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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Conflict Management in Captive Bonobos (*Pan paniscus*): Valuable Relationships,
Relationship Repair, and Third-Party Interactions with Aggressors

A dissertation submitted in partial satisfaction of the requirements for
The Degree of Doctor of Philosophy

in

Anthropology

by

Beth Peterson Roselyn

Committee in Charge:

James Moore, Chair
Suzanne Brenner
Christine Harris
Christine Johnson
Katerina Semendeferi
Shirley Strum

2015

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Chair

University of California, San Diego

2015

DEDICATION

This dissertation is dedicated to my wife, Lea Roselyn, and my parents, Don and Peggy Peterson, whose support made it possible. It is also dedicated to my daughter, Willow, the best person I know.

EPIGRAPH

The more clearly we can focus our attention on the wonders and realities of the universe about us the less taste we shall have for the destruction of our race. Wonder and humility are wholesome emotions, and they do not exist side by side with a lust for destruction.

--Rachel Carson, 1963

Luke, you're going to find that many of the truths we cling to depend greatly on our own point of view.

--Ob-Wan Kenobi, 4ABY

TABLE OF CONTENTS

Signature Page.....	iii
Dedication.....	iv
Epigraph.....	v
Table of Contents.....	vi
List of Figures.....	vii
List of Tables.....	viii
Acknowledgements.....	x
Vita.....	xi
Abstract of the Dissertation.....	xii
Introduction.....	1
Chapter 1: Conflict Management in Captive Bonobos (<i>Pan paniscus</i>): Testing the Valuable Relationships Hypothesis.....	33
References.....	76
Chapter 2: Conflict Management in Captive Bonobos (<i>Pan paniscus</i>): Testing the Relationship Repair Hypothesis	82
References.....	110
Chapter 3: Non-Aggressive Third-Party Initiated Interactions with Aggressors during Conflict in Captive Bonobos (<i>Pan paniscus</i>)	113
References.....	135
Conclusion.....	139

LIST OF FIGURES

Figure 1.1a Percentage of Conflicts Reconciled by Age-Class Combination..	72
Figure 1.1b Percentage of Conflicts Reconciled by Sex-Class Combination..	83
Figure 1.2a Probability of Reconciliation Occurring After Consolation Compared to Reconciliation Occurring in the Absence of Consolation.....	74
Figure 1.2b Probability of Consolation Occurring After Reconciliation Compared to Consolation Occurring in the Absence of Reconciliation.....	75
Figure 2.1a Comparison of Rate of Affiliation 10 Days After Reconciled Conflicts to Baseline Rate of Affiliation By Dyad.....	104
Figure 2.1b Comparison of Rate of Affiliation 10 Days After Unreconciled Conflicts to Baseline Rate of Affiliation By Dyad.....	105
Figure 2.2a Comparison of Rate of Affiliation 10 Days After Reconciled and Unreconciled Conflicts By Dyad.....	106
Figure 2.2b Comparison of Rate of Aggression 10 Days After Reconciled and Unreconciled Conflicts By Dyad.....	107
Figure 2.3a Comparison of Rate of Aggression 10 Days After Reconciled Conflicts to Baseline Rate of Conflict By Dyad.....	108
Figure 2.3b Comparison of Rate of Aggression 10 Days After Unreconciled Conflicts to Baseline Rate of Conflict By Dyad.....	109

LIST OF TABLES

Table 1.1a Predictions of Valuable Relationships Hypothesis.....	63
Table 1.1b Predictions of Relationship Security Hypothesis.....	64
Table 1.2 The <i>Pan paniscus</i> Colony at the San Zoo (San Diego, CA, United States) and Main Sub-Group Composition.....	65
Table 1.3 Inter-Animal Distances (IADs), Behaviors, and Conflict Intensity and Context.....	66
Table 1.4a Reconciliation: Number of Attracted, Dispersed, and Neutral Pairs for Recipients of Aggression; Conciliatory Tendencies per Individual ..	67
Table 1.4b Number of Conflicts Followed by PC Affiliation; Number of Reconciliations Initiated by Recipient	68
Table 1.5a Occurrence of Reconciliation and Consolation by Intensity.....	69
Table 1.5b Occurrence of Reconciliation and Consolation by Context.....	70
Table 1.6 Offered Consolation: Number of Times Each Individual Was Offered Consolation from a Third Party; Number of Attracted, Dispersed, and Neutral Pairs, Triadic Contact Tendencies per Individual.....	71
Table 2.1 Hypotheses and Predictions for Short and Long-Term Consequences of Conflict in the Presence of Absence of Reconciliation.....	99
Table 2.2 The <i>Pan paniscus</i> Colony at the San Zoo (San Diego, CA, United States) and Main Sub-Group Composition.....	100
Table 2.3 Number of Reconciled and Unreconciled Conflicts per Dyad Followed by Renewed Aggression or Not.....	101
Table 2.4 Occurrence of Renewed Aggression After Reconciled and Unreconciled Conflicts.....	102
Table 2.5 Comparison of Mean Rate of Affiliation and Aggression 10 Days after Conflict, Relationship Quality, and CCT per Dyad.....	103
Table 3.1 Summary of Key Studies on Third-Party Initiated Interactions with Aggressors in Primates.....	127

Table 3.2 The <i>Pan paniscus</i> Colony at the San Zoo (San Diego, CA, United States) and Main Sub-Group Composition.....	129
Table 3.3 Inter-Animal Distances (IADs), Behaviors, and Conflict Intensity and Context.....	130
Table 3.4 Aggressors and Conflict Dyads Receiving Third-Party Affiliation or Interference (Inverventions) During Conflicts.....	131
Table 3.5 Third-Parties Intervening with Aggressors During Conflicts by Total Interventions and First to Affiliate.....	132
Table 3.6 Third-Party Initiated Affiliation with Aggressors During Conflict by Aggressor and Third-Party Identity.....	133
Table 3.7 Comparison of Rate of Aggression Thid-Parties Received from Aggressors and the Rate of Affiliation Offered to Aggressors.....	134

ACKNOWLEDGEMENTS

I would like to thank Christine Johnson and the COGS 160 interns for data collection assistance and Kelsey Quigley for help with data entry. This research was supported, in part, by UCSD Department of Anthropology Project Bucks. Thank you to my dissertation committee, especially Jim Moore and Shirley Strum, for helpful feedback and guidance. Thank you to Christine Johnson for her mentorship and introducing me to the bonobos; Vivian Lew and the UCLA Statistical Consulting Center for help with statistics; Mike Bates and the San Diego Zoo for their support, interest, and facilitation of the research; and, most especially, I would like to thank the bonobos.

Chapters 1, 2, and 3 are being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this material.

VITA

EDUCATION

- 2015 Ph.D., Anthropology
University of California San Diego
- 2008 C. Phil, Anthropology
University of California San Diego
- 2006 M.A., Anthropology
University of California San Diego
- 2003 B.A., Anthropology and Economics
University of Kansas, Lawrence, KS

APPOINTMENTS

- 2013-Present Instructor Cabrillo College
Anthropology Department
- 2012-2013 Lecturer University of California San Diego
Making of the Modern World Program
- 2011-2012 Lecturer University of California San Diego
Anthropology Department
- 2008-2013 Associate Faculty Mira Costa College
Anthropology Department
- 2006-2012 Teaching Assistant University of California San Diego
Making of the Modern World Program
- 2005 Teaching Assistant University of California San Diego
Human Development Program
- 2004-2005 Teaching Assistant University of California San Diego
Anthropology Department

ABSTRACT OF THE DISSERTATION

Conflict Management in Captive Bonobos (*Pan paniscus*): Valuable Relationships,
Relationship Repair, and Third-Party Interactions with Aggressors

by

Beth Peterson Roselyn

Doctor of Philosophy in Anthropology
University of California, San Diego 2015
Professor James Moore, Chair

All social animals face similar problems regarding intragroup competition over access to resources, which can lead to aggressive conflicts, and are therefore expected to have evolved mechanisms for managing the costs of conflict. Reconciliation, post-conflict affiliation between former opponents, and consolation, post-conflict affiliation directed at victims of aggression by third-parties, are two of these mechanisms and have been demonstrated widely in nonhuman primates. The Valuable Relationships hypothesis (VR) argues that individuals with valuable relationships are more likely to reconcile conflicts. VR rests on the assumption that conflict damages relationships and

reconciliation serves to repair that damage. Most studies support VR but this Relationship Repair hypothesis (RR) remains untested, and while the post-conflict behavior (PCB) of chimpanzees has been widely examined, less is known about PCB in bonobos.

This dissertation serves as a test of VR and RR and data presented here also examine third-party initiated interactions with aggressors during conflict, which have not been reported in bonobos.

Analyses of the patterns of conflict management in the San Diego Zoo bonobo colony are inconsistent with both VR and RR. Overall, the group had a low rate of reconciliation (23.6% of conflicts reconciled), a low CCT (corrected conciliatory tendency; 6.71%), and there was no relationship between reconciliation and relationship quality or other relevant variables (sex of conflict participants, conflict intensity or context). Reconciled conflicts were less likely to be followed by continued aggression on the same day than were unreconciled conflicts. However, analysis of long-term patterns of interaction (10 days following conflicts) shows inconsistent support for RR. In the 10 days following unreconciled conflicts, there was no decrease in affiliation compared to baseline rates, which suggests the precipitating conflict did not damage the relationship. Similarly, in the 10 days following unreconciled conflicts, there was no change in the rate of aggression. The data presented here are more consistent with the Relationship Security hypothesis (RS), which argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation, while

insecure relationships would be more likely to be damaged by conflict and therefore more likely to reconcile.

Consolation has been well-studied in the primate conflict management literature. Less understood are third-party initiated interactions with aggressors during conflicts. The data presented here serve as a test of the four main hypotheses about third-party initiated interactions with aggressors: adults will be most motivated to offer affiliation to aggressors or interfere non-aggressively in conflicts to promote social stability, gain dominance or mating benefits, or to promote self-protection by affiliating with frequent aggressors. None of these hypotheses were supported by the analysis presented here. Nearly all of the third-party initiated interactions with aggressors during conflicts were initiated by immature individuals and were directed at one adult male.

INTRODUCTION

All social animals are presented with similar problems regarding within-group competition over resources and species are expected to have evolved mechanisms to cope with these problems. Postconflict behavior (PCB) is a major focus of nonhuman primate research, particularly reconciliation, post-conflict affiliation between former opponents, which has been demonstrated in virtually all of the species in which it has been studied (de Waal and van Roosmalen 1979; Aureli and de Waal 2000; Aureli et al. 2002; Silk 2002; but see Sommer et al. 2002; Schaffner et al. 2005; Berman et al. 2006), including several non-primates (domestic cat: van den Bos 1997; domestic goat: Schino 1998; spotted hyena: Wahaj et al. 2001; bottlenose dolphin: Weaver 2003; wolves: Cordoni and Palagi 2008; horses: Cozzi et al. 2010). The ways in which species vary in their conflict management can help clarify the aspects of post-conflict behavior that are necessary for group living to persist and what aspects are specific to a taxon's particular socioecological adaptations.

This study will examine conflict management in captive bonobos within the framework of the Valuable Relationships (VR) hypothesis, which holds that individuals with valuable relationships are more likely to reconcile conflicts (de Waal and van Roosmalen 1979). VR has two clear components: (1) reconciliation repairs relationships after conflict and (2) dyads with valuable relationships are more likely to reconcile. While the overwhelming majority of studies demonstrate support for the second component, the first component contains an assumption that is largely unexamined, i.e. that conflict damages relationships and requires reconciliation to repair them (Cords and Aureli 1996; Watts 2006). Several studies have demonstrated

that reconciliation restores tolerance after conflicts in the short-term (Cords 1992; Cords and Thurnheer 1993; Silk 1996), however, the long-term consequences of reconciliation or its absence have yet to be widely examined. This Relationship Repair (RR) hypothesis has only been explicitly tested once (Japanese macaques: Koyama 2001). Similarly, reconciliation in bonobos is understudied, particularly in comparison to chimpanzees. In one of two published studies of reconciliation in bonobos using standard methods, Palagi et al. (2004) reported results consistent with VR: female-female dyads reconciled at the highest rate, followed by female-male dyads, and dyads with strong affiliative relationships reconciled more than weak dyads. Clay and de Waal (2013) also reported support for VR, in that dyads with strong affiliative relationships were more likely to offer consolation to each other. Consolation may function as a mechanism for demonstrating investment in the relationship with the victim of aggression. Other postconflict research in bonobos has also supported VR (de Waal 1987; Hohmann and Fruth 2002), however, Fortunato (2009) presented results more consistent with the Relationship Security (RS: Cords and Aureli 2000) hypothesis than VR. RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation, regardless of the value of the relationship. RS predicts a lower rate of reconciliation than VR and that relationship quality (RQ) does not necessarily influence the rate of reconciliation.

The objectives of the present study are to (1) provide an additional test of VR and RS in bonobos (Chapter One), (2) test a critical assumption of the VR hypothesis, relationship repair (Chapter Two), and (3) report data on the occurrence of third-party

affiliation with aggressors during conflicts (Chapter Three), with the aim of furthering our understanding of PCB in bonobos and how PCB varies within and between species, particularly between bonobos and chimpanzees. Bonobos differ from chimpanzees in significant ways—the strength and significance of the dominance hierarchy, the absence of male dominance, the relative importance of female-female and female-male relationships, and the frequency and severity of aggression—that have implications for the nature of PCB in both species. Bonobos are relatively understudied and given the importance of the comparative method for constructing models of the evolution of human behavior and the over-emphasis on a chimpanzee model, it is essential to expand our understanding of our *other* closest living relative.

SECTION I: Group-Living and Conflict

Group living in primates evolved as a response to ecological and/or predation pressures, particularly for females (Wrangham 1980; van Schaik 1983). Its benefits include protection from predation (van Schaik 1983), protection from infanticidal transfer or extra-group males (Wrangham 1980; Sterck et al. 1997), and defense of resources (Wrangham 1980; van Schaik 1983; Isbell and Young 2002). These benefits, however, do not come without costs. The costs of group living emerge from conflicts of interest which can lead to aggressive competition over food (Wrangham 1980; van Schaik 1983), between potential mating partners (Parker 1979; Smuts and Smuts 1993; Gowaty 1996), over dominance status or access to social partners (Walters and Seyfarth 1987), over access to mates (Trivers 1972; Clutton-Brock et al. 1988), and over access to other resources. Traditionally, conflict has been viewed negatively, as an anti-social behavior that leads to the disintegration of social bonds and the

dissolution of groups, rather than as one component of the negotiation of group living that, along with other negotiation strategies, allows animals to manage the costs of group living (de Waal 1996, 2000).

Relationships are one of the primary mechanisms primates employ to manage group living. Relationships are investments from which partners derive fitness benefits (Kummer 1978) and can be characterized as an emergent property of the sum of interactions between individuals in which patterns emerge over time and the history of interactions influences the form of future interactions (Hinde 1976). Relationships can be measured by 3 interrelated dimensions: value—fitness benefits derived from the relationship, access to resources (food, sex, social partners) or agonistic support; compatibility—overall tenor of interactions, affiliation; and security—resistance of the relationship to change, predictability of interactions (Cords and Aureli 2000), that likely influence the costs of conflict. VR tends to rely on both value and compatibility for developing predictions about which dyads or dyad classes are more likely to reconcile. VR uses rates of affiliation to determine compatibility (typically referred to as relationship quality (RQ) in the literature) and the value of partners in specific age or sex classes is based on predictions from socioecology, e.g. male-male (MM) chimpanzee dyads are characterized as high value because they tend to be more affiliative than female-female (FF) or FM dyads (higher compatibility or relationship quality) and chimpanzee socioecology predicts males have high value relationships because males are the natal sex, increasing the likelihood they are kin. There has been some attempt at separation of compatibility from value in the literature, presenting an additional Good Relationships hypothesis (GR: Aureli et al. 1989; Kappeler and van

Schaik 1992; Palagi et al. 2004) but since affiliation, coalition formation, and support (elements of good relationships) tend to be associated with the fitness benefits of relationships, whether kin or non-kin, the general trend seems to subsume GR under VR or to make no distinction between them (Watts 2006). What this ultimately means for primates is that relationships themselves are valuable (Kummer 1978).

While conflict is an integral component of relationships and an inescapable aspect of group living, it can be a source of disturbance that disrupts patterns of tolerance or affiliation. Depending on the value of a relationship, a disturbance can have significant negative fitness consequences as a result of loss of tolerance (Kummer 1978). If a relationship is disturbed, then the predictability of the form of future interactions is decreased, creating uncertainty and stress (Aureli et al. 1989). As long as the benefits of group membership outweigh the costs, there will be selection pressures for animals to evolve non-dispersive mechanisms to cope with the negative effects of conflict (de Waal 1996; Keltner and Potegal 1997). There are various ways individuals can respond to a conflict: reconciliation; consolation, post-conflict affiliation with a third party; redirected aggression, aggression directed at a third-party by one of the former opponents; avoidance; and business as usual (Wittig and Boesch 2003). Of these, most attention has gone to reconciliation (Kappeler and van Schaik 1992; Aureli and de Waal 2000; Watts 2006).

Post-Conflict Behavior

Reconciliation: Valuable Relationships and Relationship Repair

The Valuable Relationships hypothesis (VR) has been the dominant model for the analysis of reconciliation (de Waal and van Roosmalen 1979; Kappeler and van

Schaik 1992; de Waal and Aureli 1997; Koski et al. 2007). VR argues that if conflict damages social bonds and post-conflict affiliation serves to repair those social bonds, then individuals with valuable relationships (kin, close associates) are more likely to reconcile after conflicts. There are two explicit components to VR: (a) reconciliation repairs relationships and (b) individuals with valuable relationships are more likely to reconcile. The second component of VR is generally supported in the literature: kin tend to reconcile more frequently than non-kin, associates tend to reconcile more frequently than non-associates, and coalition partners tend to reconcile more frequently than non-partners¹ (Kappeler and van Schaik 1992; de Waal and Aureli 1997; Aureli and de Waal 2000; Aureli et al. 2002; Watts 2006). However, the first component contains an underlying assumption—that conflict damages relationships and reconciliation serves to repair that damage—that has yet to be widely examined (Silk 1996; Koyama 2001; Watts 2006) and must be, in order for the function of reconciliation to be understood.

Studies of reconciliation that have focused on this relationship repair hypothesis (RR) have largely focused on *short-term* relationship repair, i.e. the short-term consequences of reconciliation, its role in reducing post-conflict (PC) stress and continued aggression (Aureli et al. 1989; Aureli and van Schaik 1991a,b; Wittig and Boesch 2003; Cooper et al. 2007; Koski et al. 2007a) and in restoring tolerance (Watts

¹ Relationships are not necessarily of equal value to both partners. This is clearest in dominant-subordinate relationships where maintaining a good relationship is potentially of greater value to the subordinate individual. Which individual values the relationship more is likely to be reflected in which individual is more likely to initiate reconciliation (Aureli and van Schaik 2000; Wittig and Boesch 2003b). Since dominance status often relies on alliances and support from others, it is also possible that a dominant individual values a relationship more if their status depends on the support of the subordinate former opponent.

1995; Castles and Whiten 1998; Wittig and Boesch 2005) and peaceful simultaneous exploitation of resources (Cords 1992; Cords and Thurnheer 1993). However, RR makes predictions about the *long-term* consequences of conflict and reconciliation that have not yet been examined (Cords and Aureli 1996; Silk 1996, 2002; Watts 2006). Silk cautioned against allowing RR to become “entrenched as dogma” (1996) and suggested that the persistence of support for RR in the absence of evidence may be “because it fits our own folk model of how and why we resolve conflicts” (Silk 2002). If conflict damages relationships and reconciliation serves to repair that damage, then conflicts that are *not* reconciled presumably should result in damaged relationships. Although this is a central tenet of RR (and VR), the only *direct* evidence for *long-term* damage or repair comes from Koyama (2001), who reports that in the 10 days following unreconciled conflicts, Japanese macaque dyads had lower rates of affiliation and higher rates of aggression compared to baseline measures while reconciled dyads experienced no relative change in affiliation and reduced aggression, i.e. reconciliation repaired their relationships. Watts (2006) echoes Silk’s earlier caution: “Results of Koyama’s (2001) study meet the [relationship repair] condition, but clearly we need more such work before we can confidently conclude that [reconciliation] repair[s] disturbances to relationships or at least maintain[s] the status quo” (1348).

Challenging RR (and VR), Silk (1996) proposed the Benign-Intent (BI) hypothesis, arguing that “the primary function of [reconciliation] is not to repair damaged social relationships...[but] to [reestablish] contact with former opponents with no implicit long-term consequences” (39). In two studies of PCB in wild female

baboons (Cheney et al. 1995; Silk et al. 1996), Silk and colleagues demonstrated that reconciliation restored tolerance (short-term repair) but that there were no long-term consequences for relationships after unreconciled conflicts, i.e. rates of affiliation and aggression after unreconciled conflicts were no different than baseline rates. Silk argued that for relationship repair to be demonstrated, there should have been an *increase* in affiliation in the 10 days PC. But, RR does not predict an *increase* in long-term affiliation, only no *decrease* (Koyama 2001). In their response to Silk (1996), Cords and Aureli agreed that the long-term consequences of reconciliation had yet to be demonstrated and suggested that “Silk’s analysis should challenge researchers to conduct more conclusive searches for such long-term effects” (1996; see also Watts 2006).

