller reservoir of built up emotional tolerance or ingrained symmetrical features to rely on when interacting (Brosnan & de Waal, 2002; Newton-Fisher, 1999). The same is true of interactions that are not driven by close social bonds. Although pairs may be familiar with each other, there may be a need to overcome social uncertainty or aversion (Bohnet, Greig, Herrmann, & Zeckhauser, 2008; Rilling et al., 2008).

3.1 The Present Study

In this study we examine relationship development and tactical associations in two newly formed groups of chimpanzees. Chimpanzees are territorial and xenophobic in the wild and encounters with individuals from neighboring groups may lead to severe injury or death (Mitani et al., 2010; Watts, 2006; Watts & Mitani, 2001; Wilson, Wallauer & Pusey, 2004). Since chimpanzees are patrilineal, emigrating females do join new groups. They are usually buffered from the most severe male aggression (but see

Watts & Mitani, 2001), but even so may receive injuries from females in their non-natal group (Kahlenberg, Thompson, Muller & Wrangham, 2008).

Captive chimpanzees, though, commonly encounter unfamiliar conspecifics when new social groups are formed due to management considerations and movement between sanctuaries or zoos. Captivity, therefore, provides us with the ability to document the step-by-step formation of a new social bonds and to examine how individuals initiate and respond to social interactions with new group members. It also allows us to observe how the formation of a dyadic dominance hierarchy translates into changes in social behaviors.

The newly formed groups in our study are a combination of familiar and unfamiliar dyads. This arrangement enables us to examine whether the benefits of maintaining pre-established relationships outweighs the costs of creating new ones. Although the former may be more predictable, an individual who develops new relationships could benefit through an increase in coalitionary support, a decrease in aggression, or an overall higher rank within the new group (de Waal, 2007). These introductions may be viewed as experiments, which allow for insight into how the costs and benefits of interacting socially influences non-human primate social behaviors.

In order to investigate this subject, we here ask three main questions. 1) How does the formation of a dominance hierarchy over time influence social behaviors in two newly formed groups of chimpanzees? 2) Do chimpanzees in a newly formed group direct most of their energy into maintaining previously familiar relationships or initiating unfamiliar ones? 3) How do characteristics such as rank or number of familiar group members influence how an individual responds to other familiar or unfamiliar individuals?

3.2 Subjects and Housing

In order to answer each question, we observed and recorded the social behaviors of chimpanzees during the formation of two new social groups at the Yerkes National Primate Research Center in Lawrenceville, Georgia. We began data collection in 2012 when the research center dissolved two existing groups living in large compounds at the Yerkes Field Station (FS) and created two new groups (FS1 and FS2) from existing members of groups at the FS and those at the Yerkes Main Center (MC). The two new groups included 31 total individuals with 15 chimpanzees in FS1 and 16 in FS2.

We were able to examine how unfamiliar dyads respond to each other in comparison to familiar ones because both new groups were comprised of smaller sub-groups of previously familiar pairs, which had recently lived together in the same group, as well as those of previously unfamiliar individuals. Therefore most subjects had a combination of familiar and unfamiliar relationship types in their new social group. For the purpose of this study we define previously familiar dyads as those living in the same group prior to relocation and unfamiliar group-mates as those that had lived separately for more than five years (Brent, Kessel, & Barrera, 1997).

Each familiar subgroup ranged in number from two to four animals. Several chimpanzees were also introduced into the new groups with no previously known group mates. Each new group was comprised of one subgroup in which four original group members stayed in their home compound and one subgroup in which four group members moved from one FS compound to the other. The rest of the members of FS1 and FS2 consisted of single individuals and subgroups brought from the MC. Table 3.1 details the composition of FS1 and FS2.

Table 3.1 The number of subgroups of familiar individuals in each compound.

Compound	4 Member Subgroups	3 Member Subgroups	Familiar Pairs	No Familiar
FS1	2	0	2	3
FS2	1	1	3	3

* For example FS1 was comprised of 2 subgroups in which 4 of the members lived in the same compound previous to introduction.

Table 3.2 indicates the composition of each newly formed group as well as lists with whom each group member was previously familiar.

Table 3.2 Background and new group location for each chimpanzee.

ID	Sex	Birthdate	Former Location	New Location	Familiar Group Mates
AR	M	5/21/91	Main Center	FS2	None
AZ	F	3/7/97	Main Center	FS1	LI
BB	F	6/14/76	FS2	FS1	CY/ST/WA
CP	M	3/30/89	FS2	FS2	DA/JL/VR
CR	F	6/1/95	Main Center	FS2	JW
CY	F	6/7/80	FS2	FS1	BB/ST/WA
DA	F	6/6/88	Main Center	FS1	None
DA	F	10/1/89	FS2	FS2	CP/JL/VR
DN	F	4/3/90	FS1	FS2	GG/MS
DW	M	3/6/93	Main Center	FS2	SY
FI	F	12/5/94	Main Center	FS1	RO
GG	F	8/27/80	FS1	FS2	DN/MS
JA	F	5/17/95	Main Center	FS2	None
JL	F	5/15/98	FS2	FS2	CP/DA/VR
JW	F	3/9/92	Main Center	FS2	CR
KT	F	10/5/89	FS1	FS1	RI/RN/TA
LI	F	3/19/94	Main Center	FS1	AZ
ML	F	6/27/81	Main Center	FS2	SU
MS	F	7/8/93	FS1	FS2	DN/GG
PE	M	8/3/2001	Main Center	FS2	None
RI	F	9/23/87	FS1	FS1	KT/RN/TA
RN	F	12/17/87	FS1	FS1	KT/RI/TA
RO	F	8/13/88	Main Center	FS1	FI
ST	M	9/8/93	FS2	FS1	BB/CY/WA
SU	F	2/17/85	Main Center	FS2	ML
SY	F	7/19/93	Main Center	FS2	DW
TA	F	9/5/95	FS1	FS1	KT/RI/RN
TR	M	8/2/89	Main Center	FS1	None
VR	F	4/18/91	FS2	FS2	CP/DA/JL
WA	F	3/19/82	FS2	FS1	BB/CY/ST
WI	M	1/12/87	FS3	FS1	None

3.3 Question 1: Is there a correlation between the formation of a dominance hierarchy over time and social behaviors in two newly formed groups of chimpanzees?

The formation of a stable dominance hierarchy is theorized to function as a means by which individuals can bypass the continuous need to reinforce relationships in order to determine who has preferential access to resources. This occurs due to an increase in the predictability of the outcome of social interactions as a social hierarchy forms (Rowell, 1974). Flack et al. (2005) experimentally substantiated this when they removed the three dominant males from a stable pigtail macaque social group. They discovered that the group hierarchy destabilized due to a decrease in policing behavior, which resulted in an increase in aggression and a decrease in affiliation. Their work suggests that without the policing of high-ranking group-members, social interactions become more high risk. Policing functions to create predictability in social interactions.

Similarly, after observing the formation of one large chimpanzee social group from two smaller groups over the course of 16 months, Schel et al. (2013) measured decreased aggression over time as the two groups became established. This implies that the need for aggression was reduced after dyads gained knowledge about their relationships and became better able to predict the outcome of an interaction. Both Seres et al. (2001) and Baker (1992) though, found continued aggression in their newly formed chimpanzee groups up to six months post group formation, calling into question the relationship between stability in a newly formed group and duration of time that has passed since group formation.

We predicted that, if the formation of a dominance hierarchy has the theorized effect of increasing the predictability of social interactions, we should see a significant decrease in aggression over time. Our expectations for grooming were less clear as grooming functions in several ways, from signaling affiliation (Sugiyama, 1988; de Waal, 1986) to relieving social tension through reconciliation (de Waal & Roosmalen, 1979). When measuring social interactions in a newly formed chimpanzee group, Baker (1992) found that when aggression decreased within a dyad, grooming also decreased. Seres et al. (2001) also observed a slight decrease in grooming in a newly formed chimpanzee group. This occurred, though, over an expanded time period of four years, and the authors did not report data from a smaller time frame. We expected that if grooming functions primarily as a means to develop and maintain social bonds, we would observe an increase over the shorter time period. If, however, grooming primarily functions as a tool to relive social tension, we expected a decrease over time. Comparing the pattern of change across both grooming and aggression helps to determine how each may function in the new group.

3.3.1 Methods

To investigate how the formation of a dominance hierarchy correlates with aggression and affiliation in each new group, we first measured change in the hierarchy over time. We achieved this by recording dyadic pant-grunts in order to determine who was signaling subordinance to whom. We chose this behavior because in chimpanzees, pant-grunts are considered the formal dominance signal and, in most cases, represent a 100% unidirectional sign of submission (Noë, de Waal, & Van Hooff, 1980). In order to obtain the number of pant-grunts between dyads, three researchers (SC, JW and MS) recorded every pant-grunt bout heard, both during systematic observations and *ad libitum*, from the first day that the complete group was housed together.

Along with measuring change in the dominance hierarchy, the same three researchers also collected behavioral data. From the first day of full group formation for both FS1 and FS2, we began to conduct 90-minute group wide observations five days per week. These observations continued for approximately 18 weeks, after which we reduced the number to two observations per group per week, stopping for each group after the group had been together for approximately one year.

The ethogram that we used for behavioral coding was based on de Waal and Van Hooff (de Waal & van Hooff, 1981) and has been in use at the Field Station in its current form since the 1980s (de Waal, 1989). Each 90-minute observation included 10 scan samples recorded every 10-minutes. We measured proximity for each sample, as defined by dyads that were within an arms reach of each other. During the observations we also counted every social behavior using *all occurrences* sampling, as well as who participated. These measures included coalitionary support and aggression, which we separated into non-contact and contact.