There are two other hypotheses related to reconciliation: Uncertainty Reduction (UR: Aureli et al. 1989) and Relationship Security (RS: Cords and Aureli 2000). UR argues that reconciliation functions to reduce post-conflict anxiety caused by the uncertainty that conflict will continue or be renewed. UR and BI make similar predictions, they simply approach reconciliation from slightly different perspectives: UR emphasizes reconciliation’s role in reducing the stress response, while BI emphasizes its role in restoring tolerance immediately after conflict. RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation (Cords and Aureli 2000). Relationship security is the degree to which the nature of a relationship will not change in response to conflict, i.e. the relationship is resistant to damage. UR has been most widely studied in macaques (Aureli et al. 1989; Aureli and van Schaik

1991b; Aureli 1997). After reconciliation, the rate of recipient self-scratching, a behavioral indicator of anxiety, decreases more rapidly than in the absence of reconciliation. Schaffner et al. (2005) reported support for RS; captive red-bellied tamarins do not reconcile conflicts and conflict does not appear to disturb relationships between individuals—they resumed pre-conflict activities immediately without any apparent change in tolerance. Schaffner et al. suggest that cooperative breeding and the very strong predation pressure tamarins experience in the wild may have selected for such a high degree of intragroup co-dependence, resulting in relationship security that daily aggression does not disturb.

Third-Party Affiliation: Consolation

Reconciliation is not the only post-conflict outcome open to former opponents. Consolation, third-party affiliation with the recipient of aggression, can be offered to or solicited by the recipient of aggression. The function of consolation is still unclear. Fraser et al. (2008) reported that consolation reduced post-conflict anxiety in chimpanzees but this has not been demonstrated in most other studies testing for it (Aureli and van Schaik 1991b; Das 2000; Watts et al. 2000; Koski and Sterck 2007). Consolation has been reported in chimpanzees (de Waal and van Roosmalen 1979; Kutsukake and Castles 2004; but see Arnold and Whiten 2001; Fuentes et al. 2002), bonobos (Clay and de Waal, 2013; Palagi et al. 2004), mountain gorillas (Watts 1995; Cordoni et al. 2006), and stumptailed macaques (Call et al. 2002).

SECTION II: Bonobos

Wild bonobos are only found in a limited area south of the Zaire River in the Democratic Republic of Congo (Kano 1980) and have been studied at five field sites:

Wamba (Kano 1980), Lomako (Badrian and Badrian 1984; White and Lanjow 1992), Lukuru (Meyers-Thompson 2002), Lui Kotal (Hohmann and Fruth 2003), and Lac Tumba (Inogwabini et al. 2008). Bonobos live in multimale-multifemale groups composed of natal males and transfer females (Kano and Mulavwa 1984; Furuichi 1997) and have a fission-fusion social structure similar to chimpanzees (*Pan troglodytes*) (Goodall 1968; Nishida 1968), although bonobos are more likely to be found in mixed sex groups and to stay in large aggregations for long periods of time (Kano 1980; Kuroda 1980; Badrian and Badrian 1984). Bonobos are generally less aggressive and excitable than chimpanzees and are characterized by more relaxed and tolerant social interactions (Kano 1980; Kuroda 1980; Badrian and Badrian 1984; Kano and Mulavwa 1984; de Waal 1997; Stevens et al. 2005a; Paoli et al. 2006; Palagi and Paoli 2007), including less emotional reactivity (Hare et al. 2007) and a more egalitarian, relaxed dominance hierarchy (Vervaecke et al. 1999; Vervaecke et al. 2000), although a great deal of variation in the linearity of the hierarchy has been reported for captive populations (Stevens et al. 2007; Paoli and Palagi 2007; Jaeggi et al. 2010). Aggression is most common among males and male-male dyads are the least affiliative, while aggression among females and between females and males is relatively infrequent (Kano 1980; Kuroda 1980; Badrian and Badrian 1984; Kano and Mulavwa 1984; ,1996; Parish and de Waal 2000) and females are more likely to aggress males than vice versa (Hohmann and Fruth 2003).

The Question of Female Dominance

Unlike the closely related chimpanzee, female bonobos form close relationships (Kano 1980; Kuroda 1980; Kano and Mulavwa 1984; Parish 1995, 1996;

Parish and de Waal 2000; de Waal 2001) and play more than other adult dyads (Palagi 2006; Palagi and Paoli 2007). Females are generally dominant to males (Kano and Mulavwa 1984; de Waal 1987; Furuichi 1997; Vervaecke et al. 1999,2000; Parish 1995, 1996; de Waal 2001; Paoli et al. 2006; Stevens et al. 2007), although there is a great deal of debate over the nature and degree of female dominance (Stanford 1998; Stevens et al. 2007; White and Wood 2007) and the relative importance of female-female relationships (Hohmann and Fruth 2002; Stevens et al. 2006). While female affiliation, coalitions, and co-attacks against males are commonly reported (Kano 1980; Kuroda 1980; , 1996; Parish and de Waal 2000), some studies report that some female-male relationships are more affiliative than some female-female and that females associate preferentially with males (Wamba: Hohmann and Fruth 2002; 5 captive colonies: Stevens et al. 2006).

Debates over female dominance appears to be related to the nature of female-female relationships. de Waal and Parish (de Waal 1987; Parish 1995,1996; Parish and de Waal 2000) argue for female dominance over males and present data from a captive colony with a high degree of affiliation among females. Since the females formed particularly close relationships, they were more likely to support one another in agonistic contests against males. Stevens et al. (2006) presented comparative data from 5 captive colonies in European zoos indicating that some female-female relationships were stronger than female-male relationships, but others were no stronger than intersexual bonds, which is consistent with wild data from Lomako (Hohmann and Fruth 2002). Stevens et al. (2007a) also reported that females occupied the highest ranks in the hierarchy but that some males dominated some females. The

low-ranking females were typically young, nulliparous, and recently introduced which would put them in a similar position as immigrant females in the wild who are low-ranking (Furuichi 1997). White and Wood (2007) characterized the hierarchy at Lomako as male deference in feeding contexts but as male dominant in dyadic intersexual interactions; females did consistently exhibit feeding priority but were not socially dominant to males.

It seems that the nature of bonobo hierarchies is highly flexible and responsive to both ecological and social conditions. Captive studies report results consistent with wild studies. Male-male relationships are always reported to be the weakest and males very rarely form coalitions or aggress females (Kano 1980; Kuroda 1980; Badrian and Badrian 1984; Kano and Mulavwa 1984; Ihobe 1992; Hohmann and Fruth 2003), which is particularly surprising since males are natal and more likely to be kin. Brothers do not preferentially associate with one another when association rates are controlled for mother-son interactions (Ihobe 1992). In fact, during periods of food scarcity it is males who are more likely to disperse from the larger social group than females (White 1998), quite the opposite of the pattern expressed in chimpanzees (Goodall 1986; Pepper et al. 1999). Female-female and female-male relationships are typically very strong, although in the wild female-male relationships are reported to be stronger (Kano 1980; Kuroda 1980; Badrian and Badrian 1984; Kano and Mulavwa 1984; Hohmann and Fruth 2003).

The degree of female dominance de Waal and Parish (de Waal 1987; Parish 1995,1996; Parish and de Waal 2000) report may be influenced by the nature of captivity and the composition of the group. The captive group at the San Diego Wild

Animal Park during de Waal's (1987) study was divided into 3 small sub-groups and during Parish's (1996) work, the study group of 13 had been recently formed from those subgroups. In the wild, immigrant females seek affiliative contacts with resident females in order to facilitate social integration (Furuichi 1989; Idani 1991). While these immigrant females are low-ranking, the fact that most of the females at San Diego would be engaging in "immigrant" behavior may have contributed to their greater tendency to form alliances with one another. Paoli et al. (2006) and Stevens et al. (2007) characterize the hierarchy as nonexclusive female dominance, which seems particularly appropriate since it is consistent with wild and captive reports.

The Dominance Hierarchy

The emphasis on dominance in the previous section belies the relative unimportance of dominance interactions in bonobos. As noted, bonobo dominance hierarchies are relatively relaxed and not strictly enforced, and bonobos likely do not possess formal dominance indicators (Stevens et al. 2005a). Dominance contests occur most often during feeding (Vervaecke et al. 1999; Vervaecke et al. 2000b). Higher-ranking individuals have priority of access to resources but are also highly tolerant of food stealing by lower-ranking individuals (de Waal 1987), although Jaeggi et al. (2010) recently reported that food sharing in 4 captive groups of bonobos was less tolerant and more unidirectional than in 3 captive groups of chimpanzees. The linearity of bonobo hierarchies is highly variable and dependent on group characteristics (Paoli et al. 2006) and measures used (Stevens et al. 2007). Linear hierarchies have been reported in wild (Wamba: Ihobe 1992) and captive groups (Planckendael and Stuggart: Franz 1999; Planckendael: Vervaecke et al. 1999;

Cincinnati: Fortunato 2009; Planckendael, Apenheul, Twycross, Wuppertal: Jaeggi et al. 2010). Vervaecke et al. (1999) reported linearity but the directionality of outcomes in competitive contests was often inconsistent in dyads. Additionally, some authors separate the female and male hierarchies, reporting unclear relationships or non-linearity for females and linearity for males (Wamba: Furuichi 1997; Apenheul: Paoli et al. 2006). Paoli et al. (2006) also reported an intersexual hierarchy with clear evidence for the presence of an alpha female and an alpha male but unclear dominance relationships for mid- or low-ranking individuals. Stevens et al. (2007) reported linear intersexual hierarchies for 6 captive groups but that the male hierarchies were all steeper than the female except for one.

Grooming tends to go up the hierarchy but rank effects on grooming received are confounded by age and sex; older individuals and females tend to have higher ranks than younger individuals and males and are groomed more frequently (Vervaecke et al. 1999, 2000b). Male rank is also heavily dependent on maternal support (Ihobe 1992). Individuals may exchange grooming for support (Vervaecke et al. 2000b), although Stevens et al. (2005b) reported that grooming was interchanged for food sharing more often than support received. The steepness of the hierarchy also influences the distribution of grooming; in groups with steep hierarchies, grooming tends to be more unidirectional whereas in shallower hierarchies grooming is more reciprocal (Stevens et al. 2005b). The relationship between the hierarchy and grooming is highly variable between groups.

While the directionality of grooming is not a reliable predictor of rank, peering (Johnson et al. 1999; Vervaecke et al. 1999; Stevens et al. 2005a) and fleeing during

agonistic interactions (Vervaecke et al. 1999) are highly unidirectional; individuals tend to peer up the hierarchy and tend to flee during agonism if they are lower in rank. Peering is a stereotyped behavior observed in bonobos in which one individual intently stares at the mouth of another while avoiding eye contact (Johnson et al. 1999). It is derived from infantile begging, although in adult animals it rarely ends in food transfer. Since rank and age are correlated, peering tends to be directed from younger animals to older ones and appears to be an affiliative behavior that increases tolerance by older or dominant individuals (Vervaecke et al. 2000), occasionally initiates affiliative interactions, and may serve to help immigrant females integrate. Stevens et al. (2005a) suggest that peering may also be about expression of interest in an object, as well as food, which could help explain instances of down-the-hierarchy peering.

Social Relationships

The dramatic differences between chimpanzees and bonobos in the strength of inter- and intrasexual social relationships are likely due to ecological variation. The relative lack of seasonality in ripe fruit availability for bonobos relative to chimpanzees (Badrian and Badrian 1984; Kano and Mulavwa 1984; Malenky and Wrangham 1994; Doran et al. 2002) reduces intragroup, particularly female intrasexual, competition for resources (Wrangham 1980). This is consistent with variation in relationship strength among chimpanzee field sites. Where chimpanzees do not experience the dramatic seasonality common to most chimpanzee sites researchers report stronger intersexual and female intrasexual relationships (Bossou: Sugiyama 1988; Sakura 1994; Tai: Boesch 1991, 1996; Boesch and Boesch-

Achermann 2000). Similarly, captive female chimpanzees are reported to be more gregarious and form closer relationships compared with wild ones due to reduced feeding competition (Preuschoft et al. 2002).

Bonobo social interactions often include sexual behavior with non-reproductive functions (de Waal 1987). Sexual contacts occur in virtually all partner combinations possible and in a variety of positions including ventro-ventral copulations between females and males (Kano 1980; Kuroda 1980; Badrian and Badrian 1984; de Waal 1987; Hohmann and Fruth 2000), ventro-ventral genital rubbing among females (“g-g rubbing”: Kano 1980; Hohmann and Fruth 2000), and genital contact among males (“rump rubbing”: Kano 1980), although this occurs much less frequently than female-male or female-female sexual contacts (Thompson-Handler et al. 1984). Kuroda (1980) proposed the “g-g rubbing hypothesis” suggesting that it functions to reduce tension, increase tolerance, and facilitate non-aggressive food transfers. Sociosexual behavior is common among bonobos during times of potential tension, particularly during feeding competition, and its occurrence promotes tolerant co-feeding (de Waal 1987) in all age-sex class dyads. Paoli et al. (2006) reported that genital contacts among females were not correlated with grooming or contact sitting in a captive colony and suggested that it may be employed as a tool for social assessment to determine a willingness to interact fairly.

Conflict and Post-Conflict Behavior in Bonobos

Among bonobos, male-male conflicts are most frequent and are most likely to occur over competition for access to estrous females (Hohmann and Fruth 2003). Female-male aggression is rarely initiated by males and occurs more often than

female-female aggression. Female-female aggression may take the form of mating harassment, with the aggressing female usurping the male from the victim. Feeding competition is also common among bonobos (de Waal 1987). While bonobos likely express agonism in competition over preferred social partners, which has been reported in chimpanzees (Wittig and Boesch 2003), it has not been explicitly studied.

Postconflict behavior in bonobos is not as well studied as that of chimpanzees. There have been four systematic studies of postconflict reconciliation in bonobos (Clay and de Waal, 2013; Hohmann and Fruth 2000; Palagi et al. 2004; Fortunato 2009), although postconflict and conflict management behaviors have been described elsewhere (de Waal 1987; Palagi et al. 2006). As previously noted, bonobos use sociosexual behaviors to reduce tension, particularly in feeding contexts (Badrian and Badrian 1984; de Waal 1987; Parish 1995; Hohmann and Fruth 2000). de Waal (1987) reported that the frequency of agonistic interactions increased during feeding and remained elevated immediately following feeding in a captive group of bonobos. Along with this increase in agonistic interactions came an increase in sociosexual and other nongrooming affiliative behaviors, suggesting a tension regulation function.

de Waal (1987) also reported that affiliative and sociosexual behaviors increased in the period immediately following conflicts relative to pre-conflict rates with 48% of conflicts followed by sociosexual behaviors. Aggressors were responsible for initiating at least 50% of all postconflict affiliative interactions and were significantly more likely to initiate reconciliation following contact aggression relative to “silent runs” and “non-contact” aggression. Grooming does not appear to play as prevalent a role in conflict management in bonobos as might be expected given the

central role of grooming in chimpanzee reconciliation (de Waal and van Roosmalen 1979; Preuschoft et al. 2002; Wittig and Boesch 2003). deWaal (1987) suggests that grooming may play a more important role in the long-term maintenance of relationships in bonobos but that sociosexual behaviors are more important in conflict management.

Hohmann and Fruth (2000) investigated the occurrence of reconciliation among female bonobos in a study testing hypotheses about the function of ventro-ventral mounting behavior (g-g rubbing) in an unprovisioned population living at Lomako. They reported that g-g rubbing functions to reconcile conflicts and regulate tension among females. Of 466 genital contacts between mature females, 30 were preceded by an agonistic encounter and in 376 contacts no agonistic encounter occurred in the preceding 15 minutes. They also reported that the frequency of g-g rubbing in the 15 minutes post-conflict was higher than in the 15 minutes pre-conflict (0.29 v. 0.07, respectively). This indicates that genital contacts are used PC, but that the majority of them occur in other contexts. Consistent with other research with bonobos, these females used sociosexual behaviors to diffuse the tension that arises in the presence of monopolizable resources.

Palagi et al. (2004) examined reconciliation and consolation in a captive group of bonobos housed at the Apenhul Primate Park, The Netherlands following the standard post-conflict/matched control (PC-MC) protocols (de Waal and Yoshihara 1983). Using PC-MC, the timing of first affiliative contact between former opponents post-conflict is compared to the timing of their first affiliative contact in a matched control period. If contact occurs earlier PC than MC, the pair is considered attracted

and the conflict reconciled. For consolation, the timing of first PC and MC affiliative contacts between the victim of aggression and a third party are compared. They also collected data on association rates in each session. A total of 251 agonistic dyadic contacts were recorded and categorized according to their intensity: level 1—threat or chase (51%); level 2—chase with submission (15%); and level 3—aggressive contact (34%). Of the 251 conflicts recorded, 167 PC-MC were collected. Palagi et al. (2004) reported a mean individual CCT² = 35.6%. If only the adult dyads are considered, the mean individual CCT = 24.8%. In female-female dyads the CCT was above the group average at 54.7%. Palagi et al. reported that their study found good support for VR. In addition to the fact that females had the highest CCT and bonobos are female-bonded, relationship quality had a significant influence on the occurrence of reconciliation. In adult friend dyads, the mean CCT = 53.3% and for weak dyads the mean CCT = 5.3%. Consolation occurred and was both solicited and offered: solicited TCT³ (third-party conciliatory tendency) = 22.8% for all individuals and = 10.9% for only adults; offered TCT = 21% and 20.6%.

Fortunato (2009) reported on 106 PC-MC pairs from a study on the captive bonobos at the Columbus Zoo, which includes former San Diego Zoo residents. This group of bonobos differs from the Apenhuel group in that they are managed in a simulated fission-fusion style which may more accurately reflect wild association patterns. Of the 12-17 individuals housed at Columbus during the 2 study periods, only the 8 adolescents and adults were included in the analysis. She defined intensity

² CCT = Corrected Conciliatory Tendency (Veenema et al. 1994). The CCT is a measure of the rate of reconciliation that corrects for differences in baseline rates of dyadic affiliation.

³ TCT = Triadic Contact Tendency (Call et al. 2002). The TCT is a measure of the rate of consolation that corrects for differences in baseline rates of dyadic affiliation.

levels slightly differently than Palagi et al. (2004): level 1—threat or charge, no contact (48%); level 2—single aggressive contact (45%); level 3—multiple aggressive contacts (6%). The mean individual CCT = 40% but there was no correlation between relationship quality and CCT or sex of opponents and CCT, contrary to Palagi et al. (2004) and the predictions of VR. The mean individual solicited TCT = 9% and the mean individual offered TCT = 35%. Fortunato reported that relationship quality between the third-party and the recipient of aggression was significantly correlated with offered consolation. Fortunato suggested that RS may be a more appropriate explanation for the occurrence of reconciliation in this group of bonobos and that this is likely related to the simulated fission-fusion management style, i.e. both high and low quality dyads are motivated to reconcile given the more insecure nature of their relationships (association patterns are subject to more variability).

Clay and de Waal (2013) reported support for VR in a study of the bonobos living at the Lola Ya Bonobo Sanctuary, Kinshasa, Democratic Republic of Congo. Their primary focus was factors associated with consolation but they reported a mean group CCT = 22.31%. The mean TCT was 34.8%. Consolation was more likely to occur after the victim had redirected aggression against another individual and third-parties were more likely to console close associates. They also reported that juveniles were more likely to be consolers than adults and that mother-reared juveniles consoled more frequently than orphaned juveniles.

SECTION III: Overview of This Study

Data were collected August 5, 2009 – December 16, 2010 at the San Diego Zoo. During the study period, the San Diego Zoo bonobo colony was composed of 10

individuals: 3 adult females, 2 adult males, 1 adolescent female, 1 juvenile female, 1 juvenile male, 1 infant female, and 1 infant male (see Table 1.2). The bonobos have indoor and outdoor enclosures and cannot move between them at will. All observations took place at the outdoor enclosure (560m²). The bonobos came out in two groups: the “morning” group approximately 9:00a.m.-12:30p.m. and the “afternoon” group approximately 12:30-4:30p.m in sub-groups of varying composition to simulate fission-fusion. Sub-group composition was also influenced by keeper and veterinary staff decisions to separate two adult females (I, O) from one of the adult males (G) after on-going severe aggression that resulted in serious injury to the adult male. Both groups had access to water and a variety of foods distributed throughout the enclosure daily by keepers, as well as liquefied foods in an artificial termite mound, and scheduled daily feeding from keepers at approximately 11:00a.m. (10:00a.m. August 2009 only) for the morning and 2:00p.m. for the afternoon. Observations took place in the morning and afternoon.

This research project grew out of long-term studies with the San Diego bonobos directed by Christine Johnson, including studies on the function of peering (Johnson et al. 1999), the dynamics of social attention and gaze interactions (Johnson and Karin-D’Arcy 2006), and the development of gestures and coordinated social interactions (Hutchins and Johnson 2009). Students enrolled in Christine Johnson’s COGS 160 Videography Studies Laboratory participated in data collection after intensive training by the author, Prof. Johnson, and experienced interns.

Questions and Predictions

CHAPTER ONE: Testing Valuable Relationships

VR predicts that dyads with more valuable relationships will be more likely to reconcile their conflicts and console one another than dyads with less valuable relationships. Alternatively, RS predicts that dyads with very secure relationships will be less likely to reconcile and that insecure dyads will be more likely to reconcile. VR has been overwhelmingly supported in the literature, however, Fortunato (2009) did not find support for VR, suggesting RS may be more appropriate for describing the post-conflict behavior of the Columbus Zoo bonobos. If high value dyads do not reconcile conflicts, RS would be supported here. Previously, support for RS has been demonstrated only in a cooperatively breeding primate (Schaffner et al. 2005) but bonobos are not cooperative breeders, requiring another possible explanation for why RS might be more appropriate for bonobos than other species. If RS is supported here, it could be influenced by the relative predictability and regularity of social life that characterizes captivity, along with the relatively low costs of conflict and feeding competition, i.e. no individual will go without resources regardless of competition.

CHAPTER TWO: Testing Relationship Repair

RR predicts that conflict damages social bonds and that reconciliation serves to repair those bonds (Koyama 2001). BI predicts that reconciliation serves only to signal the end of the conflict and resumption of tolerance and that there are no long-term consequences of reconciliation for relationships (Silk 1996). RS predicts that when relationships are very secure they are resistant to damage and will not suffer long-term consequences in the absence of reconciliation. It is expected that RR will be supported here, i.e. unreconciled conflicts will be followed by a long-term decrease in affiliation and/or increase in aggression, whereas reconciled conflicts will see no significant

long-term change in the rate of affiliation or aggression. No long-term difference in the rate of affiliation and/or aggression following reconciled v. unreconciled conflicts would support BI and would also be consistent with RS. It may be possible to differentiate between BI and RS if the long-term consequences of conflict and reconciliation differ based on the differential value of relationships or if low value dyads reconcile at a rate higher than expected.

CHAPTER THREE: Third Party Interactions with Aggressors during Conflict

Most research on conflict management has focused only on the post-conflict period and that was the original intention of this study. However, observations of third-party initiated affiliation with aggressors during the course of the conflict itself prompted me to collect data on those interactions and test their possible functions. Third-party initiated interactions with aggressors have been reported in monkeys and apes and are generally discussed within a framework of “policing” behavior that functions to promote social stability (Flack et al. 2005), although other functions have also been proposed. The dominance assurance hypothesis suggests that third party intervention functions to reinforce the third party’s dominance status “by interfering with others’ efforts to rise up the social hierarchy” (Beisner and McCowan 2013:2). The mating benefits hypothesis suggests that third party intervention functions to increase the likelihood of the third party gaining mating access to one or both of the conflict participants (Beisner and McCowan 2013). The self-protection hypothesis suggests that third party intervention functions to reduce the likelihood that aggressors will direct further aggression at the third party (von Rohr et al. 2012). These four hypotheses are tested here.

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CHAPTER 1

Conflict Management in Captive Bonobos (*Pan paniscus*): Testing the Valuable

Relationships Hypothesis

Abstract

Conflict management, particularly reconciliation and consolation, has been studied extensively in primates and other social animals. However, bonobos (*Pan paniscus*), remain relatively understudied. The Valuable Relationships hypothesis (VR) has been the dominant framework for understanding postconflict behavior (PCB) and is generally well-supported. It argues that if conflict damages social bonds and postconflict affiliation serves to repair those social bonds, then individuals with valuable relationships (kin, close associates) will be more likely to reconcile after conflicts. The primary purpose of this study is to provide an additional test of VR in captive bonobos. PCB in bonobos has been studied using standard methods (postconflict-matched control, PC-MC) in three other studies, two reported support for VR and one supported the Relationship Security hypothesis (RS), which argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and would not require reconciliation, whereas insecure relationships (of high or low value) would be more likely to be damaged by conflict and therefore more likely to be reconciled. The present study explored reconciliation and consolation using the PC-MC method, examining how relationship quality, age-sex class, conflict context, and conflict intensity influence the tendency to engage in reconciliation and/or consolation. VR is not supported by this study: there is no clear relationship between relationship quality, age-sex class, conflict context, or conflict

intensity and the occurrence of reconciliation or consolation. Furthermore, the mean of individual conciliatory tendencies (CCT), 10.11%, is dramatically lower than other studies of bonobos and most studies of chimpanzees. Aggressors and recipients of aggression were equally likely to initiate reconciliation, as were females and males. The results presented here are more consistent with RS than VR. The high security of relationships in this group is likely influenced by their history and demographics.

Introduction

Group living in primates evolved as a response to ecological and/or predation pressures, particularly for females (van Schaik, 1983; Wrangham, 1980). While living in groups provides a number of benefits (Isbell and Young, 2002; Sterck, et al. 1997; van Schaik, 1983; Wrangham, 1980), it also entails significant costs that emerge from conflicts of interest over ecological and social resources (Gowaty, 1996; Parker, 1979; Trivers, 1972; Walters and Seyfarth, 1987). Traditionally, conflict has been viewed as an anti-social behavior leading to the disintegration of social bonds rather than as one component of negotiating the costs and benefits of group living (de Waal, 1996, 2000).

Postconflict behavior (PCB) has been a major focus of nonhuman primate research since de Waal and van Roosmalen's (1979) groundbreaking study on reconciliation and consolation in captive chimpanzees. Reconciliation, postconflict affiliation between former opponents, has been demonstrated in virtually all of the species in which it has been studied (Aureli and de Waal 2000), including non-primates (domestic cat: van den Bos 1997; domestic goat: Schino 1998; spotted hyena: Wahaj et al. 2001; bottlenose dolphin: Weaver 2003; domestic dogs: Cools et al.,

2007; rooks: Seed et al., 2007; wolves: Cordoni and Palagi 2008; horses: Cozzi et al. 2010; corvids: Logan et al., 2012).

The Valuable Relationships hypothesis (VR; Table 1.1a) has been the dominant model for explaining the function and occurrence of reconciliation (Aureli and de Waal, 2000; de Waal and van Roosmalen, 1979; but see Silk, 1996, 2002 and Watts, 2006). VR argues that post-conflict affiliation repairs damage to social bonds and, therefore, dyads with valuable relationships (kin, close associates) should be more likely to reconcile after conflicts. Thus, testing VR has relied on examining the distribution of reconciliation across dyads. Relationships can be assessed using 3 interrelated dimensions: value—fitness benefits derived from the relationship (access to resources or agonistic support); compatibility—overall tenor of interactions (affiliation); and security—resistance of the relationship to change (predictability of interactions) (Cords and Aureli 2000)—that likely influence the costs of conflict. Studies of VR tend to use the term “value” to refer to what Cords and Aureli (2000) separate into compatibility and value. The compatibility component is determined, then, by rates of affiliation and the value component is based on the value of partners in specific kinship or sex classes derived from predictions from socioecology. Strong support for VR has been demonstrated in the literature: kin tend to reconcile more than non-kin, close associates more than non-associates, and coalition partners more than non-partners (Aureli and de Waal, 2000; Watts, 2006). Some authors use the Good Relationships hypothesis (GR: Aureli et al. 1989; Palagi et al. 2004) to refer to a focus on relationship compatibility separate from value as defined by fitness benefits. Since most studies consider value and compatibility together, only VR will be used here.

A significant modification to VR is the Relationship Security hypothesis (RS: Cords and Aureli, 2000; Table 1.1b), which focuses on the third relationship dimension. RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships, regardless of value, may not be damaged by conflict and would not require reconciliation, whereas insecure relationships would be more likely to be damaged by conflict and therefore more likely to be reconciled. The role of relationship security was first suggested by Cords and Aureli (1993) in work with peer-housed juvenile long-tailed macaques who were more likely to reconcile with non-kin than kin, perhaps because the kin relationships were more secure. Schaffner et al. (2005) report captive red-bellied tamarins do not reconcile conflicts and conflict does not appear to disturb relationships between individuals; monkeys resumed pre-conflict activities immediately without any apparent change in tolerance. The authors suggested that cooperative breeding and the very strong predation pressure tamarins experience in the wild may have selected for such a high degree of intragroup co-dependence, relationship security, that daily aggression does not disturb it.

If conflict damages relationships, it is possible that factors other than relationship quality may also influence the occurrence of reconciliation. Other proximate factors that may be correlated with PCB include intensity and context (Wittig and Boesch, 2003). Chimpanzees are more likely to engage in reconciliation after low intensity conflicts (Arnold and Whiten, 2001; Wittig and Boesch, 2003) and high intensity conflicts are more likely to be consoled or followed by continued aggression (Wittig and Boesch, 2003). Wittig and Boesch (2003) suggest that while high intensity conflicts may be more damaging to relationships, recipients of

aggression may be less willing to approach the initiator after these because of the increased likelihood of continued aggression. Similarly, Koski et al. (2007) reported that low intensity female-male conflicts were more likely to be reconciled than high intensity, although they did not report any significant predictors for consolation. Results from other species (long-tailed macaques: Aureli, 1992; baboons: Castles and Whiten, 1998; Moor macaques: Matsumura, 1996) have shown that reconciliation is less likely after food-related conflicts, suggesting that food conflicts are not as damaging to relationships as social conflicts. However, Wittig and Boesch (2003) reported no difference in rate of chimpanzee reconciliation after food or social conflicts suggesting it is just as beneficial for partners to restore tolerance around resources as it is to restore relationships.

Other functions of reconciliation include, or have been suggested to include: reducing post-conflict stress (Aureli et al., 1989; Aureli and van Schaik, 1991a,b; Koski et al., 2007); reducing the likelihood of renewed aggression (Aureli and van Schaik, 1991a; Wittig and Boesch, 2003); restoring tolerance (Castles and Whiten, 1998; Silk 1996; Watts, 1995; Wittig and Boesch, 2005); and facilitating peaceful simultaneous exploitation of resources (Cords, 1992; Cords and Thurnheer, 1993).

Consolation, third-party initiated post-conflict affiliation with victims, although not as widely or consistently, has been reported in the great apes (bonobos: Palagi et al., 2004; chimpanzees: Cordoni et al., 2006; de Waal and van Roosmalen, 1979; Kutsukake and Castles, 2004; but see Arnold and Whiten, 2001; Fuentes et al., 2002; Watts, 1995), stumptailed macaques (Call et al. 2002), domestic dogs (Cools et al., 2007), and corvids (Seed et al., 2007; Fraser and Bugnyar, 2010; Logan et al.,

2012). The function of consolation is still unclear. It has been hypothesized to function as a mechanism for reducing post-conflict stress (Fraser et al., 2008), but this has not been demonstrated in several studies testing for it (Aureli and van Schaik, 1991b; Das, 2000; Koski and Sterck, 2007; Watts et al., 2000). It may also function as a mechanism for indirect reconciliation through affiliation with the former opponent's kin (Aureli and van Schaik, 1991a; de Waal and Aureli, 1996; Watts et al., 2000; Wittig and Boesch, 2003; Wittig et al., 2007; but see Koski and Sterck, 2007 and Palagi et al., 2004). Consolation may also serve as a signal of investment in a relationship by a third party and sensitivity to the emotional state of others (Clay and de Waal, 2012; de Waal and Aureli, 1996).

A great deal is known about PCB in chimpanzees but bonobos are understudied and, given the important role of the comparative method for constructing models of the evolution of human behavior (Moore, 1996) and the over-emphasis on a chimpanzee model (Parish and de Waal, 2000; Zihlman, 1996), it is essential to expand our understanding of our other closest living relative. Bonobos, while similar to chimpanzees in their basic social structure, are generally less emotionally reactive (Hare, 2006; Hare et al., 2007), less aggressive, and have more relaxed social interactions (Hare et al., 2012; Kano, 1980; Kuroda, 1980), including a relaxed dominance hierarchy (Kuroda, 1984; Vervaecke et al. 1999) with at least some degree of female dominance (de Waal, 1987; Furuichi, 1997; Kano, 1998; Parish and de Waal, 2000; Stevens et al., 2007). Aggression is most common among males and male-male dyads are the least affiliative, while aggression among females and between males and females is relatively infrequent (Kano, 1980; Kuroda, 1980; Ihobe,

1992; Parish and de Waal, 2000). Bonobos use sociosexual behaviors to reduce tension, particularly in feeding contexts (de Waal, 1987) and to reconcile conflicts (Hohmann and Fruth, 2000).

There have been three systematic studies of PCB in bonobos (Clay and de Waal, 2012; Fortunato, 2009; Palagi et al., 2004) using the standard methods developed by de Waal and van Roosmalen (1979) and de Waal and Yoshihara (1983), although post-conflict and conflict management behaviors have been described elsewhere (de Waal 1987; Hohmann and Fruth, 2000; Parish, 1994). Palagi et al. (2004) examined reconciliation and consolation in a captive group of bonobos housed at the Apenhul Primate Park. They found support for VR: the overall rate of reconciliation was high and female-female dyads and dyads with close relationships had the highest rates of reconciliation. They also reported that consolation occurred at relatively high rates but they did not include data on variation in consolation based on relationship quality between the victim and third-party. Clay and de Waal (2012) also reported results consistent with VR with the bonobos at Lola Ya Bonobo Sanctuary: kinship and affiliation predicted reconciliation and consolars were more likely to have a close relationship with victims they consoled.

Fortunato (2009) reported very different results in her study of captive bonobos at the Columbus Zoo. This group is managed in a simulated fission-fusion style which may more accurately reflect wild association patterns. The overall rate of reconciliation was relatively high but there was no correlation between relationship quality or sex of opponents and the rate of reconciliation, contrary to VR. However, Fortunato did report that relationship quality between the third-party and the recipient

of aggression was significantly correlated with consolation. Fortunato suggested that RS may be a more appropriate explanation for the occurrence of reconciliation in this group of bonobos and that this is likely related to the simulated fission-fusion management style, i.e. both high and low quality dyads were motivated to reconcile given the more insecure nature of their relationships (association patterns are subject to more variability and less predictability).

The goals of the present study are to expand our knowledge of PCB in bonobos and to provide a further test of VR and RS and to examine the occurrence of consolation. VR will be supported if:

1. relationship value (fitness benefits) influences the tendency to reconcile, i.e. female-female dyads will be more likely to reconcile than female-male and male-male dyads and male-male dyads will be least likely to reconcile.
2. relationship quality (compatibility) influences the tendency to reconcile, i.e. dyads with higher rates of affiliation will be more likely to reconcile.
3. the intensity or context of a conflict influence the tendency to reconcile, i.e. high intensity and social conflicts will be more likely to be reconciled.
4. relationship value and/or quality influence the tendency for third parties to console recipients, i.e. third parties with high value and/or quality relationships with the recipient of aggression will be more likely to offer consolation to the recipient.

RS will be supported if:

5. relationship value and quality do not influence the tendency to reconcile.
6. the intensity or context of a conflict do not influence the tendency to reconcile.

7. relationship value and/or quality do not influence the tendency for third parties to console recipients.

Methods

Data were collected August 5, 2009 – December 16, 2010 from the bonobo (*Pan paniscus*) colony at the San Diego Zoo. The colony was composed of 10 individuals (Table 1.2). The bonobos have indoor (off exhibit) and outdoor (560m²) enclosures and cannot move between them at will. All observations took place at the outdoor enclosure. The bonobos came out in two groups of varying composition (Table 1.2): morning, approximately 9:00a.m.-12:30p.m., and afternoon, approximately 12:30-4:30p.m. Sub-group composition varied to simulate fission-fusion but was also influenced by keeper and veterinary husbandry decisions and remained relatively stable over time. Both groups had access to water and a variety of foods distributed throughout the enclosure daily, liquefied foods in an artificial termite mound, and scheduled daily feeding from keepers at approximately 11:00a.m. and 2:00p.m.

Data Collection

Data were collected using instantaneous scan sampling and all occurrences sampling for conflicts (Altmann 1974). Scans were collected at 2-minute intervals and included inter-animal distances (IADs) and social behavior for all visible individuals (Table 1.3). A total of 16,888 behavior scans were collected (562.93h) over 226 days.

When conflicts occurred, scan collection stopped and behavior was recorded using a digital voice recorder (DVR) to allow detailed collection on the initiator and recipient of aggression during and after the conflict. The conflict data include:

initiator, recipient, intensity (Table 1.3), context (Table 1.3), third-party contacts, and duration of aggression. The end of a conflict was determined to be after the last aggressive act as long as aggression did not resume during the 10 minute PC collection. Collecting the data with the DVR also enabled collecting data on simultaneous or co-occurring conflicts; incompletely described conflicts were discarded (N=84).

After the conflict ended, data collection switched to the postconflict-matched control method (PC-MC: de Waal and Yoshihara 1983). The recipient of aggression was the focal but both opponents were tracked. The PC data include: type and timing of the first friendly interactions among the former opponents and/or between a former opponent and a third party. On the next day possible, at about the same time of day as the conflict, the 10-minute MC collection period occurred. The MC collection was identical to the PC collection with exception of the preceding conflict and only concerned the recipient of aggression. MC collections always took place within 1 week of the PC collection.

Research Interns

Scan data were collected by the author and a group of research interns participating in COGS 160 Videography Studies Laboratory at UCSD under the guidance of Prof. Christine Johnson. All interns underwent extensive training in bonobo behavior and data collection methods with Prof. Johnson, the author, and experienced interns. Students had to pass an inter-observer reliability test (agreement at least $K = 83\%$) to participate in data collection. All conflict and PC-MC data were collected by the author.

Data Analysis

Complete PC-MC data were collected on 313 conflicts and analyses were carried out at the individual, dyadic, and group levels. Twenty-eight of 45 possible dyads had at least one conflict. Conflicts were divided by relationship quality (RQ—discussed below), sex of dyad, age of dyad (adult, immature, mixed), intensity, and context; a z-test for proportions was used to test the relationship between each of these factors and the occurrence of conflict. To determine the proportion of conflicts by sex or age of the dyad, the number of conflicts in each sex or age class was divided by the number of behavior scans in which dyads of each type were observed together. The adolescent was classified as an adult and the 2 juveniles and 2 infants were combined as immatures. FM and mixed age conflicts were also separated by initiator (F or M, adult or immature) and a z-test for proportions was used to test which age or sex class was more likely to initiate aggression. All categorical measures are adjusted for the proportion of scans during which a particular dyad or dyad type are possible.

Reconciliation

Reconciliation occurs if the former opponents engage in a friendly interaction after the conflict (de Waal and van Roosmalen 1979; de Waal and Yoshihara 1983). In order to control for baseline affiliation, Veenema et al. (1994) developed the corrected conciliatory tendency (CCT), which represents how conciliatory an individual or dyad is by considering how many conflicts are reconciled but controlling for baseline rates of affiliative interaction. To determine the CCT, the timing of affiliative PC contacts is compared to the timing of affiliative MC contacts. If contact occurs earlier PC than MC, that pair is considered “attracted” for that conflict but if the contact occurs earlier

MC than PC, the pair is considered “dispersed”. If no contact occurs in either period or the contact occurs at the same time, the pair is “neutral”. $CCT = (\text{attracted pairs} - \text{dispersed pairs}) / \text{total PC-MC pairs}$. To avoid pseudoreplication, only data on the recipient of aggression were used in this analysis. A comparison of the proportion of attracted and dispersed pairs for each individual was done using the Wilcoxon matched pair, signed-ranks test to test if reconciliation is used as a post-conflict strategy by these bonobos.

Dyadic relationship quality (RQ) was determined by calculating the total number of scans in which a dyad was grooming or sitting in contact divided by the total number of scans in which they *could* have been interacting [(groom + contact sitting)/total scans out together)].

To test the influence of RQ on reconciliation, RQ and CCTs were compared using a Wilcoxon matched pair, signed-ranks test following Palagi et al. (2004) and Fortunato (2009). Using this method, dyads were divided into two classes, close and weak, by calculating the mean RQ of all dyads and classifying dyads as close if their RQ was above the mean and weak if their RQ was below the mean. Then, for each individual, the mean CCT value for each of their close partners and weak partners was calculated separately. The Wilcoxon matched pair, signed-ranks test was then used to compare each individual’s mean CCT for the RQ classes.

Although the CCT is a measure of the *tendency* for an individual or dyad to reconcile, it is generally accepted that any PC affiliation *functions* as reconciliation (Veenema et al. 1994). Given this, for all remaining analyses the actual number of conflicts reconciled was used to examine the other correlates of reconciliation. To do

this, reconciled conflicts (followed by PC affiliation within 10 minutes) were divided by sex, age, intensity, and context. I also did an additional test of the relationship between RQ and reconciliation by dividing RQ into high, medium, and low categories and examining the number of conflicts reconciled by dyads in each category. A z-test for proportions was used to test relationships among each of the conflict characteristics and the occurrence of reconciliation. Reconciliations involving mixed sex/age class opponents were also separated by initiator (F or M, adult or immature) and a z-test for proportions was used to test which age or sex class was more likely to initiate reconciliation.

Consolation

Consolation, third-party initiated affiliation with victims, was determined for each individual and dyad using a method similar to determining reconciliation. Attracted, dispersed, and neutral pairs were determined based on the timing of PC affiliation between the recipient and a third-party and used to calculate the triadic contact tendency (TCT; Call et al. 2002).