Because all chimpanzees were allowed indoor and outdoor access during observation times, each individual was visible for a different number of scans. Both groups also occasionally had different observation times for each week. When we examined individual behaviors, we adjusted for these variations by dividing each individual’s behavioral frequencies by the percentage of time that they were visible as well as the number of observation hours (grooming, aggression) or number of scans (proximity measures). When we analyzed dyadic data we used the same calculations but divided by the percentage of time that both subjects were visible during observations. We referred to the data from these observations to answer each of the three research questions.

3.3.2 Analyses

We recorded the number and sequence of pant-grunts to calculate an Elo-rating, a method originally used in chess tournaments (Hvattum & Arntzen, 2010) that Neumann et al. (2011) originally used to determine primate hierarchies. According to Neuman et al. (2011), the outcome of Elo calculations are on an interval scale and further analysis is possible using parametric statistics. This enabled us to calculate a stability index (S) using the ratio:

$$S = \frac{\textbf{Rank changes per \# individuals present}}{\textbf{Time period}}$$

For this calculation, our denominator was 14 days, as this was the smallest measure of time that would provide us with a reliable amount of pant-grunt data between various dyads. We defined rank change as a pant-grunt that went against the expected direction. For the first interaction between each dyad there was no expected direction.

According to the stability index, a lower S score indicates a more stable group and a score of .5 represents complete instability, as this suggests that the hierarchy is reversing every other day (Neuman et al., 2011). Because S had never been calculated on newly formed chimpanzee groups, our measure was somewhat arbitrary. Therefore in order to examine stability across groups over time, and because our data were not normally distributed, we calculated a two-tailed Spearman's rank-order correlation between S and number of weeks since the group had been formed.

In order to examine changes in social behaviors in each new group over time we compiled all grooming, proximity and aggression by week separately for each group and corrected for the amount of time each subject was visible as well as total hours of observation per week. We then ran a two-tailed Spearman's rank-order correlation between social behaviors and time both up to 18 weeks and from 19 weeks to one year (41 weeks total for FS1 and 29 weeks total for FS2). There were several weeks when no observations were taken due to weather, holidays or the separation of multiple group members. This occurred, for example, when the alpha male of FS2 was injured and the group was temporarily divided up until he could be relocated. We did not count these weeks in the data analysis, therefore each group's total weeks of observations were different and less than 52. Examining behaviors over both short and long time periods allowed us to investigate how the initial impact of relocation to a new social group influenced social interactions and then to look for changes in these patterns as the hierarchy became increasingly stable.

When data points were not independent, such as dyadic points, we evaluated probabilities using a bootstrap with 5,000 repetitions (Ho, 2006). When necessary, we corrected for multiple analyses by comparing significant p-values to their Benjamini-Hochberg critical value, or false-discovery rate (FDR), where the calculated p-value must be less than the Benjamini-Hochberg critical value ((rank of p value/number of tests)* .05) in order to be considered significant (Benjamini & Hochberg, 1995). Any time data was not normally distributed we used non-parametric statistics. For all analyses we used either SPSS Version 23 or the R open-access software environment.

3.3.3 Results

The initial stability index for FS1 was 0.129 and the initial stability index for FS2 was 0.112. A two-tailed Spearman's rank-order correlation showed a significant negative correlation between the stability index and time, at 18 weeks, in both FS1 (r_s= - 0.659, N= 20, p= 0.002) and FS2 (r_s= - 0.838, N= 14, p< 0.001) indicating an increase in stability for both groups (Figure 3.1). Table 3.3 outlines the number of members in each group as well as how many hours of observation we collected.

Table 3.3 The composition of each group and number of observation hours collected

Group	**Group Members**	**Male**	**Female**	**Total Observation Hours**	**Average hours per week (overall)**	**Total Observation Hours (first 18 weeks)**	**Average hours per week (first 18 weeks)**
FS1	15	3	12	202.5	4.71	121.5	6.75
FS2	16	4	12	148.5	4.80	124.5	7.78

When investigating behaviors by weeklong period over the course of the 18 weeks that we took daily observations for both groups, we found a negative correlation between grooming and time at FS2 (r_s= - 0.629, N=16, p= 0.009). The correlation between grooming and time at FS1 was significantly negative according to the calculated p-value but not according to the permutation procedure (r_s= - 0.523, N=18, p= 0.026) so we considered this to imply no relationship. We also found no relationship between proximity and time for either group (FS1, r_s= 0.230, N=18, p= 0.358; FS2, r_s= - 0.439, N=16, p= 0.069). There was no correlation at either FS1 or FS2 between the rate of either non-contact or contact aggression and time during the first 18 weeks (FS1 non-contact aggression, r_s= 0.030, N=18, p= 0.906; contact aggression, r_s= 0.138, N=18, p= 0.584) (FS2 non-contact aggression, r_s= 0.038, N=16, p= 0.888; contact aggression, r_s= 0.312, N=16, p= 0.240).

When analyzing our data from 18 weeks to the full year at FS1 and FS2 we did not find a correlation between time and grooming (FS1, r_s= 0.441, N=23, p= 0.035; FS2, r_s= 0.088, N=13, p= 0.775), proximity (FS1, r_s= 0.153, N=23, p= 0.485; FS2, r_s= 0.445, N=10, p= 0.170), non-contact aggression (FS1, r_s= -0.069, N=23, p= 0.753; FS2, r_s= 0.346, N=13, p= 0.246) or contact aggression (FS1, r_s= - 0.134, N=23, p= 0.542; FS2, r_s= -0.034, N=13, p=0.912). Although the calculated p-value for grooming at FS1 was significant, it was not according to the permutation procedure. Even when we combined non-contact and contact aggression at FS1 and FS2 for 18 weeks as well as the rest of the year, we did not find a correlation with time (FS1, r_s= 0.104, N=18, p= 0.681; r_s= -0.145, N=23 p= 0.510; FS2, r_s= 0.218, N=16, p= 0.418; r_s= -0.006, N=13, p= 0.985).

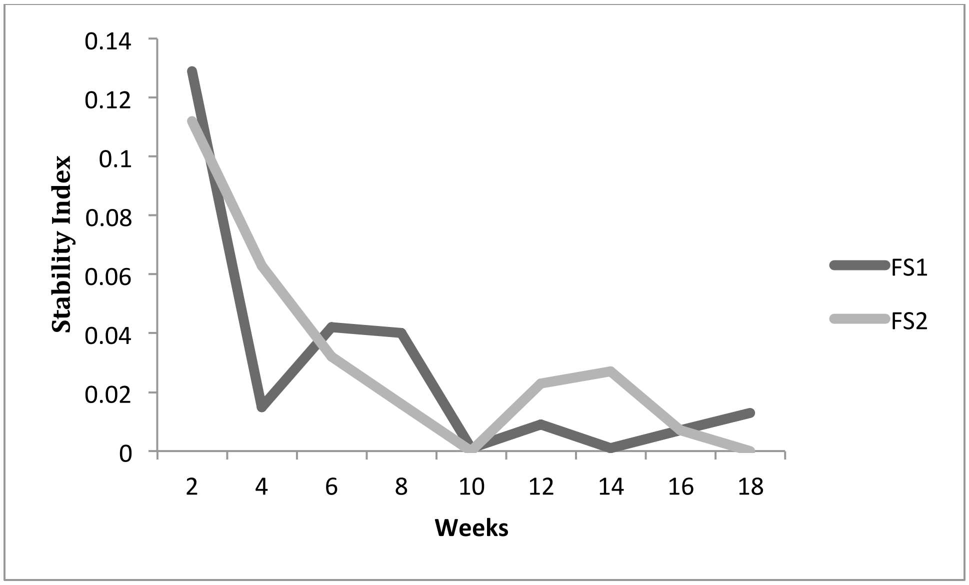


Figure 3.1 The stability index based on pant-grunts for FS1 and FS2 over the first 18 weeks of observation.

3.4 Question 2: Do chimpanzees in a newly formed group direct more affiliation, aggression and support towards familiar or unfamiliar group members?

Both newly formed groups in our study were composed of dyads that lived together previous to relocation and dyads that did not. Therefore our subjects could initiate social interactions with, as well as provide coalitionary support to, familiar individuals, unfamiliar individuals or both relationship types. Schel et al. (2013) found that when two groups of 11 chimpanzees were combined to form one large social group, almost all subjects interacted primarily with familiar group members but that social interactions between unfamiliar dyads increased over time. They also observed a decrease in aggression between unfamiliar group members whereas aggression between familiar group members remained constant.

The new groups in the Schel et al. (2013) study, though, differ from ours in that each chimpanzee had ten previously familiar group mates whereas our number was much smaller and varied between individuals. This allowed us to investigate how the number of familiar group-members may influence social behaviors. In addition, Dufour and colleagues (2011) observed the relocation of capuchin and squirrel monkeys to a new enclosure and concluded that the relationships between group members increased in affiliation. This indicates that the stress of moving may cause individuals to strengthen relationships.

Based on these findings, we predicted that a majority of affiliative social interactions in our new groups would take place between familiar dyads. We expected that most aggression would be directed towards unfamiliar group members, but this would decrease over time. Since Baker (1992) found that when there was an aggressive interaction between a familiar and unfamiliar group-member, subjects in almost 100% of cases chose to support the familiar partner, we hypothesized that coalitionary support would be biased towards familiar individuals. This is similar to that which is measured in established groups along the lines of affiliative relationships (de Waal, 2007).

Focusing on familiar partners, though, may come at the expense of increasing standing within the group as a whole. Although riskier, in some cases interacting with previously unfamiliar partners may provide greater benefits than maintaining old relationships. For a chimpanzee, a greater number of affiliative partners could mean reduced aggression, more coalitionary support and higher standing within the group. Because of this, we expected our observations to mirror those of Schel and colleagues (2013) and to see an increase in affiliative interactions between unfamiliar dyads over time.