Only 312 PC-MC pairs were used for the third-party analyses because one PC collection period was only 6 minutes, during which the former opponents reconciled, but all individuals were subsequently out of sight making that conflict ineligible for consolation observations. Additionally, 4 of 45 dyads were excluded from this analysis (GO, JO, MO, OY) because the dyad partners were never together during one of the other's conflicts. A comparison of the proportion of attracted and dispersed pairs for each individual was done using the Wilcoxon matched pair, signed-ranks test to test if consolation is used as a post-conflict strategy for these bonobos.

To test the influence of RQ on consolation, the same method was used as for reconciliation, a Wilcoxon matched pair, signed ranks test comparing TCT by close and weak RQ as per Palagi et al. (2004) and Fortunato (2009). The same analyses of other conflict variables and reconciliation were carried out using consolation. To do this, consoled conflicts (all conflicts followed by third party initiated PC affiliation) were divided by RQ (high, medium, low), sex, age, intensity, and context. To examine if consolation substitutes for reconciliation, I divided the reconciled conflicts into 2 categories, reconciliation occurring after consolation and reconciliation occurring without consolation, and the consoled conflicts into 2 categories, consolation after reconciliation and consolation without reconciliation. A z-test for proportions was used for all of these tests.

Analyses were performed using all dyads and adult only dyads. Results for both are only presented if they differ. Significance levels were all set at 5% and all tests were two-tailed. Statistical analyses were done in Excel.

Results

Conflicts

Complete PC-MC data were collected on 313 conflicts. Of 45 possible dyads, 17 (37.8%) had no observed conflicts. Conflicts were categorized by intensity level: level 1 = 54 (17.3%), level 2 = 60 (19.2%), level 3 = 199 (63.6%). Conflicts were also categorized by context: social = 61 (19.5%), aggress = 147 (47%), feeding = 50 (16%), other = 55 (17.6%). Conflicts were significantly more likely to be level 3 and to take place during on-going aggression (level 3: $z = 11.35$, $P = 0$; aggress: $z = 8.97$, $P = 0$). Conflicts were separated by sex of dyad: FF = 100, FM = 127, MM = 86. MM

dyads had significantly more conflicts than expected ($z = 7.322$, $P < 0.0001$), which is consistent with predictions that MM dyads tend to be more aggressive. FM dyads had significantly fewer conflicts ($z = -2.587$, $P = 0.004837$), which is consistent with FM dyads having high value relationships. FF conflicts were no different than the expected proportion ($z = -1.268$, $P = 0.1023$), which is inconsistent with the expectation that FF dyads would have low aggression because their relationships are of high value.

However, when looking only at adult conflicts, FF dyads had significantly fewer conflicts than expected ($z = -2.1881$, $P = 0.0143$) so the higher rate in all dyads is likely due to aggression involving immatures. There was no significant difference in the number of conflicts at each intensity level across sex classes ($\chi^2 = 7.3932$, d.f. = 4, $P = 0.1165$). With only adult dyads, there was a significant difference in the number of conflicts at each intensity level across sex classes ($\chi^2 = 15.1058$, d.f. = 4, $P = 0.0045$); pairwise comparisons show this is due to significantly fewer MM level 2 conflicts (FF v. MM 1 v. 2: $\chi^2 = 4.2067$, d.f. = 1, $P = 0.0402$; FF v. MM 2 v. 3: $\chi^2 = 12.0801$, d.f. = 1, $P = 0.0005$; FM v. MM 1 v. 2: $\chi^2 = 4.6972$, d.f. = 1, $P = 0.0302$; FM v. MM 2 v. 3: $\chi^2 = 12.9989$, d.f. = 1, $P = 0.0003$). Females initiated FM conflicts significantly more often than males, F-initiated = 87/127 (68.5%: $z = 4.171$, $P < 0.0001$) v. M-initiated = 40/127 (31.5%: $z = -4.171$, $P < 0.0001$). However, in adult only dyads there was no significant difference in sex of initiator (F = 27/50; M = 23/50).

Conflicts were also separated by age of dyad: adult = 196, immature = 42, mixed = 75. Adult conflicts were as expected given the statistical null hypothesis ($z = 1.273$, $P = 0.10$) and immature and mixed conflicts were significantly lower than expected (immature: $z = -5.62$, $P < 0.0001$; mixed: $z = 6.351$, $P < 0.0001$). Mixed age

conflicts were initiated by adults significantly more often than immatures (adult = 66: $z = 6.581$, $p < 0.0001$; immature = 9: $z = -6.581$, $p < 0.0001$). Only one immature initiated conflict against the adults, K, the daughter of the alpha female, and only against the adult males.

Reconciliation

Of 313 PC-MC pairs collected, 74 (23.6%) were followed by post-conflict affiliation between former opponents, i.e. were reconciled. For the group as a whole, 64 pairs were attracted, 43 dispersed, and 206 neutral, giving a group CCT = $(64 - 43)/313 = 6.71\%$. For each of the 10 individuals, their attracted, dispersed, and neutral pairs were sorted and the proportion of attracted and dispersed pairs for each individual were compared using the Wilcoxon matched pair signed-ranks test (Table 1.4a). All individuals had at least 1 attracted and 1 dispersed pair. The difference between individuals' attracted and dispersed pairs was not significant ($W = 10$, $N = 9$, $0.10 < P < 0.20$), which suggests reconciliation is not an important conflict management strategy for these bonobos. However, one individual (Y) had many fewer attracted than dispersed pairs; if Y is excluded from this analysis, the results are significant ($W = 3$, $N = 8$, $0.02 < P < 0.05$). The mean of individual CCTs = 10.11% ($\pm 24.28\%$). The mean CCT of only adult dyads with at least 1 conflict ($N = 11$) is 8.67%.

Occurrences of reconciliation were separated by whether the initiator of reconciliation was the aggressor or recipient of aggression (Table 1.4b). Thirty-eight reconciliations (56.7%) were initiated by the aggressor and 31 (46.3%) were initiated by the recipient of aggression (5/74 were simultaneously initiated). The difference was

not significant (aggressor-initiated: $z = 0.8156$, $P = 0.2074$; recipient-initiated: $z = -0.8156$, $P = 0.2074$).

Occurrences of reconciliation were separated by behavior used to reconcile conflict: groom, sex, play, peer, or other friendly contact. Of 74 reconciliations, 13 (17.6%) were groom, 1 (1.4%) was sex, 19/74 (25.7%) were peer, 15 (20.3%) were play, and 26 (35.1%) were other friendly contact. Other friendly contact was significantly higher than expected ($z = 3.2549$, $P < 0.0001$), sex was significantly lower than expected ($z = -4.0105$, $P < 0.0001$), and the other behaviors did not differ from the null hypothesis. The results were largely the same in adult only dyads, however, grooming was almost significantly higher than expected (28%, $z = 1.571$, $P = 0.0580$) and peering and sex were not used at all (peer: $z = -3.1436$, $P = 0.0008$; sex: $z = -3.1436$, $P = 0.0008$).

There was no relationship between RQ and CCT (group mean RQ = 7.51% +/- 7.79%; range 0 – 0.3222; Wilcoxon matched pair signed-ranks, $W = 22$, $n = 10$, $p > 0.2$). Five of 10 individuals had a higher CCT for weak relationships than close. Using adult only dyads also yielded insignificant results (Wilcoxon matched pair signed-ranks, $W = 6$, $n = 6$, $P > 0.2$). Using high, medium, and low RQ and all occurrences of reconciliation also yielded insignificant results for all dyads (high: $z = -0.6762$, $P = 0.2495$; medium: $z = 1.2584$, $P = 0.1041$; low: $z = -0.0222$, $P = 0.4911$) and adult only dyads (high: $z = -0.2974$, $P = 0.3831$; medium: $z = 0.3015$, $P = 0.3815$; low: $z = 0.2077$, $P = 0.4177$).

The reconciliation data were also separated by sex of the dyad and mean CCTs were calculated for each. For FF dyads, the mean CCT = 6.8%; FM = 5.4%; and MM

= -19.8%. FF dyads were the only category with a CCT higher than the group mean CCT (6.71%) but the difference between FF, FM, and MM CCTs was not significant (Kruskal-Wallis, $H = 0.945$, d.f., = 2, $P = 0.624$). When examining only adult dyads, FF dyads had a higher mean CCT (FF = 21.48%; FM = -3%; MM = 2.9%) but the difference between sex classes was not significant (Kruskal-Wallis, $H = 2.195$, d.f., = 2, $P = 0.334$).

Female-female dyads reconciled 26/100 conflicts (26%), FM dyads reconciled 35/127 conflicts (27.56%), and MM dyads reconciled 13/86 conflicts (15.1%) (Figure 1.1b). The FF and FM rates were not significantly different than the rate of reconciliation expected if dyad sex does not influence tendency to reconcile, while the MM rate was significantly lower than expected (FF: $z = 0.5549$, $P = 0.2894$; FM: $z = 1.0389$, $P = 0.1494$; MM: $z = -1.8609$, $P = 0.0313$). Among mixed sex dyads, reconciliation was female-initiated 22/35 times (62.9%) and male-initiated 13/35 (37.1%). Neither was significantly different from the expected distribution (F: $z = 1.5213$, $P = 0.0641$, M: $z = -1.5213$, $P = 0.0614$). Among adult only dyads, FF reconciled 20/77 (26%), FM reconciled 14/50 (28%), and MM reconciled 8/69 (11.59%). The MM rate was significantly lower than expected (FF: $z = 0.9721$, $P = 0.1655$; FM: $z = 1.1324$, $P = 0.1287$; MM: $z = -1.9908$, $P = 0.0232$). Among mixed sex adult dyads, reconciliation was female-initiated 9/14 times (64.29%) and male-initiated 5/14 (35.71%) times; neither was significantly different from the expected distribution (F: $z = 1.0690$, $P = 0.1425$; M: $z = -1.0690$, $P = 0.1425$).

Adult dyads reconciled 42/196 conflicts (21.4%), immature dyads reconciled 15/42 conflicts (35.7%), and mixed age dyads reconciled 17/75 conflicts (22.7%)

(Figure 1.1a). Immature dyads were the only age-class combination that reconciled significantly more conflicts than expected (adult: $z = -0.7294$, $P = 0.2329$; immature: $z = 1.8414$, $P = 0.0328$; mixed: ($z = -0.1988$, $P = 0.4212$). Adults initiated reconciliation with immatures 16/17 times (94.1%) and the immature initiated reconciliation only 1 time (5.9%). The difference was significant (adult-initiated: $z = 3.6380$, $P = 0.0001374$; immature-initiated: $z = -3.6380$, $P = 0.0001374$).

Occurrences of reconciliation were divided by intensity (1, 2, 3) and context (social, aggress, feeding, other) and tested for differences (Table 1.5a,b). The intensity and context of conflicts had no effect on the tendency to reconcile with all dyads. With adult only dyads, intensity has no effect on the tendency to reconcile but conflicts that took place during on-going aggression were significantly more likely to be reconciled ($z = 1.9599$, $P = 0.0250$) and feeding conflicts were significantly less likely to be reconciled ($z = -3.0290$, $P = 0.0012$).

Consolation

Of 312 PC-MC pairs included in this analysis, 147 (47.7%) conflicts were followed by third-party initiated affiliation with the recipient of aggression, i.e. consolation. For the group as a whole, there were 103 attracted pairs, 32 dispersed, and 177 neutral. This yields a group TCT = 22.76%. For each of the 10 individuals, their attracted, dispersed, and neutral pairs for consolation were sorted and the proportion of attracted and dispersed pairs for each individual were compared using the Wilcoxon matched pair, signed-ranks test (Table 1.6). All individuals had at least 1 attracted and 1 dispersed pair, except I and O who had no dispersed pairs and were excluded from this portion of the analysis. The difference between attracted and

dispersed pairs for each individual was significant ($W = 0$, $n = 7$, $P < 0.001$), suggesting consolation is a post-conflict strategy for these bonobos. The mean of individual TCTs = 24.85%. The mean TCT of adult dyads present for at least 1 of each other's conflicts = 2.86%.

Each individual's average TCTs were separated by close and weak partners and compared using the Wilcoxon matched pairs, signed-ranks test. The results were not significant for all dyads or adult only dyads. Using high, medium, and low RQ and all occurrences of consolation, high quality dyads consoled one another significantly more than expected (16.24%: $z = 3.2380$, $P = 0.0006$) and low quality dyads consoled one another significantly less than expected (6.74%: $z = -2.9050$, $P = 0.0018$) if RQ does not affect consolation. With adult only dyads, high quality dyads also consoled one another significantly more than expected (20.38%: $z = 2.8801$, $P = 0.0020$) and medium quality dyads significantly less often (1%: $z = -3.5179$, $P = 0.0002$).

An adult offered consolation to another adult significantly less often than expected (8/347 possible instances in which adults dyads were possible: $z = -5.0246$, $P < 0.0001$); an immature offered consolation to another immature significantly more than expected (36/162 possible instances: $z = 4.7969$, $P < 0.0001$); and consolation was offered in mixed dyads at the expected rate if age of dyad does not influence tendency to console (103/876 possible instances: $z = 1.0995$, $P = 0.1358$). Immatures offered consolation to adults in 81/103 instances (78.6%) and adults offered consolation to immatures in 22/103 instances (21.4%). Immatures were significantly more likely to offer consolation to adults than adults were to offer consolation to

immatures (immature-initiated: $z = 5.8134$, $P < 0.0001$; adult-initiated: $z = -5.8134$, $P < 0.0001$).

For FF dyads, consolation was offered after 37 of 378 possible instances and for FM dyads, it was offered after 94 of 764 possible instances. Neither of these are significantly different than expected values (FF: $z = -0.5209$, $P = 0.3012$; FM: $z = 1.5165$, $P = 0.0647$). For MM dyads, consolation was offered after 16 of 243 possible instances, which is significantly lower than expected if sex does not affect the rate of offered consolation but is consistent with expectations males have lower value relationships ($z = -2.0392$, $P = 0.0207$). For mixed sex dyads, females offered consolation significantly more than males ($F \rightarrow M = 65/94$, 69.1%: $z = 3.7131$, $p < 0.0001$; $M \rightarrow F = 29/94$, 30.9%: $z = -3.7131$, $P < 0.0001$). In adult only dyads, MM consolation was not significantly different than the expected value but there is only one adult MM dyad.

Occurrences of consolation were divided by intensity (1, 2, 3) and context (social, aggress, feeding, other) and tested for differences (Table 1.5a,b). The intensity and context of conflicts had no effect on the occurrence of consolation.

Of the 312 conflicts in which reconciliation and consolation could have occurred, 73 (23.4%) were reconciled only, 147 (47.11%) were consoled only, reconciliation and consolation co-occurred 37 times (11.86%), and neither reconciliation nor consolation occurred 128 times (41.03%). Of the co-occurrences, reconciliation occurred after consolation in 21 instances and consolation occurred after reconciliation in 16. Reconciliation was significantly more likely to occur in the absence of consolation than after consolation (without consolation: $z = 1.7993$, $P =$

0.03598; after consolation: $z = -1.7993$, $P = 0.03598$) (Figure 1.2a). Consolation was significantly more likely to occur in the absence of reconciliation than after reconciliation (without reconciliation: $z = 7.8333$, $P < 0.00001$; after reconciliation: $z = -7.8333$, $P < 0.00001$) (Figure 1.2b).

Discussion

The pattern of reconciliation in this group of bonobos does not appear to support VR. The mean individual adult CCT, 8.67%, is dramatically lower than others reported for bonobos (40%: Fortunato, 2009; 35.6%: Palagi et al., 2004) and even lower than most reported values for chimpanzees (discussed below). Even the rate of reconciliation (using all instances of post-conflict affiliation regardless of timing), 23.6%, is substantially lower than the CCT values for other studies. Not only did this group of bonobos reconcile relatively few conflicts compared to other studies of captive bonobos, there was no correlation between RQ and CCT.

The results presented here are more consistent with the Relationship Security hypothesis (RS: Cords and Aureli, 2000). RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation, while insecure relationships would be more likely to be damaged by conflict and therefore more likely to reconcile. RS was originally demonstrated among juvenile long-tailed macaques (Cords and Aureli, 1993) and red-bellied tamarins (*Saguinus labiatus*: Schaffner et al., 2005). Schaffner et al. (2005) hypothesized that tamarin relationships were so secure, i.e. resistant to damage, because of the nature of cooperative breeding and the importance of intra-group stability in the face of serious predation threats. The tamarin adaptation

is dramatically different than the bonobo adaptation, which makes support for RS in a large-bodied, promiscuous ape interesting.

While Palagi et al.'s (2004) results were consistent with VR—FF dyads reconciled the most and higher RQ was associated with higher CCT—Fortunato (2009) reported support for RS. Fortunato reported that reconciliation occurred at high rates for high and low RQ and independent of conflict intensity, although high intensity conflicts were very rare ($6/105 = 5.71\%$), and that the sex of opponents did not correlate with reconciliation. The high rate of reconciliation regardless of RQ suggests the relationships are more insecure. The Columbus Zoo bonobos are managed in a simulated fission-fusion style, so group composition can vary day-to-day. Fortunato suggested that this variability in group composition likely produced more uncertainty about relationship status, making relationships more insecure, and thus accounting for the high rate of reconciliation regardless of relationship quality. If this is the case, then perhaps the San Diego bonobos have more secure relationships so that, regardless of relationship quality, reconciliation was less necessary to restore predictability to relationships. The San Diego bonobos did come out in several different compositions over the study period but these did not vary significantly from one day to the next, i.e. the groups were relatively stable over time (see Table 1.2), and individuals who were not on exhibit together still had social access to each other in the indoor quarters in the evening and over night.

Clay and de Waal (2012) reported on PCB in semi-free ranging bonobos at Lola Ya Bonobo Sanctuary. The mean individual CCT = 22.31%, lower than Palagi et al. (2004) and Fortunato (2009) but higher than the present study. Clay and de Waal

reported that affiliation strongly predicted the occurrence of reconciliation and that kin reconciled at a higher rate than non-kin, consistent with VR.

The relative CCT values for each sex class in the present study are consistent with predictions for bonobos, FF dyads had the highest CCT, followed by FM, and MM dyads had the lowest, although the results are not statistically significant when examining all dyads or adults only. The value for the adult FF CCT (21%) is dramatically lower than Palagi et al. (2004) reported (54.7%) and the FM and MM values appear lower than those reported by Palagi et al. in Figure 2 (both appear to be about 10% or slightly under but exact values were not reported). Looking more closely at the FF dyads, it appears that they may have relatively insecure relationships. Two dyads, IN and IO, had 7 conflicts each and a higher than average CCT, 28.6% for both, but different RQ measures. IN have a close relationship and IO a weak relationship. The high rate of reconciliation in two dyads with different RQs suggests security may be the more salient variable. The other FF dyad, NO, had only one conflict, which was unreconciled. It is interesting to note that the two adult males are unrelated, unlike the wild pattern, but that their conflict and reconciliation patterns are consistent with some expectations for male bonobos—the two adult males had the highest rate of aggression and a very low CCT and rate of reconciliation—and inconsistent with another—the two adult males have a close relationship. The combination of low reconciliation and high relationship quality suggests they have a secure relationship. They are only one dyad, however.

It is difficult to determine a pattern of post-conflict behavior in bonobos from just 3 captive studies and 1 semi-free ranging study in which the results differ so much

but some insight can be gained by examining variation in PCB in captive and wild chimpanzees. One study in a very small ($N = 5$) group of captive chimpanzees (*Pan troglodytes*) at the Chimpanzee and Human Communication Institute had a CCT = 9.1% (calculated from published data; Fuentes et al., 2002), although differences between the sex classes of the dyads were dramatic (FF = 34.5%, FM = 16.3%, MM = 4.4%) and conform more to the expected bonobo pattern with very high rates of FF reconciliation and low rates for MM dyads. However, this group was very small with only 3 adult females and 2 adult males and its membership was unique with 4 individuals who were cross-fostered with humans and all 5 individuals trained in ASL.

In contrast, Preuschoft et al. (2002) reported a high mean individual CCT for captive chimpanzees at Yerkes, 41.2%, and high CCTs for FF (57.9%) and FM (45.7%) dyads and that high RQ was correlated with high CCT, supporting VR. It is also important to note that this group of 19 had only 1 adult male and 1 adolescent male. They suggested that the reduced feeding competition in captivity contributed to the high rate of reconciliation among females and in inter-sexual dyads, making them more bonobo-like in their behavior and relationship quality. This is consistent with wild reports of higher FF relationship quality in chimpanzees in environments with less dramatic seasonality (Boesch and Boesch-Achermann, 2000). It may be that under different ecological conditions female chimpanzees can form strong relationships with each other but those relationships are characterized by a high degree of insecurity given the greater emotional reactivity of chimpanzees relative to bonobos. The low number of adult males also likely reduced constraints on the females. In another captive chimpanzee study at Arnhem, Koski et al. (2007) reported a mean CCT =

21.6%. Unlike Preuschoft et al. (2002), however, Koski et al. (2007) reported significantly higher CCTs for MM dyads than FF dyads, similar to de Waal and van Roosmalen's (1979) original work at Arnhem, and that high RQ dyads had higher CCTs. Similar to the present study, Koski et al. (2007) reported that conflict intensity and context did not influence CCT.

Mean individual CCTs from wild chimpanzees are generally lower than from captives: 14.4% (adults only; Mahale: Kutsukake and Castles, 2004) and 12.3% (Budongo: Arnold and Whiten, 2001). Kutsukake and Castles (2004) reported higher MM CCT than FF (26.4%) and FM (20.6%) but the results were not significant, contrary to VR. Kutsukake and Castles also reported that it was the lowest quality dyads that had the highest CCT values, which they suggested is more consistent with RS. Arnold and Whiten (2001) also reported results inconsistent with VR—MM dyads did not reconcile significantly more often than FM dyads (FF dyads did not reconcile at all but only 10% of the 120 conflicts were FF) and when examining all possible dyads and there was no correlation between RQ and CCT. Wittig and Boesch (2003) reported results more consistent with VR for Tai chimpanzees: dyads with high quality relationships reconciled more than other dyads and FM dyads reconciled at high rates (they suggest that Tai chimpanzees may consider mating partners valuable and other work has shown strong intersexual bonds in Tai chimpanzees; Boesch and Boesch-Achermann, 2000). The current results lie near the low end of chimpanzee CCTs and CCTs reported in red-fronted lemurs (6.4%, calculated from published data, *Eulemur fulvus rufus*: Kappeler, 1993), Guinea baboons (7.1%, *Papio papio*: Petit et al., 1997), and rhesus macaques (8.1%, *Macaca mulatta*: Call et al., 1996). All of these results

suggest the PCB in bonobos and chimpanzees is more complex and variable than can be accounted for by VR and RS.

While dominance relationships were not considered here, the results do support the arguments that female and male bonobos are at least co-dominant and that bonobos have a relaxed dominance hierarchy. For all mixed sex dyads, females initiated FM conflicts significantly more than males, although the difference was not significant in adult only dyads. Females and males initiated reconciliation equally after mixed sex conflicts, as did aggressors and recipients of aggression. This suggests recipients of aggression did not perceive any risk of continuing aggression when approaching the aggressor.

Consolation

VR predicts that individuals with high quality relationships will be more likely to offer consolation to one another; the data presented here provide ambiguous support for VR and leave further questions about the function of consolation. There was no correlation between TCT and RQ but when using all instances of consolation instead of TCT, it was found that high RQ dyads engaged in consolation more than other dyad types, which is consistent with VR, and MM dyads engaged in consolation significantly less than other dyad types but in the adult-only male dyad there was no difference. Fortunato (2009) reported similarly mixed results: high RQ dyads were more likely to offer consolation to each other, supporting VR, but the sex class of dyads was not correlated with consolation. Fortunato reported a mean individual TCT = 35%, which is higher than the present study but lower than the TCT for the Apenhuel group. Clay and de Waal reported a mean individual TCT = 22.31%, similar

to the present study, and that close associates and kin were more likely to offer consolation.

de Waal and Aureli (1996) have suggested that consolation may substitute for reconciliation, which is supported here given the very low rate of reconciliation and higher rate of consolation (group TCT = 23%; proportion of conflicts followed by third-party initiated affiliation = 47.7%). Reconciliation and consolation were alternatives; consolation was less likely following reconciliation and vice versa (cf. Fraser and Aureli, 2008 in chimpanzees). Consolation also requires an awareness of and sensitivity to others' emotional states and the high rate of consolation here supports the idea that bonobos have sophisticated emotional awareness of others (Clay and de Waal, 2012).

Consolation was more likely to be offered in immature dyads than adult or mixed dyads and less likely to be offered in adult dyads. In mixed dyads, immatures were also more likely to offer consolation to the adult than adults were to offer consolation to an immature. In the present study, consolation was offered in MM dyads less often than in FF or FM dyads. Similarly, in mixed sex dyads, females were significantly more likely to offer consolation to males than males to females. Intensity and context had no effect on the occurrence of offered consolation.

Clay and de Waal (2012) also reported that immatures were more likely to offer consolation than adults. This suggests awareness of the emotional states of others emerges early in bonobo development. Clay and de Waal reported that consolation reduced PC self-scratching rates in recipients of aggression, suggesting consolation

functions to reduce PC anxiety. The present study did not examine PC anxiety, in part because only one individual consistently showed any clear signs of PC anxiety.

Conclusion

The very low rate of reconciliation in this group, combined with the lack of a relationship between relationship quality or sex and reconciliation, supports the conclusion that RS is a more appropriate explanation for reconciliation in these bonobos and that relationship security and post-conflict behavior are influenced by group demographics and history.

Examining the present results in the context of the variation in patterns of reconciliation and consolation in bonobos and chimpanzees suggests that, while the PC-MC method and VR have proven to be powerful tools for understanding conflict management in social animals, there are additional proximate factors that need to be taken into account before drawing firm conclusions about the nature of conflict management in any particular species. Palagi et al. (2004: 27) suggest that “it seems premature to make generalizations regarding a given species on the basis of comparisons among a limited number of studies”; they suggest that personality and group history are also important variables that should be taken into consideration and the results presented here support that conclusion. It is also possible that the PC-MC method, which has been very productive over the last 3 decades, is inadequate for describing the complexity of how conflict, reconciliation, and relationships intersect with each other. The diversity in patterns of post-conflict behavior in *Pan* is beginning to be established but there is still a great deal of work to do in order to understand that diversity.

Chapter 1, “Conflict Management in Captive Bonobos (*Pan paniscus*): Testing the Valuable Relationships Hypothesis,” is being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this material.

Table 1.1a Predictions of Valuable Relationships Hypothesis
RQ = Relationship Quality; CCT = Corrected Conciliatory Tendency

low RQ	→	↓ low rate of reconciliation/CCT
high RQ	→	↑ high rate of reconciliation/CCT

Table 1.1b Predictions of the Relationship Security Hypothesis

		VALUE/COMPATIBILITY	
		Low	High
SECURITY	Low	↑ high rate of reconciliation/CCT	↑ high rate of reconciliation/CCT
	High	↓ low rate of reconciliation/CCT	↓ low rate of reconciliation/CCT

Table 1.2 The *Pan paniscus* Colony at the San Diego Zoo (San Diego, CA, United States) and Main Sub-Group Composition

Name	Initial	Sex	Age Class	DOB	Mother/Father
Lana	N	F	Adult	13 April 79	Linda/Kakowet
Lolita	O	F	Adult	20 April 89	Louise/Vernon, nursery
Ikela	I	F	Adult	27 Nov 91	Louise/Akili, nursery
Yenge	G	M	Adult	25 Dec 82	Salonga/Mato, Frankfurt
Junior	J	M	Adult	14 Jan 95	Lana/Maiko
Mchumba	B	F	Adolescent*	22 Dec 00	Lolita/Congo
Kesi	K	F	Juvenile*	15 Aug 04	Lana/Yenge
Makasi	M	M	Juvenile*	22 April 04	Loretta/Jumanji, San Diego Safari Park, nursery
Mali	Y	F	Infant*	4 Sep 07	Ikela/Yenge, rejected
Tutapende	T	M	Infant*	29 Oct 07	Lolita/Yenge, rejected, adopted by Ikela

Group	Dates	% Time
BINJKYT	8/10/2009 – 9/16/2009	8%
INGJKYMY	10/14/2009-11/8/2009	6%
NGJKYM	9/28/2009-12/16/2010	52%
BINOKT	9/14/2009-12/3/2010	34%

*The adolescent was included with the adults in analysis and the 2 juveniles and 2 infants were combined as immatures.

Table 1.3 Inter-Animal Distances (IADs), Behaviors, and Conflict Intensity and Context

IAD Code	
0	in contact
1	within arm's reach
3	just beyond lunge distance
5	far
Behaviors	
<i>AFFILIATIVE</i>	
carry	Carry another ventrally or dorsally
contact	Any other friendly contact
groom	With hand(s) and/or mouth
peer (+)	Stare at mouth of eater (+ get food)
play	Wrestle, tickle, chase etc. with other
sex	Any genital contact with other (except grooming)
<i>AGGRESSIVE</i>	
aggress	Threaten, charge, chase, serious bite, hit, etc.
displace	Displace another from its place
display	Push or drag branch & charge, agent only if undirected (<i>not</i> conflict); if directed, charge
Conflict Intensity	
1	threat or charge
2	chase
3	aggressive contact, long chase, multiple aggressive incidents
Conflict Context	
social	conflicts beginning while either or both of the participants were engaged in any nonaggressive social interaction, e.g., grooming, playing, or sex
other	conflicts beginning any other contexts: unknown, over an object, access to the mound, non-feeding keeper presence, or first coming out of or going back in to off-exhibit area
feeding	conflicts beginning during the keeper's approach to the enclosure for feeding, during feeding, or during the period immediately following feeding while individuals were still consuming the foods thrown
aggress	conflicts beginning with a directed display or during on-going aggression, including redirection, support, and new conflicts with new participants that began soon after or during other conflicts

Table 1.4a Reconciliation: Number of Attracted, Dispersed, and Neutral Pairs for Recipients of Aggression; Conciliatory Tendencies per Individual
 This table presents each individuals' number of attracted (A), dispersed (D), and neutral (N) pairs, their total number of conflicts, CCT value $[(A-D)/Total]$.

Individual	A	D	N	Total	CCT
N	5	2	6	13	23.08%
O	3	0	3	6	50.00%
I	1	1	2	4	0.00%
G	3	5	17	25	-8.00%
J	12	5	63	80	8.75%
B	15	4	58	77	14.29%
K	7	1	7	15	40.00%
M	10	9	35	54	1.85%
Y	4	13	8	25	-36.00%
T	4	3	7	14	7.14%
Mean of Individual CCTs					10.11%

Table 1.4b Number and Percent of Conflicts Followed by PC Affiliation; Number and Percent of Reconciliations Initiated by Recipient

This table presents each individuals' number of conflicts followed by post-conflict affiliation (PCAI) with the former opponent, the percentage of conflicts followed by PCAI, the number of reconciliations they initiated, and the percentage of reconciliations they initiated.

Individual	#PCAI	%PCAI	Initiated	%Initiated
N	5	15.38%	8	57.14%
O	3	33.33%	2	66.67%
I	1	44.90%	13	59.09%
G	4	13.68%	3	23.08%
J	14	20.63%	15	57.69%
B	16	23.71%	4	17.39%
K	8	33.93%	11	57.89%
M	12	25.40%	9	56.25%
Y	6	24.00%	1	16.67%
T	5	40.00%	3	50.00%

Table 1.5a Occurrence of Reconciliation and Consolation by Intensity
 This table shows the number of conflicts reconciled and consoled at each intensity level, the total number of conflicts at each intensity level, the percent of conflicts reconciled or consoled at each intensity level, and the results of the z-test for proportions. None of the results are significant.

Intensity	Reconciled	Total	%Reconciled	z	P
1	16	54	29.6%	1.0355	0.1502
2	13	60	21.7%	-0.3601	0.3594
3	45	199	22.6%	-0.3417	0.3663
Total	74	313			

Intensity	Consoled	Total	%Consoled	z	P
1	27	53	50.94%	0.5582	0.2883
2	29	60	48.33%	0.1890	0.4250
3	91	199	45.73%	-0.3919	0.3476
Total	147	312	47.11%		

Table 1.5b Occurrence of Reconciliation and Consolation by Context

This table shows the number of conflicts reconciled and consoled in each context, the total number of conflicts in each context, the percent of conflicts reconciled or consoled in each context, and the results of the z-test for proportions. None of the results are significant.

Context	Reconciled	Total	%Reconciled	z	P
social	16	61	26.2%	0.4756	0.3172
other	15	55	23.6%	0.3163	0.3759
feeding	11	50	22%	-0.2733	0.3923
aggress	33	147	22.4%	-0.3405	0.3667
	74	313			

Context	Consoled	Total	%Consoled	z	P
social	29	60	48.33%	0.1890	0.4250
other	26	55	47.27%	0.0233	0.4907
feeding	24	50	48%	0.1253	0.4501
aggress	68	147	46.26%	-0.2081	0.4175
Total	147	312	47.11%		

Table 1.6 Offered Consolation: Number of Times Each Individual Was Offered Consolation from a Third Party; Number of Attracted, Dispersed, and Neutral Pairs, Triadic Contact Tendencies per Individual

This table presents data on the number of times an individual was offered consolation (friendly PC affiliation initiated by a third party). It includes each individuals' number of attracted (A), dispersed (D), and neutral (N) pairs, their total number of conflicts, TCT value $[(A-D)/Total]$, number of conflicts followed by PCAI initiated by a third party (#TPOC), and the percentage of conflicts followed by PCAI initiated by a third party (%TPOC).

Individual	A	D	N	Total	TCT	#TPOC	%TPOC
N	3	3	7	13	0	7	53.85%
O	1	0	5	6	16.67%	2	33.33%
I	2	0	2	4	50%	2	50%
G	6	1	18	25	20%	7	28%
J	26	10	44	80	20%	38	47.5%
B	24	4	48	76	26.32%	33	43.42%
K	5	2	8	15	20%	9	60%
M	18	9	27	54	16.67%	28	51.85%
Y	11	2	12	25	36%	13	52%
T	7	1	6	14	42.86%	8	57.14%
Group	103	32	177	312	22.76%		
Mean of Individual TCTs					24.85%		

Figure 1.1a Percentage of Conflicts Reconciled by Age-Class Combination

*Immature dyads reconciled significantly more conflicts than expected ($z = 1.8414$, $P = 0.0328$).

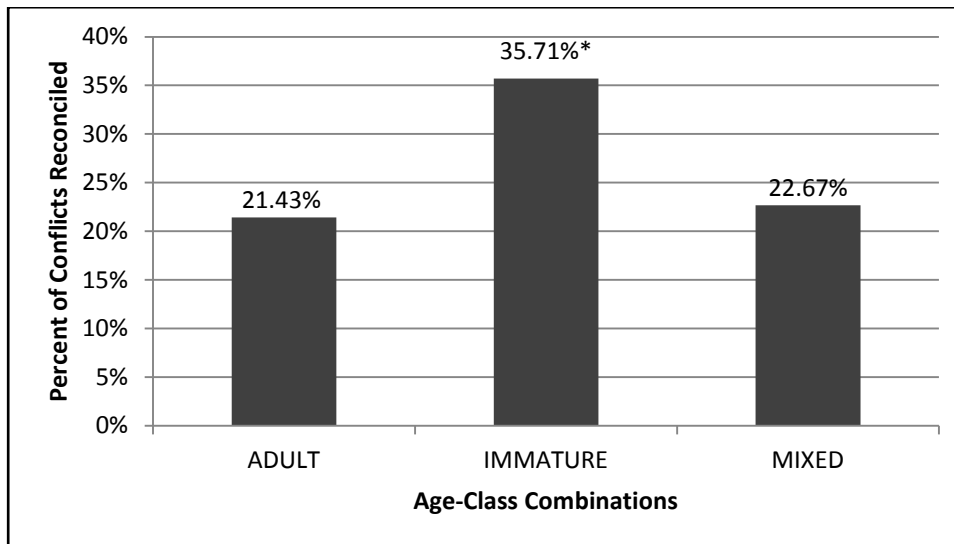


Figure 1.1b Percentage of Conflicts Reconciled by Sex-Class Combination
*MM dyads reconciled significantly fewer conflicts than expected ($z = -1.8609$, $P = 0.0313$).

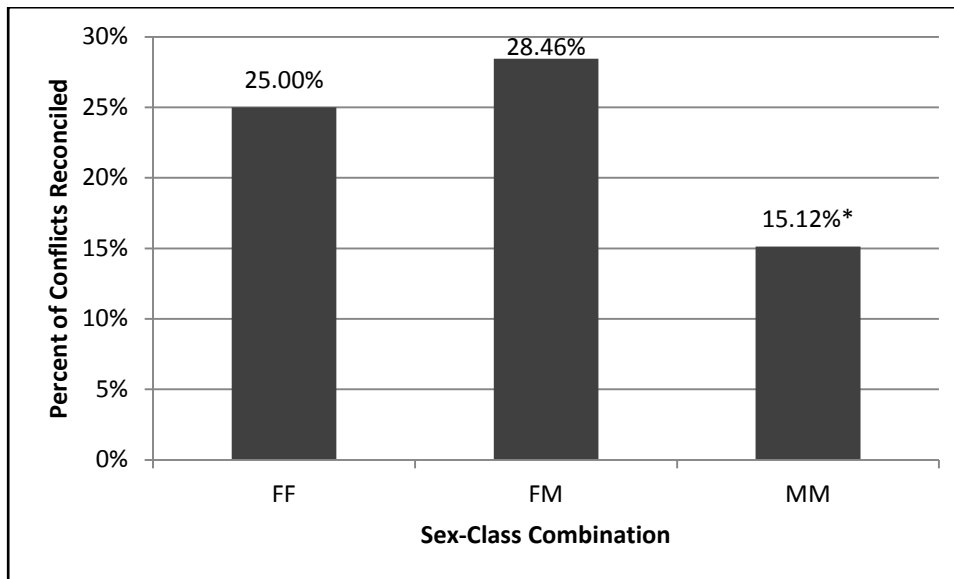


Figure 1.2a Probability of reconciliation occurring after consolation compared to reconciliation occurring in the absence of consolation.

* The differences are significant (after consolation: $z = -1.7993$, $P = 0.03598$; without consolation: $z = 1.7993$, $P = 0.03598$).

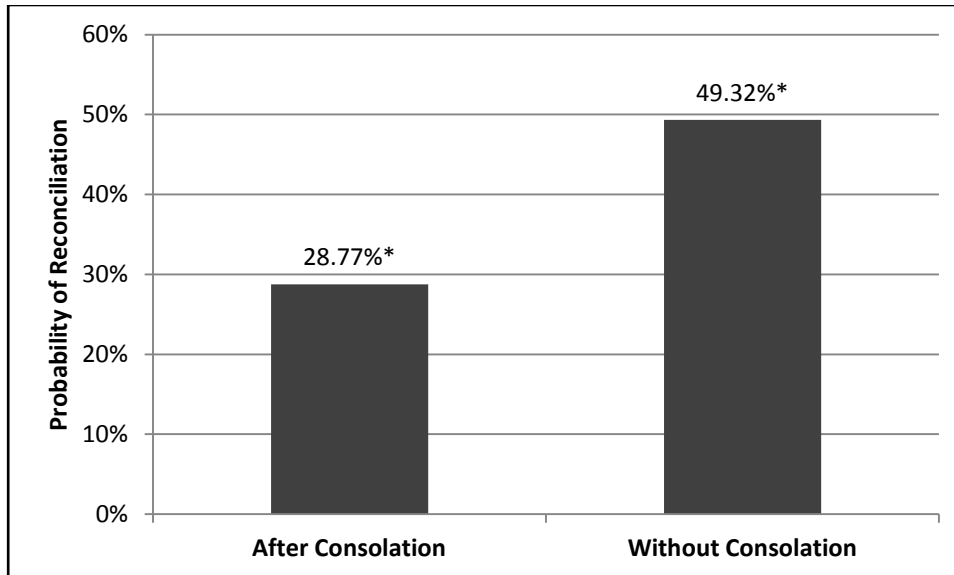
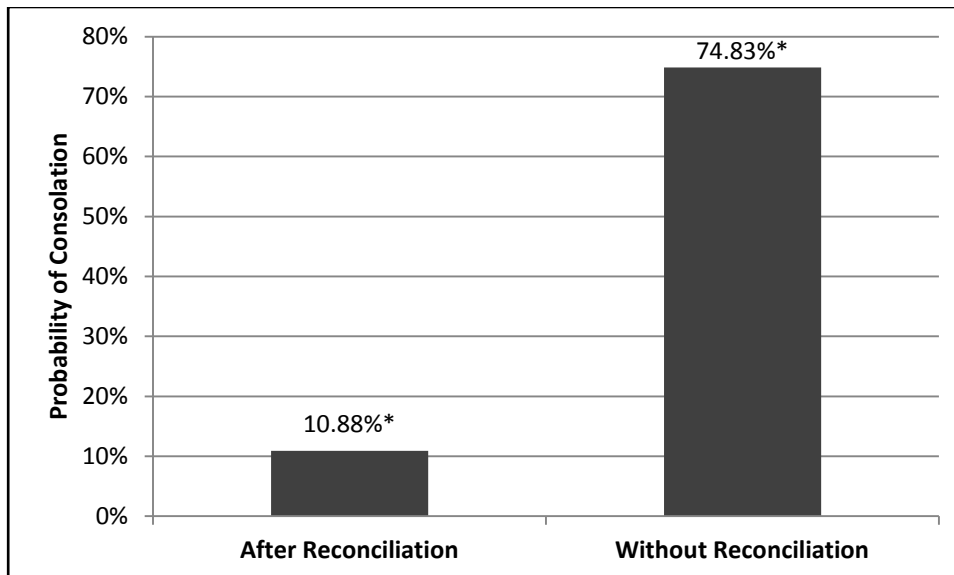


Figure 1.2b Probability of consolation occurring after reconciliation compared to consolation occurring in the absence of reconciliation

*The differences are significant (after reconciliation: $z = -7.8333$, $P < 0.00001$; without reconciliation: $z = 7.8333$, $P < 0.00001$).