3.4.1 Analyses

In order to analyze our observational data we recorded, for all possible dyads, the number of directional grooming bouts, number of times dyads were sitting within close proximity to each other, aggressive interactions and instances of coalitionary support. We then adjusted this data for the amount of time that both members of each dyad were visible during observations and the number of hours of observations for each time period. In order to correct for the unequal number of familiar and unfamiliar group-members for each individual, we averaged each subject's data across all unfamiliar and familiar partners.

In order to compile enough behaviors to compare relationships across time we divided each year into 4 time periods (P1, P2, P3, P4). P1, P2 and P3 consisted of six weeks each and consisted of daily observations, whereas P4 comprised the remainder of the year from 19 weeks on and consisted of bi-weekly observations (see Methods). We then compared the mean rate per hour of grooming and mean number of proximity scans for all dyads using a Wilcoxon signed-rank test to determine differences between relationship types. We then used a Friedman test to determine differences across time periods within relationship type. We accounted for multiple analyses on the same data by using a Benjamini-Hochberg correction.

In order to examine the direction of agonistic interventions between familiar and unfamiliar opponents we calculated a support index as per de Waal and Luttrell (1988), defining ‘pro’ as an intervention in favor of the familiar contestant against the unfamiliar one, and ‘contra’ as the opposite:

Support index = (pro-contra)/(pro+contra)

This index, calculated for each individual, ranges from -1 to 1 with -1 indicating complete support for unfamiliar contestants and a score of 1 indicating complete support for familiar contestants. A score of zero indicates equal support given to both familiar and unfamiliar contestants when they confront each other. We only examined instances of support where a chimpanzee intervened in an ongoing interaction between one familiar individual and one unfamiliar individual. In this instance the chimpanzee providing the support had to choose to intervene for or against a familiar group mate. Once a support index was calculated for each individual we ran a sign test across all possible subjects to determine whether there was a significant difference in support pro or contra familiar group-members. We then calculated the pooled percentage of pro support and examined this for each group over time.

In addition, we examined whether directional grooming was reciprocal between familiar and unfamiliar partners. To do this we examined *all occurrence* directional-grooming behaviors from the observations calculating the mean rate of grooming per hour for each member of every dyad. We then transposed the data and used a two-tailed Pearson product-moment correlation to assess whether each individual's score correlated with how much their partners groomed them. We examined this for both familiar and unfamiliar relationship types and ran a bootstrap analysis with 5,000 repetitions in order to account for the fact that dyadic data points are not independent (Ho, 2006; Peugh, DiLillo & Panuzio, 2013).

In order to visually inspect the relationships between individuals and the trends over time we plotted a social network of directional rates per hour of grooming for each dyad. We used a program in the R environment called igraph to map each individual, their number of social ties and the strength of those ties over time. We measured group cohesion via the degree of the network (Barrat & Randall, 2004) using the formula 2E/N where E is the number of grooming dyads and N is the number of chimps in each group.

3.4.2 Results

Across both new groups there were a total of 38 dyads of previously familiar individuals (9.50%) and 398 dyads of previously unfamiliar individuals. There were 14 familiar dyads (7.60%) in FS1 and 24 familiar dyads (11.00%) in FS2. In FS1 there were 182 unfamiliar dyads and in FS2 there were 216 unfamiliar dyads.

3.4.2.1 Social behaviors

When examining the mean hourly rate of grooming of familiar dyads (M= 0.293; SD= .368) versus unfamiliar dyads (M= 0.145; SD= .092) using a Wilcoxon signed-rank test over the entire year there was no significant difference between the two relationship types (Z= -1.47, p= 0.143). We did, though, find a significant difference between the mean percent of time in proximity for familiar (M= 0.424; SD= .264) and unfamiliar (M= 0.245; SD= .086) dyads (Z= -3.46, p<.001), with significantly more familiar individuals sitting in proximity to each other than unfamiliar individuals. A Wilcoxon signed-rank test also revealed significantly more aggression, as measured by mean hourly rate, between unfamiliar dyads (M= 0.159; SD= .334) than familiar dyads (M= 0.019; SD= .038) (Z= -3.65, p< .001). See figure 3.2.

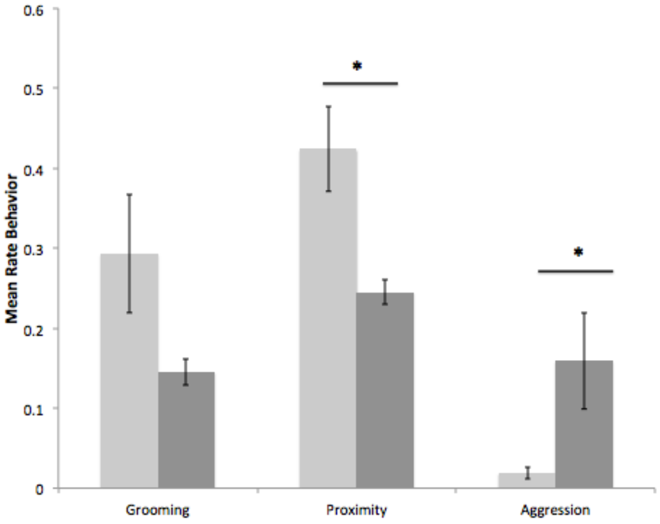


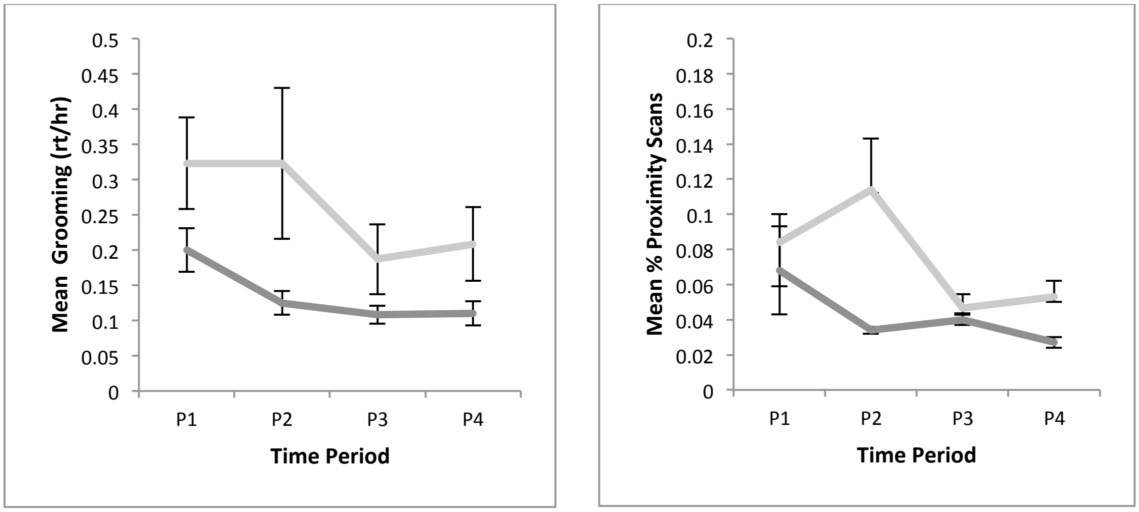
Figure 3.2 The mean rate per hour of grooming and aggression and mean percent proximity scans per hour for familiar (light gray) and unfamiliar dyads (dark gray).

In no period did we find differences in the mean hourly rate of grooming of familiar dyads versus unfamiliar dyads (P1, *Z*= -1.34, *p*= 0.174; P2, *Z*= - 0.955, *p*= 0.339; P3, *Z*= - 0.309, *p*= 0.757; P4, *Z*= -1.247, *p*= 0.212). We did, however find a significant bias towards familiar dyads sitting in proximity to each other in P2 (*Z*= -3.32, *p*= 0.001). Although the p-values were also significant for familiar dyads sitting in proximity to each other in P1 and P4, due to our adjustments for multiple analyses we could not consider them so (P1, *Z*=-2.22, *p*= 0.026; *p*= 0.026 > fdr= 0.017; P4, *Z*= -2.04, *p*= 0.042; *p*= 0.042 > fdr= 0.017). There was no significant difference for P3 in whether familiar dyads sat in proximity to each other more than unfamiliar dyads (P3, *Z*= -0.256, *p*= 0.798).

There was an overall effect of grooming between familiar dyads and time period (x^2 (3) = 14.20, *p*= 0.003). Pairwise analyses revealed that familiar pairs groomed more in P1 than they did in P3 (*Z*= 1.22, *p*< 0.005) but that there was no difference in grooming between P1 and P2 (*Z*= 0.420, *p*= 1.00), P1 and P4 (*Z*= 0.840, *p*= 0.129), P2 and P3 (*Z*=

0.800, *p*= 0.171), P2 and P4 (*Z*= 0.420, *p*= 1.00) or P3 and P4 (*Z*= -0.380, *p*= 1.00). There was also an overall effect of grooming between unfamiliar dyads and time period (x^2 (3) = 19.50, $p < 0.001$). Pairwise analyses revealed that unfamiliar pairs groomed more in P1 than they did in P3, (*Z*= 1.17, $p < 0.003$) or P4 (*Z*= 1.23, $p < 0.001$) but that there were no differences between P1 and P2 (*Z*= 0.400, *p*=1.00), P2 and P3 (*Z*= 0.767, *p*= 0.129), P2 and P4 (*Z*= 0.833, *p*= 0.075) or P3 and P4 (*Z*= 0.067, *p*=1.00).