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CHAPTER 2

Conflict Management In Captive Bonobos (*Pan paniscus*): Testing the Relationship

Repair Hypothesis

Abstract

The Valuable Relationships hypothesis has been well-supported in studies of reconciliation in non-human primates. It argues that individuals will be more likely to reconcile conflicts with valuable partners in order to repair the damage done by conflict. However, VR is based upon the assumption that conflict damages relationships and reconciliation serves to repair that damage. While this Relationship Repair hypothesis may make intuitive sense, the assumption needs to be explicitly tested before becoming entrenched as conventional wisdom. The present study serves as a test of RR in a group of captive bonobos at the San Diego Zoo. While reconciled conflicts were less likely to be followed by continued aggression on the same day than unreconciled conflicts, which is consistent with RR, results of the analysis of long-term patterns of interaction were inconsistent with RR. RR predicts that in the long-term following unreconciled conflicts, there will be a decrease in affiliation and an increase in aggression relative to baseline rates of interactions. However, the data presented here show no change in the rate of affiliation or aggression in the 10 days following unreconciled conflicts, suggesting the conflict did not damage the relationships. RR also predicts that following reconciled conflicts, affiliation rates will either increase or at least stay the same compared to baseline rates of affiliation. The results presented here are consistent with this prediction, rates of affiliation after reconciled conflicts did not differ from baseline rates. However, RR also predicts that

aggression will decrease or at least stay the same in the long-term after reconciled conflicts and the results presented here show that aggression actually *increased* in almost all dyads after reconciled conflicts.

Introduction

All social animals are faced with similar problems regarding within-group competition over resources and species are expected to have evolved mechanisms to cope with these problems (Aureli and de Waal, 2000). Postconflict behavior (PCB) is a major focus of nonhuman primate research, particularly reconciliation (postconflict affiliation between former opponents), which has been demonstrated in virtually all of the species in which it has been studied (Aureli and de Waal, 2000; Aureli et al., 2002; de Waal and van Roosmalen, 1979; Silk, 2002; but see Berman et al., 2006; Sommer et al., 2002), including several non-primates (domestic cat: van den Bos, 1997; domestic goat: Schino, 1998; spotted hyena: Wahaj et al., 2001; bottlenose dolphin: Weaver, 2003; domestic dogs: Cools et al., 2008; wolves: Cordoni and Palagi, 2008; horses: Cozzi et al., 2010; rooks: Seed et al., 2007). Although the *occurrence* of reconciliation has been well documented, questions remain about its *function* (Koyama, 2001; Silk, 2002; Watts, 2006).

The Valuable Relationships hypothesis (VR) has been the dominant model for explaining the occurrence of reconciliation (de Waal and van Roosmalen, 1979). VR argues that if conflict damages relationships and post-conflict affiliation serves to repair those relationships, then individuals with valuable relationships (kin, close associates) are more likely to reconcile after conflicts. VR has two clear components: (1) reconciliation repairs relationships after conflict and (2) dyads with valuable

relationships are more likely to reconcile. The overwhelming majority of studies demonstrate support for the second component: kin tend to reconcile more frequently than non-kin, close associates tend to reconcile more frequently than non-associates, and coalition partners tend to reconcile more frequently than non-partners (Aureli and de Waal, 2000; Aureli et al., 2002; de Waal and Aureli, 1997; Kappeler and van Schaik, 1992; Watts, 2006; but see Arnold and Whiten, 2001; Kutsukake and Castles, 2004; Schaffner and Caine, 2000; Schaffner et al., 2005). However, the first component contains a largely unexamined assumption, i.e. that conflict damages relationships and requires reconciliation to repair them (RR: Relationship Repair hypothesis) that must be tested in order for the function of reconciliation to be understood (Cords and Aureli 1996; Koyama, 2001; Silk, 2002; Watts, 2006).

Studies of reconciliation that have focused on RR have largely focused on the *short-term* consequences of reconciliation: its role in reducing continued or renewed aggression and restoring tolerance (Aureli and van Schaik, 1991a,b; Castles and Whiten, 1998; Cheney et al., 1995; Silk et al., 1996; Watts, 1995; Wittig and Boesch, 2003; Wittig and Boesch, 2005) and peaceful simultaneous exploitation of resources (Cords, 1992; Cords and Thurnheer, 1993) immediately following conflict. However, RR makes predictions about the *long-term* consequences of conflict and reconciliation that have not yet been widely demonstrated (Cords and Aureli 1996; Silk 1996, 2002; Watts 2006).

If relationships are investments from which partners derive fitness benefits (Kummer 1978) and they can be characterized as an emergent property of the sum of interactions between individuals in which patterns emerge over time, then the history

of interactions necessarily influences the form of future interactions (Hinde 1976). The reconciliation literature has yet to demonstrate this in regard to conflict and reconciliation. Silk cautioned against allowing RR to become “entrenched as dogma” (1996:39) and suggested that the persistence of support for RR in the absence of evidence may be “because it fits our own folk model of how and why we resolve conflicts” (Silk, 2002:21). If conflict damages relationships and reconciliation serves to repair that damage, then conflicts that are *not* reconciled presumably should result in damaged relationships. Although this is a central tenet of RR, it has explicitly been examined in only two studies (Koyama, 2001; Silk et al., 1996) and supported in one (Koyama, 2001).

In a study of PCB in female baboons, Silk et al. (1996) demonstrated that grunting by aggressors reconciled conflicts in the short-term by facilitating infant handling, sitting in proximity, and reducing the likelihood of renewed aggression. They also examined long-term social interactions between former opponents, comparing the rates of affiliation and aggression in the 10 days following reconciled and unreconciled conflicts. They predicted that reconciled conflicts would be followed by an increase in affiliation and a decrease in aggression, while unreconciled conflicts would show damage to the relationship, i.e. less affiliation and more aggression. However, Silk et al. (1996) reported no consistent difference in aggression and affiliation after reconciled or unreconciled conflicts and that that the rate of aggression was actually higher in reconciled dyads. In light of these results, Silk (1996:39) proposed the Benign-Intent (BI) hypothesis, arguing that “the primary function of

[reconciliation] is not to repair damaged social relationships...[but] to [reestablish] contact with former opponents with no implicit long-term consequences.”

Koyama (2001) has thus far provided the only clear support for RR in the long-term. Koyama, following a critique of Silk et al.'s (1996) methods by Cords and Aureli (1996), compared the rates of affiliation and aggression in the 10 days following conflicts to baseline measures of dyadic affiliation and aggression instead of directly comparing the 10 days following reconciled and unreconciled conflicts. In this study of free-ranging Japanese macaques, Koyama (2001) reported that in the 10 days following unreconciled conflicts, dyads engaged in less affiliation and more aggression compared to baseline rates, while reconciled conflicts were followed by reduced aggression and a return to baseline rates of affiliation. Watts (2006:1348) echoes Silk's earlier caution: “Results of Koyama's (2001) study meet the [relationship repair] condition, but clearly we need more such work before we can confidently conclude that [reconciliation] repair[s] disturbances to relationships or at least maintain[s] the status quo.”

An additional hypothesis related to reconciliation is also relevant here: Relationship Security (RS). RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation (Cords and Aureli 2000). Relationship security is the perception that the nature of a relationship will not change in response to conflict, i.e. the relationship is resistant to damage. If relationships are secure, then there will likely be no long-term consequences for unreconciled conflicts.

The primary objective of this study is to provide an additional test of the Relationship Repair hypothesis. RR predicts that conflict damages social bonds and that reconciliation serves to repair those bonds (Table 2.1). BI predicts that reconciliation serves only to signal the end of the conflict and resumption of tolerance and that there are no long-term consequences of reconciliation for relationships. RS predicts that when relationships are very secure they are resistant to damage and will not suffer short- or long-term consequences in the absence of reconciliation. If RR is supported, it is expected that: (1) unreconciled conflicts will be more likely to be followed by renewed aggression than reconciled conflicts (also consistent with BI) and there will be a long-term decrease in affiliation and/or increase in aggression after unreconciled conflicts, (2) whereas reconciled conflicts will see no significant long-term change in the rate of affiliation or aggression. BI would be supported if reconciled conflicts are less likely to be followed by renewed aggression but there are no long-term differences in the rate of affiliation and/or aggression following reconciled v. unreconciled conflicts. RS will be supported if (1) there is no consistent difference in the rate of renewed aggression after reconciled or unreconciled conflicts and (2) there is no consistent difference in long-term affiliation and aggression after reconciled or unreconciled conflicts.

Methods

Data were collected August 5, 2009 – December 16, 2010 from the bonobo (*Pan paniscus*) colony at the San Diego Zoo. The colony was composed of 10 individuals (Table 2.2). The bonobos have indoor (off exhibit) and outdoor (560m²) enclosures and cannot move between them at will. All observations took place at the

outdoor enclosure. The bonobos came out in two groups of varying composition (Table 2.2): morning, approximately 9:00a.m.-12:30p.m., and afternoon, approximately 12:30-4:30p.m. Sub-group composition varied to simulate fission-fusion but was also influenced by keeper and veterinary husbandry decisions and remained relatively stable over time. Both groups had access to water and a variety of foods distributed throughout the enclosure daily, liquefied foods in an artificial termite mound, and scheduled daily feeding from keepers at approximately 11:00a.m. and 2:00p.m.

Data Collection

Data were collected using instantaneous scan sampling and all occurrences sampling for conflicts (Altmann 1974). Scans were collected at 2-minute intervals and included inter-animal distances (IADs) and social behavior for all visible individuals (Table 2.2). A total of 16,888 behavior scans were collected (562.93h) over 226 days.

When conflicts occurred, scan collection stopped and behavior was recorded using a digital voice recorder (DVR) to allow detailed collection on the initiator and recipient of aggression during and after the conflict. The conflict data include: initiator, recipient, intensity (Table 2.3), context (Table 2.3), third-party contacts, and duration of aggression. The end of a conflict was determined to be after the last aggressive act as long as aggression did not resume during the 10 minute PC collection. Collecting the data with the DVR also enabled collecting data on simultaneous or co-occurring conflicts; incompletely described conflicts were discarded (N=84).

After the conflict ended, data collection switched to the postconflict-matched control method (PC-MC: de Waal and Yoshihara 1983). The recipient of aggression was the focal but both opponents were tracked. The PC data include: type and timing of the first friendly interactions among the former opponents and/or between a former opponent and a third party. On the next day possible, at about the same time of day as the conflict, the 10-minute MC collection period occurred. The MC collection was identical to the PC collection with exception of the preceding conflict and only concerned the recipient of aggression. MC collections always took place within 1 week of the PC collection.

Research Interns

Scan data were collected by the author and a group of research interns participating in COGS 160 Videography Studies Laboratory at UCSD under the guidance of Dr. Christine Johnson. All interns underwent extensive training in bonobo behavior and data collection methods with Dr. Johnson, the author, and experienced interns. Students had to pass an inter-observer reliability test (agreement at least $K = 83\%$) to participate in data collection. All conflict and PC-MC data were collected by the author.

Data Analysis

Reconciliation occurs if the former opponents engage in a friendly interaction after the conflict (de Waal and van Roosmalen 1979; de Waal and Yoshihara 1983). To test whether reconciliation reduced the likelihood of renewed aggression, conflicts were divided by reconciled and unreconciled then the proportion of conflicts followed by renewed aggression (any subsequent aggression in the same dyad on the same day)

in each category were compared using χ^2 . First conflicts for any dyad that occurred less than 1 hour before observations ended for the day were excluded from this analysis in order to ensure sufficient time for renewed aggression to be observed. Of 313 recorded conflicts, 188 first conflicts met these criteria.

To test the Relationship Repair hypothesis, conflicts were divided by reconciled and unreconciled then within each category the mean rates of affiliation and aggression for each dyad in the 10 days after conflicts were compared to mean baseline rates of affiliation and aggression, following Koyama (2001). Of the 313 conflicts for which complete PCMC data were collected, only 69 conflicts were included in this analysis in order to ensure enough observation days were available and to avoid sampling the same conflict more than one time. First, conflicts that occurred within 10 days of the beginning and end of the study period were excluded, then conflicts that occurred within 10 days of a change in group composition were excluded, to ensure that there would be enough observation days to determine rate of affiliation 10 days after each conflict. Similarly, conflicts were excluded if there were fewer than 100 scans in which the dyad was possible in the 10 days after the conflict. Second, multiple conflicts per dyad per day were collapsed into one data point. For these conflicts, the last conflict of the day was used to classify the conflicts as reconciled or unreconciled. Third, in order to ensure that none of the 10 day post-conflict periods overlapped with each other for a particular dyad, conflicts that occurred during the 10 days after another conflict were excluded from this analysis with preference given to keeping reconciled conflicts since there were fewer of them. Only dyads with at least 1 reconciled and 1 unreconciled conflict were used in this

analysis. As a result, 13 dyads with 33 reconciled conflicts and 36 unreconciled conflicts were used in this analysis.

After determining which conflicts would be included in the analysis, rates of affiliation and aggression in the 10 days after each conflict and adjusted baseline rates of affiliation and aggression were calculated. The same methods as Chapter 1 were used to determine rate of affiliation (# of scans grooming or sitting in contact/total scans possible for a dyad) with 2 differences. First, to determine the rate of affiliation in the 10 days PC, only those 10 days were considered. Second, the 10 days used for the PC measure were excluded when determining the adjusted baseline rate of affiliation for comparison. Then, for each dyad, the mean rate of affiliation in the 10 days PC and mean adjusted baseline rate of affiliation over all conflicts were calculated. The same method was used to determine the rates of aggression in the 10 days PC and the adjusted baseline rates of aggression. A Wilcoxon matched-pairs signed ranks test (Koyama 2001) was used to test for differences. The reconciled conflicts test was two-tailed since there is no specific direction of difference predicted; the unreconciled conflicts test was one-tailed since RR predicts a specific direction of difference, a decrease in affiliation and an increase aggression. I also followed Silk et al.'s (1996) method and used a one-tailed Wilcoxon matched-pairs signed ranks test to test for differences in the rate of affiliation in each dyad in the 10 days after reconciled and unreconciled conflicts; the same test was done for the rate of aggression.

The data on rates of affiliation and aggression after reconciled and unreconciled conflicts, as per Silk et al. (1996), are also presented with data on dyadic CCTs and relationship quality. Veenema et al. (1994) developed the corrected

conciliatory tendency (CCT), which represents how conciliatory an individual or dyad is by considering how many conflicts are reconciled but controlling for baseline rates of affiliative interaction. To determine the CCT, the timing of affiliative PC contacts is compared to the timing of affiliative MC contacts. If contact occurs earlier PC than MC, that pair is considered “attracted” for that conflict but if the contact occurs earlier MC than PC, the pair is considered “dispersed”. If no contact occurs in either period or the contact occurs at the same time, the pair is “neutral”. $CCT = (\text{attracted pairs} - \text{dispersed pairs}) / \text{total PC-MC pairs}$. To avoid pseudoreplication, only data on the recipient of aggression were used in this analysis. Dyadic CCTs were classified as high if they were above the group mean and low if they were below the group mean.

Dyadic relationship quality (RQ) was determined by calculating the total number of scans in which a dyad was grooming or sitting in contact divided by the total number of scans in which they *could* have been interacting [(groom + contact sitting)/total scans out together]. Dyads were divided into two classes, close and weak, by calculating the mean RQ of all dyads and classifying dyads as close if their RQ was above the mean and weak if their RQ was below the mean.

Results

The data on dyadic CCTs and relationship quality are presented in Table 2.4.

Short-Term Consequences—Renewed Aggression

RR and BI predict that reconciled conflicts will be less likely to be followed by renewed aggression than unreconciled conflicts. Of the 188 conflicts used in this analysis, 42 (22.3%) were followed by reconciliation and 146 (77.7%) were unreconciled (Table 2.5). Of the 42 conflicts followed by reconciliation, 4 (9.5%)

were followed by renewed aggression and 38 (90.5%) were not. Of the 146 conflicts that were unreconciled, 38 (26%) were followed by renewed aggression and 108 (74%) were not. The unreconciled conflicts were significantly more likely to be followed by renewed aggression than the reconciled conflicts ($\chi^2 = 5.1205$, $N = 188$, $P = 0.0236$).

Long-Term Consequences—Affiliation

RR predicts that rates of affiliation will not change in the long-term after reconciled conflicts. Six dyads decreased affiliation in the 10 days following reconciled conflicts and 7 dyads increased affiliation (Figure 2.1a); however, the difference between the mean rates of affiliation across dyads was not significant. Overall, mean rates of 10 day PC affiliation after reconciled did not differ significantly from the mean adjusted baseline rates, which is consistent with predictions from RR (Wilcoxon matched-pairs signed ranks, $W = 35$, $n = 13$, $p > 0.2$).

RR predicts that affiliation will decrease in the long-term after unreconciled conflicts. Seven dyads decreased affiliation in the 10 days after unreconciled conflicts and 6 increased affiliation in the 10 days after unreconciled conflicts (Figure 2.1b); however, the difference between the mean rates of affiliation across dyads was not significant. Overall, mean rates of 10 day PC affiliation after unreconciled did not differ significantly from the mean adjusted baseline rates, which is inconsistent with predictions from RR (Wilcoxon matched-pairs signed ranks, $W = -11$, $N = 13$, $z = -0.37$, $p > 0.2$, one-tailed test).

Comparing the rate of affiliation in the 10 days after reconciled conflicts to the rate of affiliation after unreconciled conflicts, 3 dyads showed a decrease in affiliation

and 10 showed an increase or no change, but the differences were not significant, which is consistent with RR (Figure 2.2a; Wilcoxon matched-pairs signed ranks, $W = 30$, $N = 13$, $z = 1.07$, $P = 0.1423$, one-tailed test).

Long-Term Consequences—Aggression

RR predicts that rates of aggression will not change in the 10 days following reconciled conflicts. Nine dyads increased aggression in the 10 days following reconciled conflicts and 4 decreased aggression in the 10 days following reconciled conflicts (Figure 2.3a), however, mean rates of 10 day PC aggression after reconciled conflicts did not differ significantly from the mean adjusted baseline rates, which is consistent with predictions from RR (Wilcoxon matched-pairs signed ranks, $W = 27$, $n = 13$, $p > 0.2$).

RR predicts that rates of aggression will increase in the long-term after unreconciled conflicts. Ten dyads decreased aggression in the 10 days after unreconciled conflicts and 3 dyads increased aggression in the 10 days after unreconciled conflicts (Figure 2.3b). Overall, mean rates of 10 day PC aggression after unreconciled conflicts did not differ significantly from the mean adjusted baseline rates, which is inconsistent with predictions from RR (Wilcoxon matched-pairs signed ranks, $W = 38$, $N = 13$, $z = 1.31$, $p = 0.0951$, one-tailed test).

Comparing the rate of aggression in the 10 days after reconciled and unreconciled conflicts yielded significant results (Figure 2.2b; Wilcoxon matched-pairs signed ranks, $W = 46$, $N = 11$, $P = 0.0217$, one-tailed test), however, the difference is in the opposite direction of the predictions—aggression *increased* after

reconciled conflicts in 10/11 dyads and decreased in only 1/11. Two dyads were excluded from this analysis because they had 0 conflicts in both conditions.

Discussion

The results presented here provide minimal support for the Relationship Repair and appear more consistent with BI and/or RS. First, in the short-term, both RR and BI predict that reconciliation will reduce the likelihood of renewed aggression. This prediction is supported by this study. Reconciled conflicts were significantly less likely to be followed by further aggression on the same day than unreconciled conflicts. RS suggests that, even in the absence of reconciliation, dyads will resume normal interactions or at least not engage in further aggression (Schaffner et al., 2005), which is not supported here. It does appear, then, that reconciliation is an important strategy for reducing the likelihood of short-term renewed aggression but this result does not differentiate between RR and BI.

RR predicts that reconciliation repairs relationships and that reconciled conflicts, in the long-term, will be followed by no change in the rate of affiliation and unreconciled conflicts will be followed by a long-term decrease in affiliation. The first component is supported here using Koyama's (2001) method; reconciled conflicts were not followed by any significant changes in the rate of affiliation when compared to baseline rates of affiliation. This result is consistent with RR but does not differentiate between the three competing hypotheses; no change in the rate of affiliation after reconciled conflicts is also consistent with both BI and RS. RR predicts that unreconciled conflicts will be followed by a long-term decrease in affiliation, i.e. show damage, but the results here show no change in the rate of

affiliation after unreconciled conflicts. These results are inconsistent with RR, consistent with BI and RS, but do not differentiate between BI and RS.

RR predicts that reconciled conflicts will be followed by a long-term *decrease* in aggression and unreconciled conflicts will be followed by a long-term increase in aggression compared to baseline rates. Using Koyama's (2001) method, the present study does not support this prediction of RR. Reconciled conflicts were not followed by a decrease in the long-term rate of aggression. It may be, however, that reconciled conflicts do not have to be followed by a *decrease* in aggression to be considered repaired. If relationship repair is about restoring a relationship to its baseline rates of interaction, then no significant difference between the rate of aggression in the 10 days after a conflict and the baseline rate could indicate repair. However, 9 dyads showed an *increase* in the rate of aggression after *reconciled* conflicts so, although the results were not statistically significant, it does not appear that reconciliation reduced the rate of aggression in the long-term or returned it to baseline rates. Unreconciled conflicts were not followed by an increase in aggression, either, contrary to RR. In fact, 10 dyads showed a *decrease* in the rate of aggression in the 10 days after unreconciled conflicts, although the results were not significant (although, $P = .0951$, which some might report as a statistical trend).

Using Silk et al.'s (1996) method, comparing the rate of affiliation after reconciled and unreconciled conflicts (rather than to a baseline measure) showed no significant difference, which is consistent with RR. However, this result is also consistent with BI and RS, which predict no long-term consequences for relationships. Contrary to prediction, aggression was significantly more likely to increase in the 10

days after *reconciled* conflicts than after unreconciled ones. Ten of the 11 dyads in this analysis showed an increase in aggression in the 10 days after reconciled conflicts.

RR is an important component of the Valuable Relationships hypothesis and is not supported here. Previous analysis showed no correlation between CCT and RQ for this group of bonobos (Chapter 1). If VR were supported, dyads with close relationships would be expected to have a CCT higher than the group mean CCT and weak dyads would be consistently more likely to have a low CCT (Table 2.4). Only 4 of the 13 dyads fit this pattern and the results from the last chapter clearly show that relationship quality is not correlated with reconciliation.

The Relationship Security hypothesis suggests that security is a more salient variable in determining reconciliation than relationship value or quality. The results from Chapter 1 appear to be more consistent with that hypothesis; however, the only measure of relationship security presented there is the rate of reconciliation, i.e. a high rate of reconciliation, regardless of relationship value or quality, suggests an insecure relationship and a low rate of reconciliation suggests a secure relationship. CCT alone, however, is an insufficient measure of security. RS suggests that secure relationships are resistant to damage and, therefore, should not show long-term consequences after reconciled or unreconciled conflicts. The data presented in this chapter suggest that the relationships among the San Diego Zoo bonobos are secure, bolstering the claims of Chapter 1; conflict, reconciled or not, appears not to have any consistent impact on the form of future interactions in a dyad.

As discussed in Chapter 1, support for VR in *Pan* is inconsistent, at best. Palagi et al. (2004) reported support for VR in a captive group of bonobos and a

relatively high CCT; Clay and de Waal (2012) also reported support for VR in a group of semi-free-ranging bonobos but reported a much lower mean CCT than Palagi et al. (2004); Fortunato (2009) reported a high mean CCT and support for RS in another captive group. Studies of chimpanzees in the wild and captivity have also varied in their support for VR (see previous chapter for details).

These results and the behavioral flexibility of *Pan* suggest that our understanding of PCB and the nature of relationships in our two closest living relatives is limited. Other variables, such as personality and group history, should be integrated more effectively into our analyses and it may be that gross measures such as grooming rates over time may not be sensitive enough to detect more subtle changes in relationships. Social network and systems analysis may allow us to gain finer grained insights into the nature of primate relationships and more complete understanding of PCB.

Chapter 2, “Conflict Management in Captive Bonobos (*Pan paniscus*): Testing the Relationship Repair Hypothesis,” is being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this material.

Table 2.1 Hypotheses and predictions for short and long-term consequences of conflict in the presence or absence of reconciliation

Hypothesis	PCB	Short-Term Aggression	Long-Term Aggression and Affiliation
Relationship Repair	Reconciled	renewed aggression less likely	baseline affiliation, reduced aggression
	Unreconciled	renewed aggression more likely	decreased affiliation, increased aggression
Benign-Intent	Reconciled	renewed aggression less likely	no long-term consequences
	Unreconciled	renewed aggression more likely	no long-term consequences
Relationship Security	Reconciled	no difference	no long-term consequences
	Unreconciled	no difference	no long-term consequences

Table 2.2 The *Pan paniscus* Colony at the San Diego Zoo (San Diego, CA, United States) and Main Sub-Group Composition

Name	Initial	Sex	Age Class	DOB	Mother/Father
Lana	N	F	Adult	13 April 79	Linda/Kakowet
Lolita	O	F	Adult	20 April 89	Louise/Vernon, nursery
Ikela	I	F	Adult	27 Nov 91	Louise/Akili, nursery
Yenge	G	M	Adult	25 Dec 82	Salonga/Mato, Frankfurt
Junior	J	M	Adult	14 Jan 95	Lana/Maiko
Mchumba	B	F	Adolescent*	22 Dec 00	Lolita/Congo
Kesi	K	F	Juvenile*	15 Aug 04	Lana/Yenge
Makasi	M	M	Juvenile*	22 April 04	Loretta/Jumanji, San Diego Safari Park, nursery
Mali	Y	F	Infant*	4 Sep 07	Ikela/Yenge, rejected
Tutapende	T	M	Infant*	29 Oct 07	Lolita/Yenge, rejected, adopted by Ikela

Group	Dates	%Time
BINJKYT	8/10/2009 – 9/16/2009	8%
INGJKYMY	10/14/2009-11/8/2009	6%
NGJKYM	9/28/2009-12/16/2010	52%
BINOKT	9/14/2009-12/3/2010	34%

*The adolescent was included with the adults in analysis and the 2 juveniles and 2 infants were combined as immatures.

Table 2.3 Number of Reconciled and Unreconciled Conflicts Per Dyad Followed by Renewed Aggression or Not

Dyad	Reconciled		Unreconciled	
	Renewed	Not Renewed	Renewed	Not Renewed
BI	0	2	3	4
BJ	1	1	4	7
BK	0	1	0	4
BN	0	1	8	16
BT	0	1	0	1
GI	0	1	0	0
GJ	1	2	15	18
GK	0	2	1	4
GM	0	0	0	3
GN	0	2	1	2
IJ	0	4	2	4
IM	0	1	0	1
IN	0	3	0	3
IO	0	2	0	2
JK	0	1	0	1
JM	0	3	0	3
JN	0	0	0	3
KM	1	4	1	6
KT	0	2	0	0
KY	0	1	2	4
MN	1	0	1	13
MY	0	2	0	3
NO	0	0	0	1
NT	0	1	0	3
NY	0	1	0	1
OT	0	0	0	1
	4	38	38	108

Table 2.4 Occurrence of Renewed Aggression After Reconciled and Unreconciled Conflicts

	Renewed Aggression	Not Renewed
Reconciled	4	38
Unreconciled	38	108

$\chi^2 = 5.1205$, $P = 0.0236$, $N = 188$

Table 2.5 Comparison of Mean Rate of Affiliation and Aggression 10 Days after Conflict, Relationship Quality, and CCT Per Dyad

Dyad	Mean rate of Affiliation 10 days after conflict	Mean rate of Aggression 10 days after conflict	RQ	CCT
	Rec:Unrec	Rec:Unrec		
BI	<	>	weak	high
BN	>	>	weak	high
IN	>	>	close	high
IO	<	<	weak	high
GJ	>	>	close	low
BJ	>	>	weak	low
GN	>	<	close	low
IJ	>	>	close	high
GK	>	>	weak	high
JM	>	>	weak	high
KM	>	>	weak	low
KY	>	<	close	low
MY	<	>	close	low

Figure 2.1a Comparison of Rate of Affiliation 10 Days After Reconciled Conflicts to Baseline Rate of Affiliation By Dyad

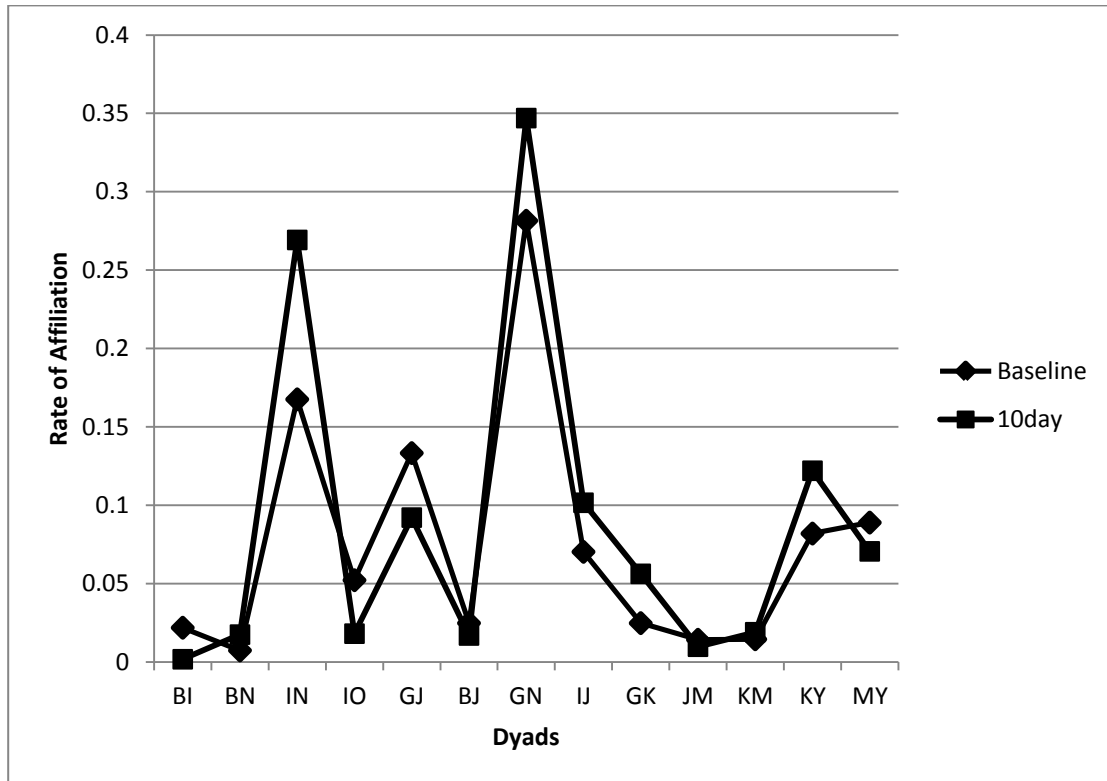


Figure 2.1b Comparison of Rate of Affiliation 10 Days After Unreconciled Conflicts to Baseline Rate of Affiliation By Dyad

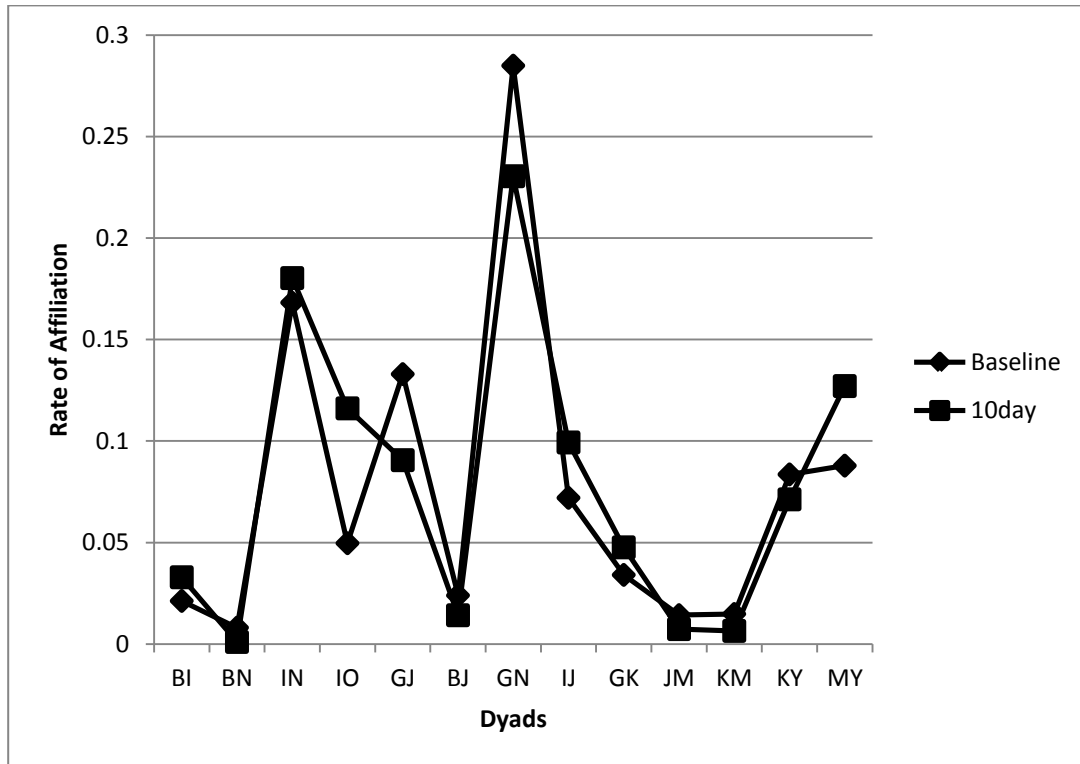


Figure 2.2a Comparison of Rate of Affiliation 10 Days After Reconciled and Unreconciled Conflicts By Dyad

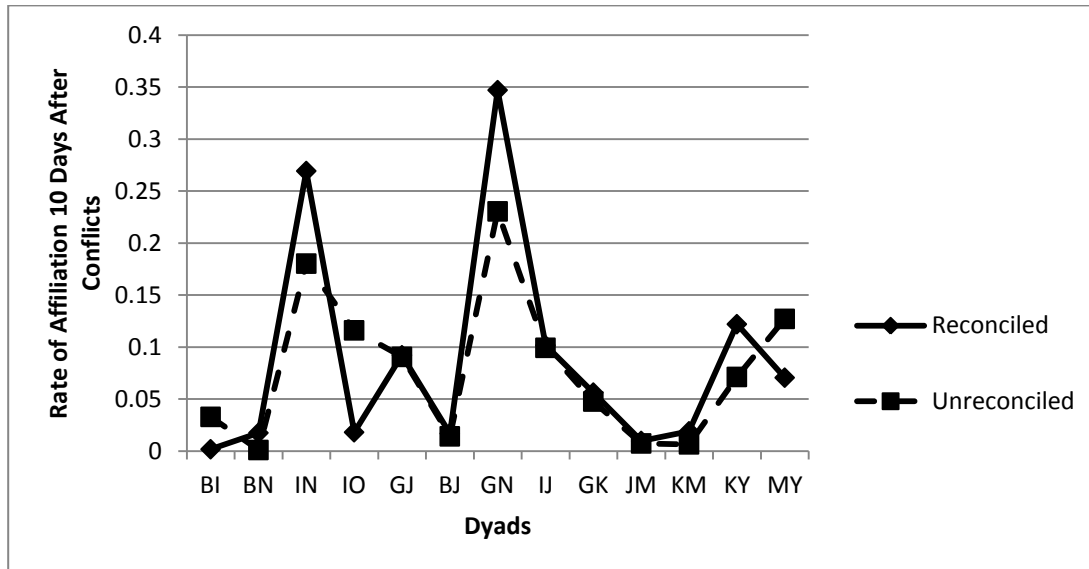


Figure 2.2b Comparison of Rate of Aggression 10 Days After Reconciled and Unreconciled Conflicts By Dyad

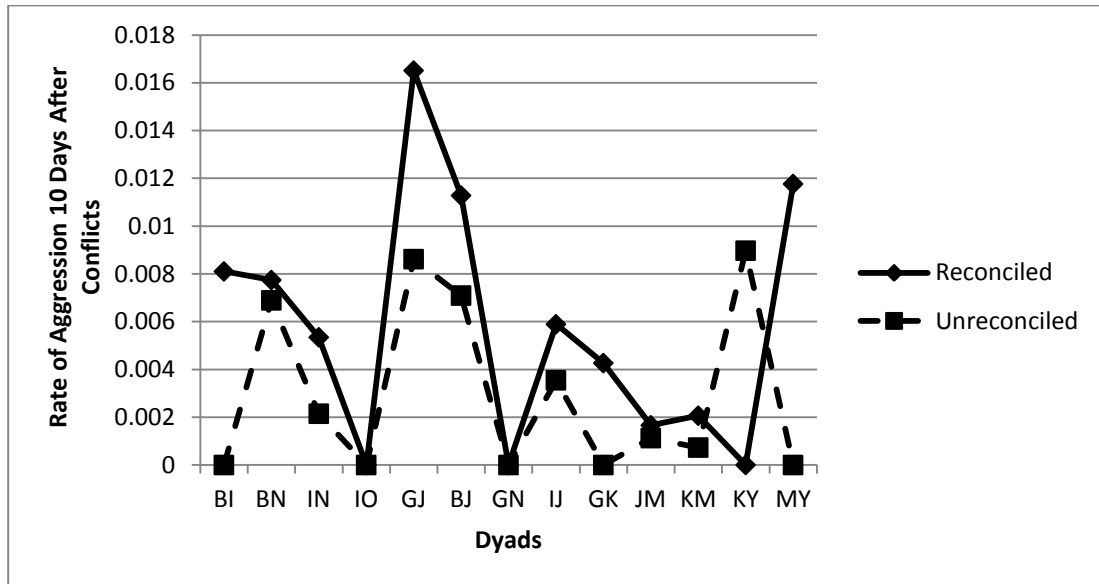


Figure 2.3a Comparison of Rate of Aggression 10 Days After Reconciled Conflicts to Baseline Rate of Aggression By Dyad

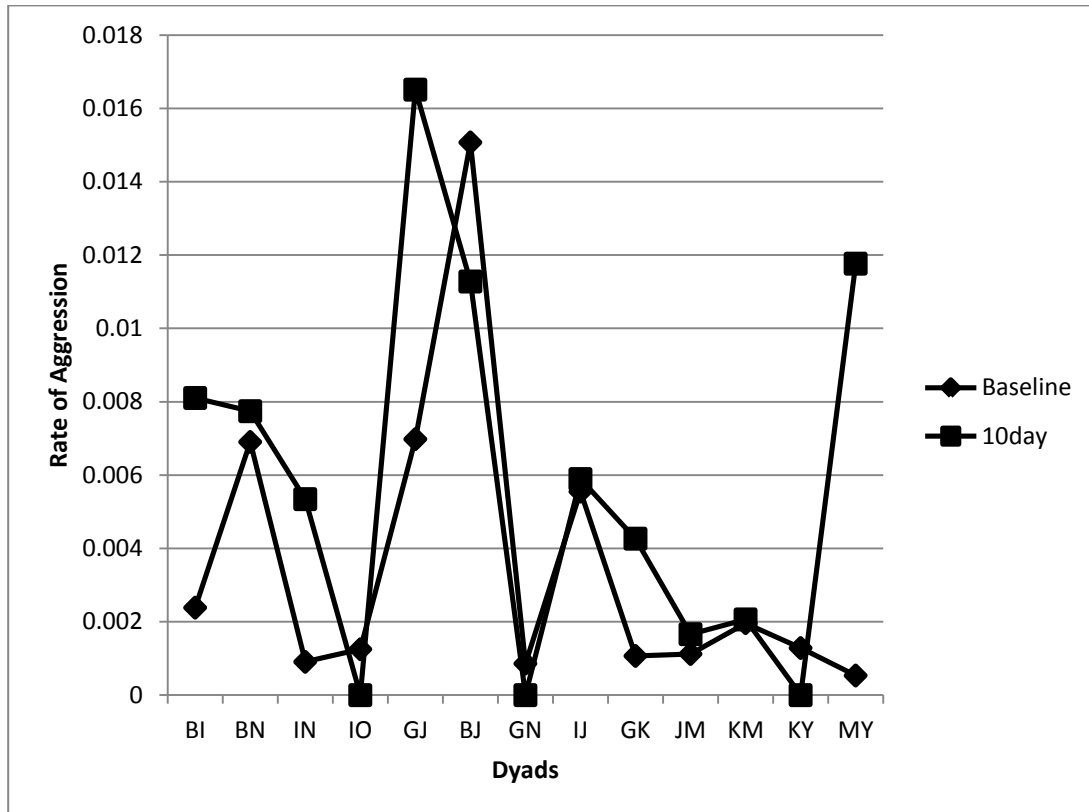
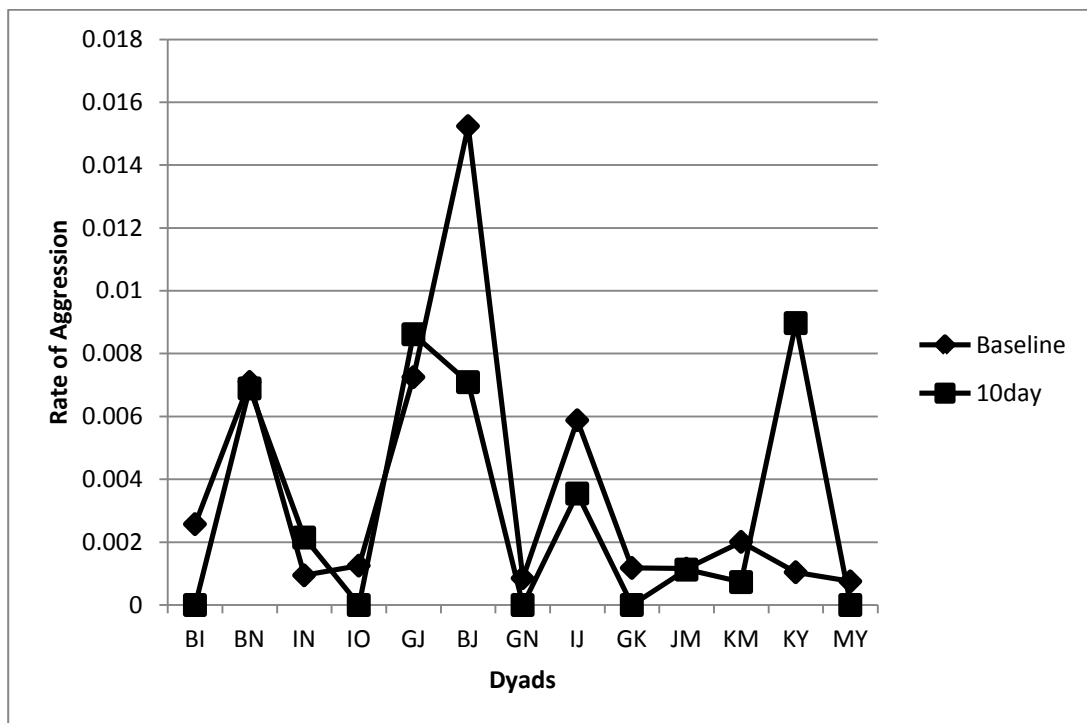


Figure 2.3b Comparison of Rate of Aggression 10 Days After Unreconciled Conflicts to Baseline Rates of Aggression By Dyad



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CHAPTER 3

Non-Aggressive Third-Party Initiated Interactions with Aggressors during Conflict in Captive Bonobos (*Pan paniscus*)

Abstract

Reconciliation and consolation are two well-studied areas of primate conflict management behavior. Less work has been done on third-party initiated interactions with aggressors during conflict. Previous work on this topic has suggested that these interactions may serve to promote social stability, reinforce an individual's dominance status, improve an individual's mating access to a conflict participant, or reduce the likelihood that the aggressor will direct aggression at the third party. This study tests these hypotheses in the San Diego Zoo colony of bonobos by examining third-party initiated affiliation and non-aggressive interference and finds that none are an effective explanation of third-party initiated interactions with aggressors. Of the 61 instances of third-party initiated affiliation with aggressors, 90.2% were initiated by immature individuals and 77% were immature individuals affiliating with just 1 aggressor, an adult male. These results are inconsistent with the first 3 hypotheses since they predict adults will be the mostly likely parties to initiate affiliation with aggressors. The results are also inconsistent with the self-protection hypothesis, which predicts third-parties affiliate with their own frequent aggressors as a way to reduce the likelihood of receiving aggression, because G very rarely initiated aggression against any of the immatures. G was the only individual in the group to show consistent, clear evidence of stress during and after conflicts, whether he was the aggressor or the victim. It is possible that the immature individuals were motivated to affiliate with him in an effort

to calm him. If this is the case, it demonstrates that the capacity for empathy emerges early in bonobos and that young individuals can be motivated to act in response to the emotional states of others.