There was no difference over time period in the mean percent of proximity scans for familiar individuals (x^2 (3) = 7.32, *p*= 0.062). We did, though, find a difference over time period in the mean percent of time in proximity for unfamiliar individuals (x^2 (3)= 17.052, $p < 0.001$). Pairwise analyses revealed that unfamiliar individuals spent more time in proximity in P1 than P4 (*Z*= .903, *p*= 0.035) and P3 than P4 (*Z*= 1.32, $p < 0.001$). There was no difference in mean percent of time spent in proximity between P1 and P2 (*Z*= -0.419, *p*=1.00), P1 and P3 (*Z*= 0.226, *p*=1.00), P2 and P3 (*Z*= -0.645, *p*= 0.295) or P2 and P4 (*Z*= 0.677, *p*= 0.233). Figures 3.3 and 3.4 show the relationship between familiar and unfamiliar dyads in each time period for grooming and proximity.



Figures 3.3 and 3.4: The mean hourly rate per dyad of grooming (left) and mean percent proximity scans (right) for time periods 1-4. The gray lines represent familiar dyads and the black lines represent unfamiliar dyads. Both graphs include standard error bars. Note that the scales are different for the two graphs.

There was significantly more overall aggression between unfamiliar dyads than familiar dyads in P1, P3 and P4 (P1, Z= -2.66, p= 0.008; P3, Z= -2.95, p= 0.003; P4, Z= -3.41, p= 0.001). The calculated p-value in P2 was significant for more aggression between unfamiliar dyads than between familiar dyads but due to multiple analyses it was not significant (Z= -2.09, p= 0.036, p= 0.036> fdr = 0.017). We found no differences within relationship category over time (Familiar x^2 (3)= 4.71, p= 0.194; Unfamiliar, x^2(3)= 7.04, p= 0.071). Figure 3.5 shows the relationship over time for aggression between familiar and unfamiliar dyads.

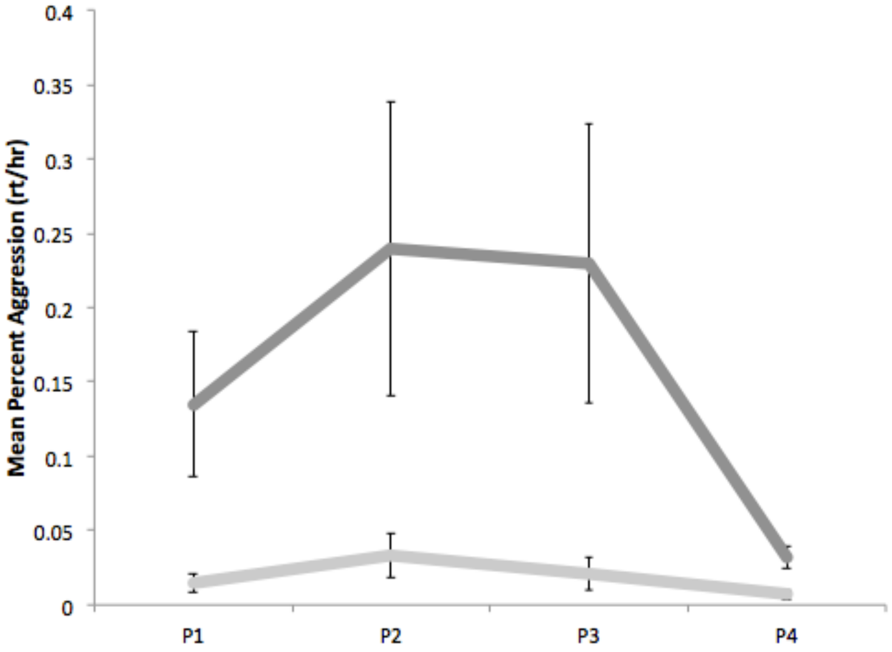


Figure 3.5 Mean percent rates of aggression for familiar (light gray) and unfamiliar (dark gray) dyads.

3.4.2.2 Support

In order to analyze agonistic interventions, we only counted instances where an individual intervened in an encounter between an individual that was familiar to them and an individual that was unfamiliar (N=77). Overall 71% of support instances were directed towards familiar individuals with 62% of support instances directed towards familiar individuals during P1 and 80% during P4. See figure 3.6. When we calculated a support index for each individual across all time periods and used a sign test to examine for an overall significant difference between pro support and contra support we found a non-significant trend towards pro support ($p = 0.057$).

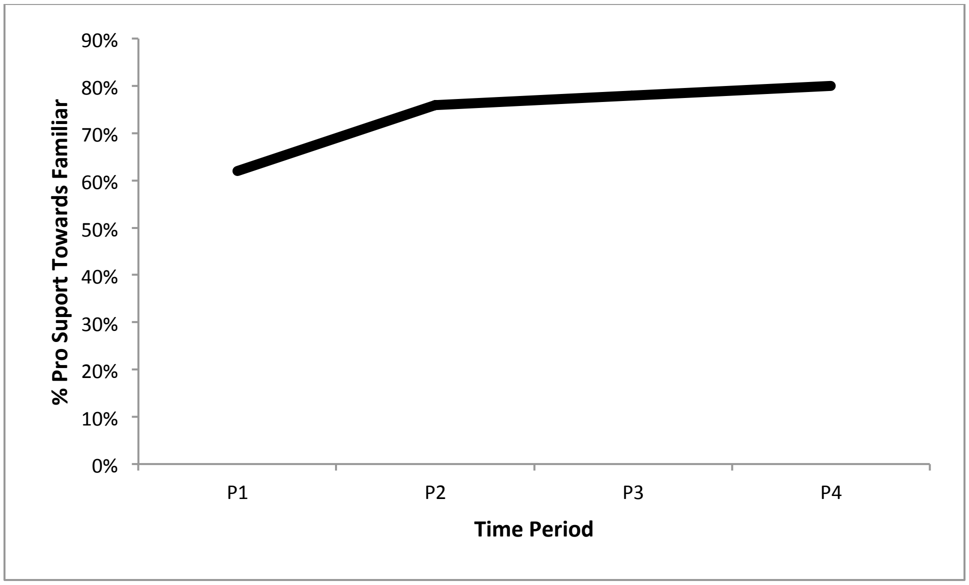


Figure 3.6 The percent of pro support towards familiar individuals for each time period.

3.4.2.3 Top Grooming Partners

In order to further explore the relationship between familiar and unfamiliar individuals we calculated the relationship type of each subject's top three grooming partners in the first time period. We calculated the top three grooming partners only for individuals in the group that had familiar group mates. To do this we measured the relationship types of the partners to which each individual directed their top grooming rates per hour. Out of 78 potential grooming partners, 54 (69.23%) were directed towards unfamiliar individuals and 24 (30.77%) were directed towards familiar individuals. According to a binomial test significantly more of an individual's top three grooming partners were unfamiliar ($p<.001$). See figure 3.7. We also found that 47.50% of the top unfamiliar grooming partners were male group members. When calculating the relationship type of each individual's top three grooming partners by available dyad in the group, as outlined in Table 3.4, 57.89% of possible familiar female dyads were in each other's top three grooming positions. This meant that when available dyads were taken into consideration, the percentage of top three grooming spaces was biased towards familiar individuals.

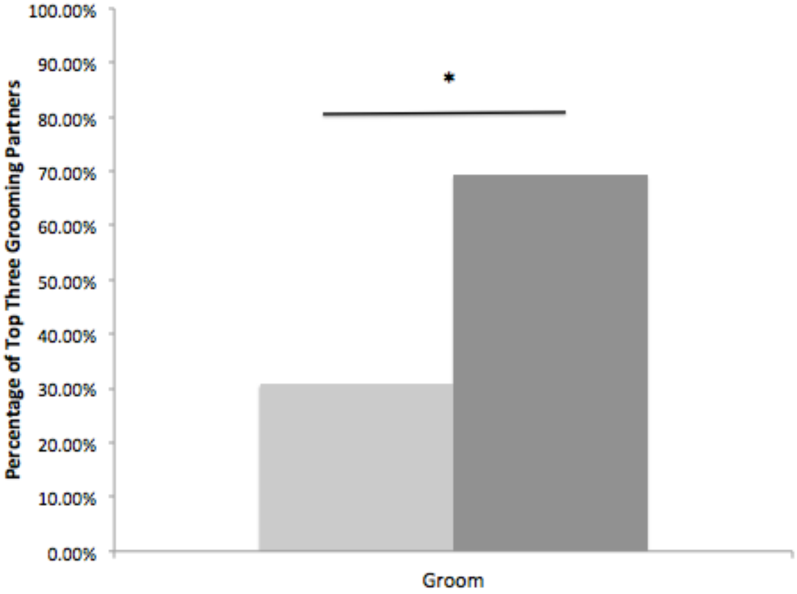


Figure 3.7. The relationship type of the top three grooming partners for each individual. Percentage is out of 78 possible partners. Familiar is light gray and unfamiliar is dark gray.

Table 3.4 The percentage of top three grooming partners by number of available dyads in the group.

	Familiar Males	Unfamiliar Males	Familiar Females	Unfamiliar Females	Familiar Mixed	Unfamiliar Mixed
# of Dyads in Group	0	8	38	207	14	96
# of Top 3 Grooming Partners	_ _ _	3	22	26	2	25
% of Top 3 Grooming Partners by Dyad	_ _ _	37.50%	57.89%	12.56%	14.29%	26.04%

3.4.2.4 Reciprocity

Grooming within unfamiliar dyads was reciprocal during all time periods (P1, $r(400)= 0.504$, $p< 0.001$; P2, $r(400)= 0.425$, $p< 0.001$; P3, $r(400)= 0.384$, $p< 0.001$; P4, $r(364)= 0.417$, $p< 0.001$) as was grooming within familiar dyads (P1, $r(47)= 0.427$, $p< 0.002$; P2, $r(47)= 0.560$, $p< 0.001$; P3, $r(47)= 0.613$, $p< 0.001$; P4, $r(40)= 0.406$, $p< 0.004$). We found no clear-cut increases or decreases in reciprocity as evidenced by figure 3.8.

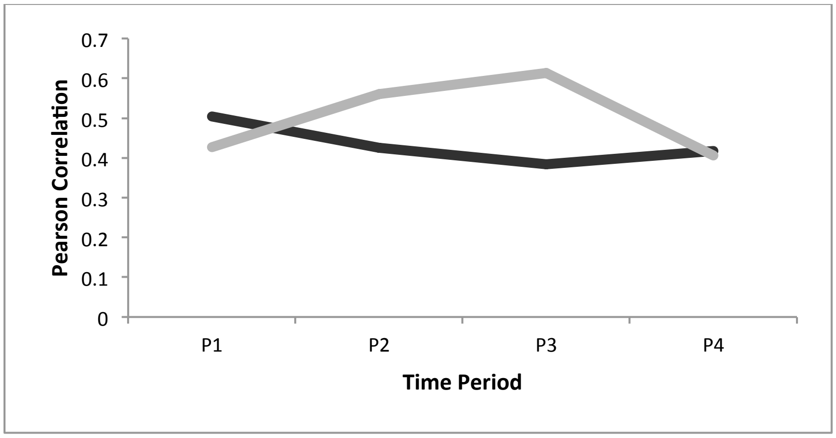


Figure 3.8. The Pearson correlation coefficients for reciprocity plotted against time period for familiar (grey) and unfamiliar (black) dyads.

3.4.2.5 Social Network Graphs

The social network, Figures 3.9 and 3.10, make obvious the qualitative differences between the two groups in group cohesion as well as relationship strengths over time. The strength of relationships in FS1 decrease over time while they increase over time in FS2. In FS1, though, the degree of the network increases over time (P1

11.06; P2 12.93; P3 12.8; P4 16.77), with the highest possible degree, or most cohesive measure of the group, being 28. In contrast, the degree of the network decreases in FS2 (P1 16.38; P2 13.75; P3 7.25; P4 9.2) with the highest possible degree being 30.

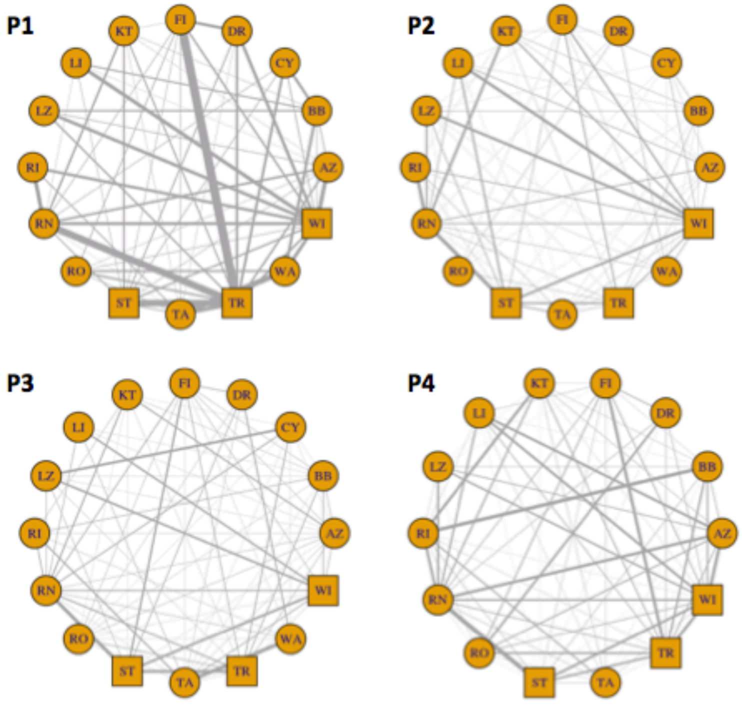
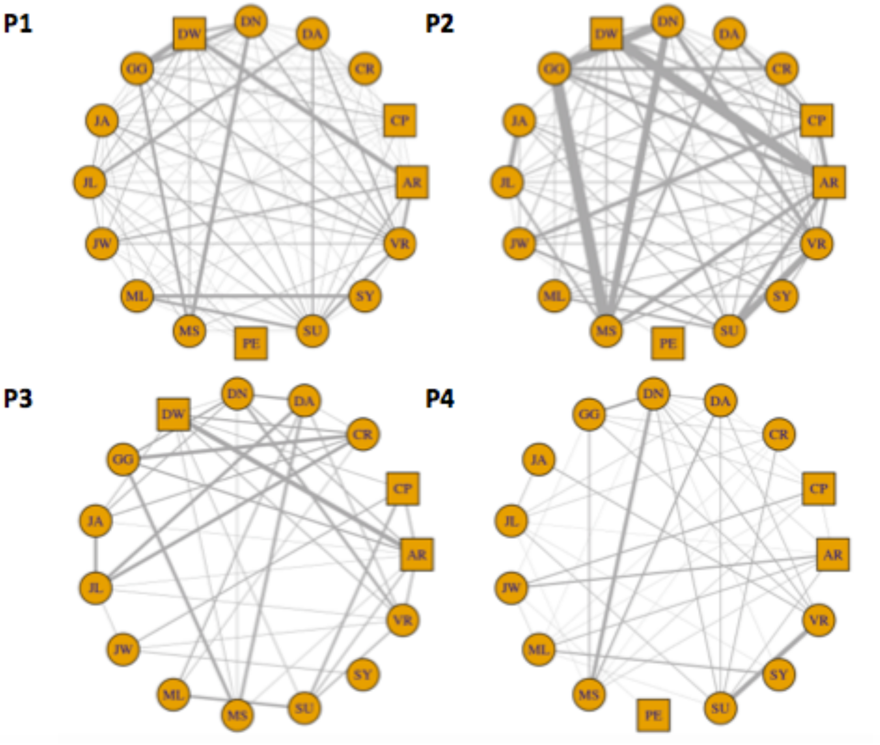


Figure 3.9. A social network figure of FS1 for Periods 1-4. Squares represent males and circles represent females. Thicker lines represent a greater frequency of grooming.



3.10. A social network figure of FS2 for Periods 1-4. Squares represent males and circles represent females. Thicker lines represent a greater frequency of grooming.

3.5 Question 3: How do individual characteristics, such as rank or number of familiar group members, influence how an individual responds to other familiar or unfamiliar individuals?

To further investigate where chimpanzees in a newly formed group invest their social effort, we looked for an interaction between relationship type and either rank or size of familiar subgroup. The relationship between these factors and relationship type can elucidate how individuals balance the costs and benefits of social interactions. Those with a larger familiar subgroup, for example, may gain enough benefits from their already familiar partners that there is no motivation to strengthen relationships with unfamiliar group members. This would suggest that the benefits from maintaining multiple familiar relationships might outweigh the potential costs of investing in new partners.

A similar social strategy may be why Schel and colleagues (2013) found that even after several years, two subgroups of chimpanzees in a newly formed group remained essentially separate with little social interaction between them. Given that each subgroup consisted of 11 familiar group mates, an individual could possibly obtain all social benefits from members of the familiar group with little reason to spend energy on unfamiliar group members. Rank may also play a role in what relationship type individuals associate with, as higher-ranking group mates may spread out their social efforts as a political strategy in order to maintain a high rank.

3.5.1 Analyses

In order to determine whether or not there was a relationship between the rank that they would ascertain after 18 weeks and association with familiar or unfamiliar group members, we ran two-tailed Spearman's rank-order correlations.

3.5.2 Results

There was no correlation between an individual's rank and whether they groomed familiar group members ($r_s = 0.107$, N=25, $p= 0.611$) or unfamiliar group members ($r_s= -0.346$, N=25, $p= 0.091$). There was no correlation between the number of familiar individuals a chimpanzee had in the group and how high their rank ($r_s= 0.038$, N=31, $p= 0.841$).

3.6 Discussion

As predicted, each group stabilized over time as the hierarchy was established. This conclusion is limited, though, because it is difficult to ascertain whether an initially high stability index is due to instability in the group or whether it is due to the fact that the formula that we used takes several data points before it produces an accurate measure of stability. For example, our formula may not identify a strongly dominant member of a dyad until several interactions have been recorded even though the hierarchy may have, in reality, been established previous to our observations.

Another factor that could have influenced group stability was the relocation, due to aggression, of the alpha male in FS2 16-weeks after group formation, as well as the natural death of two females in FS1 during P4. An advantage of the Elo-rating, though, is that it is not disrupted by the gain or loss of individuals in a group and in-fact, can help to show how these factors influence group stability. Nevertheless, it is possible that the loss of individuals in the group may have influenced group stability and behavior without being reflected in the stability-index measure.

Even though we measured an increase in stability over time we did not find that this translated into the predicted increase in affiliation or decrease in aggression. In fact, over the course of the first 18 weeks we observed a decrease in grooming in one group. This pattern may suggest that the initial rates of grooming were particularly high in this group in order to relieve the social tension and stress that was produced from relocation and early group formation. Dufour et al. (2011) and Gust et al. (1991) observed similar behaviors in capuchins, squirrel monkeys and rhesus monkeys after relocation as they saw that affiliation increased from the old location to the new one (Dufour, Sueur, Whiten, Buchanan-Smith, 2011; Gust et al., 1991).

The fact that aggression did not decrease, as predicted, during the first 18 weeks of group stabilization may indicate that the chimpanzees did not rely on aggression in order to establish dominance. If they had relied on contest competition in order to establish the hierarchy, we should have observed a pattern of decreasing aggression in line with increasing stability. It is possible that they instead relied on submissive signals and more subtle behaviors, such as displacements. This may be a necessary strategy in a situation, in which individuals may have been uncertain about a group-mates resource holding potential and who would have the advantage in an aggressive encounter (Arnott & Elwood, 2008). It is also possible though that the unchanged patterns of aggression signal continued instability in the group throughout the first 18-weeks.

Over the course of a full year we, again, did not observe the expected increase in mean hourly rates of grooming at FS1 or FS2. Our observed rates of aggression also, again, went against our predictions. Instead of finding a decrease in aggression over time, there was no change in either non-contact or contact aggression. When Seres et al. (2001) observed the formation of two new social groups they discovered that mild aggression increased over time but severe aggression decreased. The authors interpreted this pattern according to the relational model of conflict resolution whereby an increase in the ability to reconcile makes minor acts of aggression less risky and diffuses tension prior to the manifestation of severe aggression. Seres et al. (2001) observed a sharp decrease in severe aggression from year one to year two, which remained low through year four. Since we only recorded data from our social groups for one year, with intense data collection only encompassing about 4.5 months it is possible that we did not observe our groups frequently enough or for enough time to see a similar change in aggression. Schel and colleagues (2013), though, did see a decrease in aggression over the course of 16 months indicating that this pattern can be found within timeframes shorter than several years.

Even though our statistics did not reveal interpretable group wide patterns in terms of grooming over time, visualization through graphing the grooming networks showed that FS1 and FS2 had opposite strategies in terms of relationship strengths and number of ties across the four time periods. In FS1 the cohesion of the group increased over time, but the strength of the ties decreased, while in FS2 group cohesion decreased over time while the strength of the ties initially increased and then decreased. These patterns could indicate the need to balance number of partners with relationship strength and that increasing investment with a few individuals comes at the cost of the number of possible relationships. It is important to note that this cost is not due to the available time for grooming, as that limit is reached around 40 individuals (Lehmann, Korstijens & Dunbar, 2007) and anecdotally, the chimpanzees only groomed during a small proportion of the time that we observed them. Instead we most likely see this pattern due to other factors influencing relationships within the group and further investigation is warranted either within our existing data set or on other groups in order to elucidate what these factors might be.

When investigating relationship formation between unfamiliar dyads and relationship maintenance between familiar dyads in a newly formed group of chimpanzees we found that, overall, familiar dyads spent more time in proximity with each other but not more time grooming. When examined over time there were no significant differences for either measure or within relationship type. This may indicate that individuals did not focus exclusively on trusted relationships in order to buffer against the threat that unfamiliar individuals might produce, and suggests that chimpanzees either disregard relationship when choosing with whom to affiliate or that they strategically affiliate with unfamiliar group mates while maintaining familiar relationships. Our data suggests that it is the latter as evidenced by the prominent number of unfamiliar grooming partners in many of our subjects top three grooming spots.

Our findings could also indicate that social tension was still high during our entire observation period, causing grooming and proximity to remain higher than predicted between unfamiliar dyads. It is possible that the chimpanzees didn't settle into the predicted behavioral patterns until after data collection stopped. In the future we could examine this by analyzing data collected after one year.

The fact that individuals directed significantly more grooming towards unfamiliar group mates in their top three grooming spots than familiar ones is quite meaningful. Although the number of unfamiliar top grooming partners was not greater than chance, there is ample evidence to suggest that in general chimpanzees do not associate with each other randomly (de Waal, 1989; Mitani, 2009). This indicates that our group members were investing in new relationships while maintaining old ones. In this way they may have been mitigating the costs of unpredictable social interactions by keeping the benefits of having strong social bonds with familiar individuals.

It is unclear, though, as to what individual characteristics motivate an unfamiliar individual to seek out another. Given how many unfamiliar males were top grooming partners in relation to the overall number of males versus females, it may be that individuals associate preferentially with males due to their size and status. Another option is that males more often reciprocate grooming or support, making them a better social investment. Often, in the wild, immigrant females seek out males in their new groups, gaining protection from aggressive females as well as mating opportunities (Kahlenberg, Thompson, Muller & Wrangham, 2008). This also may be a form of grooming up the hierarchy in order to keep an individual close who may potentially provide support as is observed in monkey species (Schino, 2001; Ventura, et al., 2006).

We did find that there was, in general, significantly more grooming and proximity within both familiar and unfamiliar dyads in early time periods than in later ones. This could, again, indicate initially high affiliation rates due to social instability that decreases as relationships become increasingly predictable. It would be interesting to follow these measures for a longer period of time to see if eventually the patterns between unfamiliar dyads begin to differ from the patterns between familiar dyads.

Since grooming and proximity are considered low cost social interactions (Brosnan & de Waal, 2002), we also examined higher cost behaviors such as aggression and support. These types of interaction are higher cost due to the greater potential for injury and higher social cost of unreciprocated coalitionary support. Because of this we predicted that we would see differences in aggression and support between familiar and unfamiliar individuals. We did find the predicted difference in aggression as there was significantly more aggression between unfamiliar dyads that between familiar ones. This did not change over time.

Because aggression has the potential for higher costs, it should occur less frequently than lower cost social interactions, as indeed we observed. In our study aggression occurred at about 1/3 the rate of affiliative interactions. In the newly formed groups one individual may not know the physical strength of an unfamiliar group mate or how many familiar partners each has in the group that could provide support upon an aggressive attack. This uncertainty may repress aggression as it does in other situations where it is not advantageous such as during crowding (Aureli & de Waal, 1997).

When calculating the percentage of support instances that our subjects directed towards familiar individuals, we found that on average 77% of interventions were in support of a familiar partner. This meant that there was no significant difference in the number of support instances that were pro familiar partners versus those that were con familiar partners. This is very notable given Baker's (1992) discovery that when a familiar and unfamiliar group member was in conflict, interventions were overwhelmingly directed in favor of the familiar group member. In reviewing which individuals supported against familiar group mates in our groups, there were no patterns. This finding, along with those of affiliation, indicates that the chimpanzees in our study used characteristics other than simply relationship type to determine how to behave during social interactions.

In general, the size of familiar subgroups did not influence social behaviors in the way that we predicted. We discovered no correlation between the size of an individual's familiar subgroup and their rank in the group, indicating that knowing more individuals in the group did not translate into more social power. We also did not find a correlation between an individual's rank and their association with familiar or unfamiliar individuals.

This indicates that there may not be an advantage for higher-ranking individuals to spend more effort developing relationships than maintaining already formed ones.

In our study we observed that both relationship types were reciprocal, presumably for different reasons. Reciprocity between unfamiliar dyads could indicate that chimpanzees in early relationships keep closer track of the costs and benefits of social interactions. Since we included individuals that do not ever groom each other in our analysis, though, it most likely demonstrates that mutual avoidance is a social strategy used by unfamiliar individuals.

Our discovery that familiar relationships were reciprocal is surprising as, often, when individuals are closely bonded minor inequities in the costs and benefits of social interactions are well tolerated. This finding is complemented by Brosnan, Schiff, & de Waal's (2005) conclusions that more closely bonded chimpanzees are more forgiving of inequity. Our observations could indicate that relationships are maintained via symmetry based reciprocity or that during times of social stress even familiar relationships need mutual reinforcement. This may also illustrate that although the familiar chimpanzees knew each other in their old groups, they may not have been close affiliative partners and reciprocal interactions may signify relationship building as opposed to relationship maintenance. Further analysis of these factors could help to elucidate whether this is the case.

Our results reinforce previous findings that the flexible and complex social repertoire of chimpanzees enables them to respond to novel social situations based on past dyadic interactions as well as asses and respond to fluid relationship quality (Aureli & Schaffner, 2002; Hinde, 1976; Melis, Hare, & Tomasello, 2006; Seyfarth & Cheney, 1984; Trivers, 1971; de Waal, 1997b; de Waal & Luttrell, 1988). In the future we hope to see additional data on how unfamiliar relationships form and develop over time in chimpanzees. This could both further enlighten us as to how individuals mitigate social risk as well as help to inform how new chimpanzee groups are created and managed.

Because relocating chimpanzees and forming new social groups is disruptive and has potential to result in injuries (Alford, Bloomsmith, Keeling & Beck, 1995; McDonal, 1994) the implications of new group formation are important to consider. Ideally our data would have provided well-defined patterns of behavior and a reference for future group formations. Unfortunately this was not the case, and the only conclusions that we can draw in terms of management implications are that every situation is unique and often chaotic. We can also conclude that it may take more than a year for groups to stabilize and that dyadic relationships continue to evolve. Nevertheless, our data suggest that chimpanzees are very capable of using flexible social behaviors and high cognitive abilities to mitigate the costs and benefits that arise from living in a newly formed social group.

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4. DISCUSSION

In this dissertation I examined factors influencing relationship maintenance and formation in chimpanzees by means of two separate studies, a key feature being the use of both an observational as well as an experimental paradigm. These distinct methodologies enabled us to investigate the role of relationship and social risk on choices made in a controlled environment as well as observe how they influence social behaviors in a group-wide setting. The results of the two studies complimented each other in that relationship did not appear to strongly influence social behaviors in either. This implies that, in some cases, the short term costs and benefits of an interaction may be more important than how long individuals know each other or how much time they spend together.

The experimental study (Chapter 2) used a trust-game paradigm to ask whether chimpanzees distinguish social risk from economic risk while controlling for factors such as inequity aversion and prosocial tendencies. Because we used quantitative instead of qualitative rewards, we were able to separate the role of reward and relationship in predicting a subject's tendency to take social risks. In addition we established a foundation for Engelmann et al.'s (2015) argument that chimpanzees establish trusting relationships by providing evidence for differences between social risk and economic risk. Specifically, we found that chimpanzees are more averse to social risk than to non-social risk. Based on these results, we can argue that although risk and reward may be more important than relationship in predicting social behaviors, chimpanzees do differentiate the risks and rewards in the social realm from those in the non-social realm.

This is important for claiming that chimpanzees build dyadic trust (Engelmann et al., 2015), as opposed to simply treat conspecifics as a tool to gain resources.

The observational study (Chapter 3) took advantage of management decisions at the Yerkes National Primate Research Center to separate pre-existing groups of chimpanzees, re-arrange them, and put them back together in new configurations after adding additional group-members. This study supplemented the knowledge gained from our experimental paradigm by enabling us to observe the social behaviors of chimpanzees that were only recently introduced to each other and thus in the process of forming relationships. Although this scenario would not happen naturally, observing social group formation allowed us to examine how learning to predict the actions of another individual, through the formation of a dominance hierarchy and spending time in the same group, influences social behaviors.

From an ultimate perspective, social relationships provide fitness benefits (Silk, 2003; Silk et al., 2009; 2010), but these two studies add to the small amount of information that is known at the proximate level about how reward, relationship and uncertainty influence social interactions. By investigating social risk, as opposed to simply how past social interactions influence future ones, we begin to understand not only how chimpanzees balance potential costs and benefits, but that they have means by which they can overcome uncertainty in order to maximize the potential of social partners. As either uncertainty and/or costs rise, the use of demanding cognitive mechanisms such as scorekeeping and even theory of mind may be adaptive when interacting socially. An emotional heuristic such as trust, though, functions to decrease uncertainty and removes the need to assess the costs and benefits of an interaction (Colquitt, Scott, & LePine, 2007; Dirks & Ferrin, 2001).

4.1 Irrational Biases and Trust

Because it maximizes resources, evolution should theoretically select for economically rational behavior. Economically irrational decision-making is ingrained, though, in both humans and NHPs (Santos & Chen, 2009). Still, studies continue to question whether NHPs make economically rational decisions within the social realm, such as their ability to interact in a tit-for-tat fashion or engage in reciprocity, finding mixed results (Brosnan et al., 2009; Clutton-Brock, 2009; de Waal, 1989, 1997; Pelé, Dufour, Thierry, & Call, 2009; Stevens & Hauser, 2004; Yamamoto & Tanaka, 2009). If social decision-making, though, is subject to similar irrational biases as economic decision-making then the expectation for individuals to behave in ways that maximize their payouts in social experiments is tenuous. When NHPs fail at these types of tasks, the implication is that it is beyond their cognitive capabilities. Although this may be the case, the results of the trust game study add to existing literature in NHPs that suggests irrational social decision-making may also play a role (Brosnan & de Waal, 2003; Horner, Carter, Suchak, & de Waal, 2011).

In Chapter 2 we found that chimpanzees, like humans, fall victim to irrational decision-making within the realm of social risk in that they overvalue a loss that results from a social interaction. This implies that aspects of decision-making about risk in the social realm are subject to different costs and benefits than those of economic decision-making. These costs and benefits most likely stem from a combination of the inherent value of relationships as well as the emotional response that interacting with another individual elicits. Our findings suggest that chimpanzees, like humans, may use emotional shortcuts, such as trust as defined by Rousseau in Chapter 1, as a heuristic to evaluate risks in the social domain and indicate that selection pressures similar to those in humans may have influenced how these risks are assessed.

Trust is valuable in situations where investing in an individual can lead to a benefit but where, simultaneously, the opportunity exists to be taken advantage of, which could result in a loss of resources (Hwang & Burgers, 1997). An appropriate level of trust can benefit an individual in two important ways. First, taking social risks provides an opportunity for greater rewards than avoiding social exchanges. This can lead to the stabilization of social systems by encouraging cooperation and mediating the relationships between individuals, creating an environment that encourages interaction (Colquitt, Scott, & LePine, 2007; Dirks & Ferrin, 2001). Second, trust allows an individual to make a relatively accurate and fast assessment in a situation where slow reaction and incorrect judgment could result in wasted energy or lost resources (Colquitt, Scott & LePine 2007). One who is willing to trust another becomes free to allocate cognitive resources to aspects other than social monitoring and does not need to continuously reassess the risks and rewards in a relationship.

There are several ways that correctly gauging whether or not to invest in a partner could result in a cost or a benefit. If one correctly trusts another individual, they have the potential to benefit through social interactions such as cooperation, reconciliation or affiliation. If they correctly mistrust they can benefit through avoiding energetic cost or even injury. On the other hand, a negative social outcome could result in some cost to the individual such as a reduction in access to resources. If an individual, though, incorrectly mistrusts a social partner there could be the opportunity costs of benefit from a social interaction and a partner with whom to interact.

Whether or not those who trust actually gain more than those who do not is unclear, though. By modeling social risk-taking behaviors in humans Engle-Warnick and Slonim (2006) concluded that the payoff for trusting a partner is greater than the payoff for distrusting. Eckel and Wilson (2004) though, found that subjects who invested in a partner only received, on average, the same amount that they gave, suggesting that those who made trusting choices did not profit. In order to investigate this subject, a further study could ask how accurate chimpanzee subjects are at predicting whether their partner will make social or prosocial choices and what factors they attend to in order to decide.

In risk-taking experiments, the act of taking a risk is often seen as evidence that the subject has a positive expectation of the outcome (Colquitt, Scott & LePine, 2007; Cox 2004; Mayer, Davis & Schoorman, 1995; Skyrms, 2004). It is clear, though, that one can act in a way that makes them vulnerable to a negative outcome without high expectations for a positive outcome. Humans, for example, play the lottery even with extremely small odds of winning. Decision-making about social interactions can function in the same way in that, if the rewards are great enough, the risk of a negative outcome may be worth the reward. Therefore we can consider that although a state such as trust can act as a gauge of wiliness towards vulnerability, the act of making oneself vulnerable indicates that either there is a positive expectation of the outcome, or the rewards have been judged to be worth the risk. In our economic trust game, we found high variability between individuals in their willingness to take risks. This could mean that certain individuals have a predisposition towards risk, but could also imply that some are simply more reward driven. In this case the salience of gaining the highest number of bananas outweighs any negative consequences from losing due to chance or the actions of a social partner.

4.2 Relationship Formation and Maintenance

As expectations develop in a dyad and a relationship develops it subsequently needs to be maintained, requiring time and energy (Lehmann, Korstjens, & Dunbar, 2007). Disruptions such as a change of environment and new social influences could impact preexisting relationships by making them stronger or by weakening them. Capuchins and squirrel monkeys increased their social interactions when moved to new enclosures (Dufour, Sueur, Whiten & Buchan-Smith, 2011). Students who moved together to new schools, though, allowed old relationships to decay and replaced old friends with new ones (Hardy, Bukowski, & Sippola, 2002; Saramäki et al., 2014). This is primarily because the factors that encouraged a close relationship in an old environment did not necessarily encourage one in a new environment. In contrast, the subjects in Chapter 3 both maintained old friends at rates higher than chance but also had a high percentage of unfamiliar top grooming partners. This strategy makes economic sense as it enabled them to take advantage of the benefits of both maintaining predictable relationships as well as gaining additional benefits from more uncertain sources.

Although the chimpanzees invested most of their energy in familiar individuals, a high proportion of top grooming partners were unfamiliar. This outcome could arise due to two different but not mutually exclusive scenarios. The first is that the benefits of interacting with a relatively unknown individual outweighed the potential costs. The other is that uncertainty about the relationship was low. It is important to note that low levels of uncertainty about a relationship do not always indicate a positive outcome. An individual can be fairly certain, for example, that if they approach another for food the outcome will be negative. Because many of the top unfamiliar social partners were male we assume that the benefits of these interactions outweigh the potential costs, that males are particularly predictable as affiliative partners or there exists some combination of the two.

Because interacting socially is generally considered low cost (Brosnan & de Waal 2002; Schino 2007; de Waal 1997) we might expect for the chimpanzees in newly formed social groups to spread their social effort across as many group mates as possible. Although the social network diagrams in Chapter 3 indicated that almost all dyads interacted socially to some degree, anecdotally we noticed that the chimpanzees we observed spent a large percentage of their time resting as opposed to actively investing in social relationships. In humans, social communication is focused on a small number of people as opposed to being spread out over a large network, suggesting that at a certain point the benefits of having a greater number of affiliates plateaus (Roberts & Dunbar, 2011). This could occur because there is a limit to what an affiliate can provide, which may not increase in relation to an increase in number of close partners (Sutcliffe, Dunbar, Binder, & Arrow, 2012).

Since relationships have both costs and benefits, the chances that benefits will not outweigh the costs may also increase as the number of relationships increase. Empirically, benefits predicted time spent with close friends while costs predicted time spent with casual friends in college age humans, implying that more distant relationships are more costly than closer relationships (Hays, 1989). This means that it is not worth the effort of maintaining too many relationships if the same number of benefits can be gained from fewer. In addition, because social risk is different from non-social risk we assume that the chimpanzees in our new social groups are, in general, more sensitive to the outcomes of negative and positive interactions in the social realm than they would be to purely economic influences. This irrational bias towards aversion to social risk may mean that, although it could pay off for individuals to direct a greater amount of their social energy in getting to know an unfamiliar individual, this is not how they behave.

Another notable finding is that the individuals in our newly formed groups did not always support the familiar partner when intervening between a familiar and unfamiliar group mate who were engaged in an agonistic interaction. Although evidence has been found for reciprocity in grooming and food sharing, the reciprocal exchange of support in coalition formation is a particularly risky behavior. During coalitionary support an individual is exposed to risk from both agonistic aggression as well as exploitation from the coalitionary partner if nothing is gained from providing the support.

Chimpanzees are thought to form coalitions based on strategic social decisions and actively seek out or avoid specific individuals for these purposes (de Waal, 1984, 2007; Newton-Fisher, 1999). De Waal (1978), who examined coalitions, found that support was reciprocal in 19 out of 20 pairs. Watanabe and Smuts (1999) concluded that up to seven percent of attempts to greet and form coalitions in male olive baboons were met with an agnostic response from a potential coalitionary male. The authors also discuss that up to 25% of these interactions were incomplete because either the initiator did not follow through with the encounter or the recipient turned away. These findings indicate that evaluating whether to form a coalition is a time where uncertainty may influence the decision. From an ultimate perspective, these this suggests that it is adaptive for chimpanzees to not only respond to the benefits that a relationship provides but also to evaluate the costs and level of uncertainty in it.

4.3 Future Studies

Due to the neophobic character of chimpanzees (Watts, 2004; Wrangham, 1999), as well as how our subjects were housed, the pairs in our trust game study knew and had relationships with each other. This factor created limitations such as the potential for relationships to change during the course of the study but is also one of the strengths of working with captive NHPs. Although human trust games are commonly played in an iterated form in order to investigate how relationships are established (Berg, Dickhaut, & McCabe, 1995; Camerer & Weigelt, 1988; King-Casas et al., 2005), these games are almost always played with a stranger or a computer.

Because there are no trust-game studies in humans where participants have pre-existing relationships with their partners, we cannot measure the influence of relationship versus reward when humans make decisions about social risk. This gap in knowledge could be filled using iterated trust-games between human dyads that are familiar and those that are not, allowing us to explore how bonds form and how already established bonds influence social risk. Using this paradigm we could also investigate the interaction between reward, relationship and time. If we repeat the game several times with the same unknown partner and manipulate relationship development, we might find that the influence of reward decreases over time as people form a relationship. This would be similar to the finding that NHPs are more tolerant of a loss arising from those with whom they have closer relationships (Brosnan, Schiff & de Waal 2005; Schino & Aureli 2009).

In addition to exploring the role of reward and relationship on socially risky decisions, it would also be fruitful to investigate how social and non-social decision-making differ. Why, for example, are chimpanzees not more prone to social risk than to non-social risk given their gregarious nature, as opposed to our finding of the opposite? Humans who ate highly palatable chocolate as well as very bitter chocolate rated these experiences as both more and less enjoyable when another person ate the food with them and the authors concluded that both positive and negative experiences are enhanced through social interactions (Boothby, Clark, & Bargh, 2014). This could imply that if we tested a sufficient number of subjects, we might find a relationship between outcome and social versus non-social risk where both positive outcomes as well as negative outcome are overvalued.

4.4 Conclusion

One of the main focuses of this dissertation was what factors influence socially risky decision-making in chimpanzees. In order to explore this topic we modified a human trust game, a paradigm which asked a subject to choose between a social but uncertain option by passing a token to her partner or a non-social option that resulted in a constant reward. Trust is defined here as the willingness to take a social risk on another individual that is based on a positive expectation of the outcome of an interaction, and we operationalized this via the subjects' choice to pass a token to a partner (Rousseau et al., 1998). Our results revealed several striking outcomes.

We found that chimpanzees are more averse to social risk than non-social risk, a finding that parallels comparable studies in humans. This provides evidence that, as in humans, the domain of social risk may be separate from the domain of non-social risk via neural and hormonal processes. In humans, fMRI evidence suggests that specialized neural mechanisms separate risky social decision-making from risky non-social decision-making. Because conscious chimpanzees cannot undergo fMRI like humans, the best way to investigate the evolutionary origins of these mechanisms is through behavioral studies such as the one employed here. These provide us with insight as to whether humans are indeed uniquely social and whether we employ means of social decision-making that are different from those of our most closely related species. Similarity between chimpanzees and humans implies shared evolutionary adaptations that shape both ape and human social economic decision-making.

Although our paradigm was similar to that of Englemann et al. (2015) and Englemann & Hermann (2016) on chimpanzees, our conclusions were quite different.

This was most likely because these earlier studies covered dyadic relationships, which were either positive or negative. Our study examined a more narrow range of relationships, since we could only use a subset of compatible pairs that were willing to hand each other tokens or accept them. Remarkably, within this subset, relationship quality outside the experiment did not seem to matter, a finding similar to the prosocial choice study of Horner et al. (2011) on the same chimpanzee colony.

Instead of focusing on relationship quality, our paradigm mimicked relationship formation and trust building during the experiment itself. Our large number of sessions allowed us to investigate the process by which individuals learn how to predict the behavior of another. We conclude that chimpanzees weigh early social interactions more heavily than later ones. This finding is akin to the importance of "first impressions" in humans (Berg, 1984) and further study is needed to determine the duration of these first impressions (at least within the experimental context) and how easily they are changed.

Our results also showed a correlation between a subject's willingness to take a social risk and their willingness to take a non-social risk in the trust game. This reveals the importance of personality and individual differences on general risk preferences. Work on human identical and fraternal twins suggests that that, in part, a genetic predisposition towards risk drives these preferences (Cesarini et al., 2008). In general, correlations in individual preferences for social and economic risk indicate that although the domains may utilize distinct decision-making processes, they have overlapping characteristics that can be assessed in similar ways. These are primarily that the benefits of an outcome have been deemed to outweigh the costs as opposed to a disregard for the degree of uncertainty in a situation (Soane & Chmiel, 2005).

Results of this study imply that each chimpanzee has a predetermined attitude about risk that influences their social decision-making but that they weigh social losses as greater than non-social losses of the same magnitude. One explanation for this difference, which has also been found in humans (Bohnet & Zeckhauser, 2004; Rilling et al., 2004), is that social risk comes with an emotional cost not present in purely economic games. It is not certain exactly what this cost stems from, but may be due to inequity aversion, damage to the relationship or assigning blame to the other individual for a negative outcome (Bohnet et al., 2008; Rilling, King-Casas & Sanfey, 2008). This response is present in many different human cultures and here we argue it exists in chimpanzees as well (Bohnet et al., 2008). This indicates that it is an important aspect of primate social decision-making and may be adaptive by helping to keep an individual from being take advantage of in a social relationship, mediating when to stop investing in another individual. This study is an important addition to literature that addresses the influence of animal emotions on decision-making.

According to the social brain hypothesis, the cognitive requirements needed to accurately predict the outcome of a social interaction have driven the evolution of advanced reasoning abilities throughout the primate lineage (Dunbar & Shultz, 2007; Whiten & Byrne, 1988). An increase in uncertainty about the outcome of an interaction requires flexible decision-making and selects for the ability to correctly evaluate the costs and benefits of a social interaction. Although theories about reciprocity and social decision-making are well established in chimpanzees, the studies in this dissertation add to the sparse data about how social relationships develop and what induces change.

In time periods of social uncertainty and change the employment of emotional heuristics, such as trust, are most useful in reducing the cognitive requirements of keeping track of the costs and benefits of a relationship (Brosnan & de Waal, 2002; Suchak & de Waal, 2012). Because a time of relationship change is most likely when the highest uncertainty, and therefore cognitive demand, is present in social decision-making this time period is important on which to focus.

In this dissertation we also reported on the formation of two new social groups of chimpanzees. Although several studies have investigated aspects of new group formation, most only focused on the process of dyadic introductions or only recorded data for a limited amount of time (Alford, 1994; Baker, 1992; Bloomsmith et al., 1999; Brent et al., 1997; Seres et al., 2001). Our research was unique in that we observed each group for a full year allowing us to investigate how new relationships changed over time. Our findings that chimpanzees invest heavily in unfamiliar relationships add to the existing literature on how chimpanzees strategically manage the social realm. It also provides important information for what social interactions to expect during the formation of similarly composed groups.

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5. APPENDIX I

An additional influence on the percentage of risky choices that our subjects made may have been the position of the risky options relative to the safe option. Due to constraints within the testing facility we could not counterbalance the location of the risky and safe options. Because of this the social and non-social risk options were nearest to the partner and the safe box was farthest away. With particularly prosocial dyads this may have increased the percentage of risky choices, albeit equally in both conditions, if the subject chose to position herself close to her partner.

Keeping these factors constant, though, decreased any possible confusion that may have come from switching the locations of the choices around for each trial. It also ensured that the social condition was similar to the non-social condition as the position of the risky option in each condition was less than 1 meter away from the other and we could not change the location of the mesh between the subject and partner. This enabled us to ensure that our comparison was accurate.

We could even argue that the position of the safe and risky options encouraged a bias towards the safe box. This box was in exactly the same position for both the social and non-social conditions where the risky option was to the side of the subject in one condition and to the front in another. If the subjects made choices based purely on the number of times they had been reinforced for each choice, they would likely gravitate towards the safe box.

In an attempt to overcome the potential for positional bias in our partners we created an apparatus that enabled us to change the position of the boxes with each trial. The advantage to this was that for partners who made choices based on position they ended up choosing prosocial 50% of the time and selfish 50% of the time, meaning that we did not have partners that only chose prosocial or selfish based on the position of the boxes. One limitation to this apparatus, though, was that since the boxes constantly moved, it may have made it more challenging for the partners to learn the meaning of each. Because of this, as well as the fact that both choices rewarded the partner equally, we only had two partners that seemed to learn the meaning of the boxes and choose prosocial a majority of the time. Although, learning the meaning of the boxes and making selfish choices are not mutually exclusive so it is not possible to directly interpret an individual's understanding of the boxes by the percentage of prosocial and selfish choices that they made.