Introduction

Conflict management has been one of the most popular and productive areas of primatological research for the last 3 decades and for good reason: relationships are investments from which partners derive fitness benefits (Kummer 1978), suggesting that mechanisms for coping with the costs of conflict are an important part of the primate adaptation (de Waal 1996, 2000). Most research into conflict management has focused on reconciliation and consolation. Reconciliation, postconflict affiliation between former opponents, has been demonstrated in virtually all of the species in which it has been studied (Aureli and de Waal 2000), including non-primates (domestic cat: van den Bos 1997; domestic goat: Schino 1998; spotted hyena: Wahaj et al. 2001; bottlenose dolphin: Weaver 2003; domestic dogs: Cools et al., 2008; rooks: Seed et al., 2007; wolves: Cordoni and Palagi 2008; horses: Cozzi et al. 2010). Consolation, postconflict affiliation between the recipient of aggression and a third-party, has also been demonstrated, although not as widely or consistently, in the great apes (bonobos: Palagi et al., 2004; chimpanzees: Palagi et al., 2006; de Waal and van Roosmalen, 1979; Kutsukake and Castles, 2004; but see Arnold and Whiten, 2001; Fuentes et al., 2002; Watts, 1995), stumptailed macaques (Call et al. 2002), domestic dogs (Cools et al., 2008), and corvids (Seed et al., 2007; Fraser and Bugnyar, 2010; Logan et al., 2012). Consolation can be offered (initiated by the third party) or solicited (initiated by the recipient of aggression). Both of these forms of conflict

management concern the post-conflict period and include the victim of aggression. Less work has been done examining social interactions that occur *during* conflict and that are directed at the aggressor.

Third-party initiated interactions with aggressors have been reported in monkeys and apes and can take the form of aggressive, affiliative, or neutral interactions (e.g, interposition), although the current study focuses only on affiliative and neutral interactions (collectively termed interventions). These interactions are generally discussed within a framework of “policing” behavior that functions to promote social stability (Flack et al. 2005), although other functions have also been proposed. The dominance assurance hypothesis suggests that third party intervention functions to reinforce the third party’s dominance status “by interfering with others’ efforts to rise up the social hierarchy” (Beisner and McCowan 2013). The mating benefits hypothesis suggests that third party intervention functions to increase the likelihood of the third party gaining mating access to one or both of the conflict participants (Beisner and McCowan 2013). The self-protection hypothesis suggests that third party intervention functions to reduce the likelihood that aggressors will direct further aggression at the third party (von Rohr et al. 2012).

Third-Party Initiated Interactions with Aggressors in Monkeys and Apes

The social stability hypothesis has received the most support in the literature (see Table 3.1). Researchers report that the third-parties tend to be high-ranking (Beisner and McCowan 2013; Flack et al. 2005, 2006; Petit and Theirry 1994; Ren et al. 1991; van Rohr et al. 2012; Watts 1997), interventions occur most frequently during high-intensity conflicts or are associated with reducing the intensity of conflicts

(Beisner and McCowan 2013; Flack et al. 2005, 2006; Petit and Theirry 1994), and interventions in one group of captive chimpanzees (*Pan troglodytes*) were also more likely to occur during periods of social instability, e.g. introduction of new members and male rank reversal (van Rohr et al. 2012).

Not all interventions are performed by high-ranking individuals, though. Tajima and Kurotori (2010) reported intervention by an adult female and juvenile male in conflicts directed at a new female in a small group of captive orangutans and infants and females in 2 bimale groups of gorillas intervened in male-male conflicts simply by getting in between the males (Sicotte 1995). Yamagiwa (1987) reported that aggressive policing of conflicts initiated by older, higher ranking males against younger males in a long-lasting all-male band was performed by younger males in support of the victim of aggression.

While third-party initiated interactions with aggressors have not been widely examined, the species in which it has been reported tend to be ones in which one or a few individuals can have a strong influence on the nature of group interactions, i.e. the dominance hierarchy is relatively important and/or uni-male social organization. This raises interesting questions about whether or not third-party interventions occurs in bonobos who tend to have a relaxed dominance hierarchy (Kuroda 1980; Vervaecke et al. 1999; but see Stevens et al. 2008) and multimale-multifemale social organization. Their close phylogenetic relationship to chimpanzees, in which policing has been reported, however, suggests that they may engage in this complex third-party interaction.

The main goal of the present study is to examine whether or not third-party initiated non-aggressive interactions with aggressors occur in bonobos and under what circumstances and to test the four hypotheses that have been proposed:

1. Predictions from social stability: If social stability is the primary function of third party intervention, then it is expected that conflicts with intervention will be of shorter duration than conflicts without intervention and intervention will be more likely to be performed by adults with high rank.
2. Predictions from dominance assurance: If dominance assurance is the primary function of third party intervention, then it is expected that third parties will intervene in the conflicts of social competitors, i.e. adults will intervene in conflicts involving other adults of the same sex.
3. Predictions from mating benefits: If mating benefits are the primary function of third party intervention, then it is expected that adult males will intervene in conflicts involving adult females.
4. Predictions from self-protection: If self-protection is the primary function of third party intervention, then it is expected that frequent recipients of the aggressor's aggression will be more likely to intervene.

Methods

Data were collected August 5, 2009 – December 16, 2010 from the bonobo (*Pan paniscus*) colony at the San Diego Zoo. The colony was composed of 10 individuals (Table 3.2). The bonobos have indoor (off exhibit) and outdoor (560m²) enclosures and cannot move between them at will. All observations took place at the outdoor enclosure. The bonobos came out in two groups of varying composition:

morning, approximately 9:00a.m.-12:30p.m., and afternoon, approximately 12:30-4:30p.m. Sub-group composition was manipulated to vary as a way to simulate fission-fusion but was also influenced by keeper and veterinary husbandry decisions and remained relatively stable over time. Both groups had access to water and a variety of foods distributed throughout the enclosure daily, liquefied foods in an artificial termite mound, and scheduled daily feeding from keepers at approximately 11:00a.m. and 2:00p.m.

Data Collection

Data were collected using instantaneous scan sampling and all occurrences sampling for conflicts (Altmann 1974). Scans were collected at 2-minute intervals and included inter-animal distances (IADs) and social behavior for all visible individuals (Table 3.3). A total of 16,888 behavior scans were collected (562.93h) over 226 days.

When conflicts occurred, scan collection stopped and behavior was recorded using a digital voice recorder (DVR) to allow detailed data collection on the aggressor and victim during and after the conflict. The conflict data include: aggressor, victim, third-party initiated contacts with aggressor and victim, and duration of aggression (de Waal and Yoshihara 1983). The end of a conflict was determined to be after the last aggressive act as long as aggression did not resume for 10 minutes. Collecting the data with the DVR also enabled collecting data on simultaneous or co-occurring conflicts. Data were collected on 397 conflicts, 84 of which were incompletely described and were discarded retroactively.

Aggressive contacts with aggressors are not part of this analysis as they were considered new conflicts in support of the victim and the focus here is non-aggressive

interactions. Neutral interactions, termed interference here, include interposition (physically getting in between aggressor and victim), obstacle (non-aggressive, non-affiliative contact that appears meant to stop rather than harm the aggressor) the aggressor, and attempting to take display branches or stop the aggressor's display by grabbing the display branches. Interposition has been reported in the literature (Sicotte 1995; Tajima and Kurotori 2010) but obstacle and attempts to take display branches are reported here for the first time. Affiliative interactions include friendly contacts such as embrace, groom, or sexual contacts (Table 3.3).

Research Interns

Scan data were collected by the author and a group of research interns participating in COGS 160 Videography Studies Laboratory at UCSD under the guidance of Prof. Christine Johnson. All interns underwent extensive training in bonobo behavior and data collection methods with Prof. Johnson, the author, and experienced interns. Students had to pass an inter-observer reliability test (agreement at least $K = 83\%$) to participate in data collection. All conflict data were collected by the author.

Data Analysis

Of 313 conflicts with complete data, 39 (12.5%) included third-party initiated affiliation with the aggressor, third-party interference, or both. Of the total number of conflicts, 32 (10.2%) included third-party initiated affiliation with the aggressor, 15 (4.8%) included third-party interference, 24 (7.7%) included affiliation without interference, and 7 (2.2%) included interference but no affiliation (2.2%). Given the

relatively small sample size, third-party initiated affiliation and interference (collectively termed intervention) were considered together for most analyses.

Conflicts were divided by which aggressors received third-party intervention, which third parties intervened with conflicts and to which aggressors they directed the intervention, and how often the third party was the first to offer affiliation (in most cases where third-party interventions occurred, multiple third parties participated). Conflicts with third-party interventions were also divided by the age and sex of the aggressors and third-parties, as well as the age and sex combinations of the conflict dyads and aggressor-third-party dyads. The only adolescent in the group was considered with the adults.

Social Stability Hypothesis

Predictions of the social stability hypothesis were tested comparing the duration of conflicts with and without intervention using a Kruskal-Wallis test and the age of interveners (adult v. immature) were compared using a z-test for proportions.

Dominance Assurance

Predictions of the dominance assurance hypothesis were tested by comparing the age combination of the aggressor-third-party dyad (adult-adult, adult-immature, immature-immature) using a z-test for proportions. Adolescents might also be concerned with their emerging role in the dominance hierarchy but there was only 1 adolescent and she was grouped with the adults.

Mating Benefits

Predictions of the mating benefits hypothesis were tested by comparing the sex combination of the aggressor-third-party dyad and compared using a z-test for proportions.

Self-Protection Hypothesis

Predictions of the self-protection hypothesis were tested by examining the rate of aggression received by the third-party from the aggressor compared to the third-party's tendency to intervene. Dyads were divided into 2 classes of aggression, high and low, by calculating the mean rate of aggression each aggressor initiated against their victims and classifying dyads as high if the rate of aggression the third-party received from the aggressor was above the mean and low if it was below the mean.

Results

Thirty-nine conflicts included third-party interventions. Of these, 32 (82%) included third-party initiated affiliation, 15 (38.5%) included interference, 24 (61.5%) included affiliation but not interference, and 7 (17.9%) included interference but not affiliation. Affiliation and interference were directed at 4 aggressors, G, I, J, and N with 6 distinct conflict dyads represented (see Table 3.4). A significant majority of the conflicts were male-male (FF = 2, $z = -3.7365$, $p < 0.00001$; FM = 2, $z = -3.7365$, $p < 0.00001$; MM = 35, $z = 7.4730$, $p < 0.000001$) and among adults (adult = 38, $z = 8.492$, $p = 0$; mixed = 1, $z = -4.0762$, $p < 0.0001$; immature = 0, $z = -4.4159$, $p < 0.00001$). Seven individuals initiated third-party affiliation with 61 total affiliations in 32 conflicts and 2 individuals interfered in 15 conflicts (see Table 3.5).

Social Stability Hypothesis

Conflicts with interventions were significantly longer than conflicts without interventions: mean with intervention = 463s, mean without intervention = 95s (Kruskal-Wallis, adjusted $H = 6.6.31$, d.f. = 1, $p = 0.01002$). Immature individuals initiated affiliation with aggressors significantly more often than adults: adults = 6 ($z = -6.2738$, $p < 0.00001$); immature = 55 ($z = 6.2738$, $p < 0.00001$). Looking more closely at which individuals initiated affiliation with which aggressors, three of the juveniles, K, M, and Y initiated affiliation most and G was the most frequent recipient of affiliation (see Table 3.6); their affiliation with G accounts for 77% of all instances of affiliation. All of the interference was initiated by 2 juveniles, K and M. K interfered with G in 11 conflicts and with J in 4 and M interfered with G in 1 conflict; no adults engaged in interference behavior. These results do not support the social stability hypothesis.

Dominance Assurance Hypothesis

Immature individuals offered affiliation to adult aggressors significantly more than any other age combination: adult dyad = 5 ($z = -4.1646$, $p < 0.0001$); mixed age dyad = 56 ($z = 9.6873$, $p = 0$); immature dyad = 0 ($z = -5.5227$, $p < 0.000001$). Two immature individuals interfered in 15 adult conflicts and no adults performed interference behaviors. These results do not support the dominance assurance hypothesis.

Mating Benefits Hypothesis

Male-male conflicts were the most likely to receive third-party initiated affiliation from both female and male third parties while conflicts involving females received significantly lower than expected affiliation: female third-party-FF conflict =

1, $z = -3.1493$, $p < 0.001$; female third-party-FM conflict = 0, $z = -3.4928$, $p < 0.001$; female third-party-MM conflict = 37, $z = 9.2188$, $p = 0$; male third-party-FF conflict = 2, $z = -2.8057$, $p < 0.01$; male third-party-FM conflict = 1, $z = -3.1493$, $p < 0.001$; male-third-party-MM conflict = 20, $z = 3.3783$, $p < 0.001$. Interference only occurred in MM conflicts. These results do not support the mating benefits hypothesis.

Self-Protection Hypothesis

In examining the rate of aggression each third-party received from each aggressor to whom they offered affiliation, there were only 2 third-parties that directed affiliation at frequent aggressors: B→I (18 conflicts initiated by I toward B) and M→J (11 conflicts initiated by J toward M; see Table 3.7) and these two individuals only directed affiliation at these aggressors once each. The other 8 third-party-aggressor dyads were dyads in which aggression occurred at a low rate. The three dyads with the highest rates of affiliation during conflicts had very low rates of aggression. These results do not support the self-protection hypothesis.

Discussion

The results of this study do not support any of the current hypotheses proposed for third-party affiliation or interference with aggressors during conflicts, each of which predicts that adults will be more likely to engage in intervention behaviors. The data demonstrate an overwhelming majority of interventions in this group of bonobos were conducted by immature individuals (92.1%), not adults. Additionally, 3 of the 4 immature individuals are orphans who do not benefit from the social support of their mothers, making their intervention in conflicts among adults rather surprising because of the potential risks. Most of the interventions occurred during conflicts among the

two adult males, meaning the orphans were comfortable approaching the adult males during aggression without fearing they would be victims of that aggression. G is the father of K, T, and Y, which could mitigate some of the risk of approaching him during aggression, although it is unclear what bonobos understand about paternity and he is not the father of M, who also interacted with him during aggression. K is also the daughter of the oldest female in the group, N, and that may provide her with greater social power and support, so it is possible that her interventions, particularly the interference, may fit into a policing function and support the social stability hypothesis. If that were the case, however, it would be surprising that she is the *only* individual in the group to consistently police MM conflicts.

Since this study does not offer support for any of the proposed hypotheses, it calls into question the function of intervention with aggressors during conflict. One individual, G, received 86.9% of interventions. Why was this one individual so often the recipient of affiliation during conflicts?

Stress, physiological arousal, is a common response to conflict and is particularly expected in victims of aggression. In primates, evidence of physiological arousal includes piloerection, self-scratching, self-grooming, or stereotypic behaviors and many studies of conflict management have examined how the stress response is affected by post-conflict affiliation, particularly in macaques and chimpanzees (Aureli, 1997; Aureli et al., 1989; Aureli and van Schaik, 1991a,b; de Waal and Aureli, 1997; Koski and Sterck 2007). Typically, these studies find that post-conflict affiliation, especially with the former aggressor, reduces evidence of the stress response in victims. While most studies of these studies have focused on the post-conflict stress

response in victims of aggression, aggressors also experience PC stress (*Papio anubis*: Castles and Whiten, 1998; *Macaca fascicularis*: Das et al., 1997, 1998; *Macaca fuscata*: Schino et al., 2007; *Papio hamadryas*: Romero et al., 2009). Evidence of physiological arousal was not systematically recorded in this study but G was the only individual to consistently show any clear evidence of stress. During conflicts G would often pace, scream, tap his chest, solicit contact from other individuals by screaming with a bared teeth expression, and/or auto-groom. It may be that the intensity of G's stress response, even as the aggressor, explains why he received the majority of interventions, particularly third-party initiated affiliation, although no precedent for this has been reported in the literature.

Empathy has been suggested as the motivation for offering consolation to victims of aggression (de Waal and Aureli, 1996) and I would speculate it is a possible motivation for offering affiliation to aggressors, particularly if the aggressor shows a high level of stress and is clearly more stressed than the victim. Clay and de Waal (2013) reported a high rate of consolation initiated by juvenile bonobos at Lola Ya Bonobo, suggesting that the capacity for empathy is at least present in young bonobos. The suggestion that the immature individuals in this group were motivated to offer affiliation to an aggressor by empathy is speculative and requires testing with systematic data on the stress response in aggressors during conflict but the fact that affiliation was offered near exclusively to the only clearly stressed aggressor is highly suggestive.

Early emergence of the capacity for empathy may offer an explanation as to why juveniles offer consolation to victims of aggression and affiliation to aggressors

but it does not address why these behaviors were less likely to be expressed by adults in this group. It is highly unlikely that the capacity for empathy diminishes as individuals age so another explanation for the relatively low participation by adults is required. It may be that adults have a more complex set of social concerns that influence their behavior; adults may have to take more factors into consideration before offering affiliation in these contexts.

Nevertheless, none of the previously proposed hypotheses for third-party affiliation and/or interference with aggressors are supported by this study. It is important to note that this is the first time this behavior has been reported in bonobos, the behavior was relatively rare in this group, and one study of one captive population cannot definitively answer any question or rule out any possibility. Follow-up research with this group and comparisons to other captive and wild populations of bonobos is required before any strong conclusions can be drawn.

Chapter 3, “Non-Aggressive Third-Party Initiated Interactions with Aggressors during Conflict in Captive Bonobos (*Pan pansiscus*),” is being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this material.

Table 3.1 Summary of key studies of third-party initiated interactions with aggressors in primates

Species	Setting	Hypotheses Tested	Conclusions
Golden Monkeys (<i>Rhinopithecus roxellanae</i>) Ren et al. 1991	Captive	Social Stability	Males intervene in female conflicts to maintain harmonious female relationships and directed aggressive and non-aggressive intervention at both conflict parties.
Tonkean Macaques (<i>Macaca tonkeana</i>) Petit and Thierry 1994	Captive	Social Stability	Aggressive and non-aggressive contacts were used to end conflicts and aggressors were preferentially targeted; non-aggressive contacts more successful. Males intervened more than females and interveners tended to be higher ranking.
Pigtailed Macaques (<i>Macaca nemestrina</i>) Flack et al. 2005	Captive	Social Stability	High rate of intervention in conflicts, particularly by high ranking individuals, reduced conflict intensity and duration. Interventions were directed at both conflict parties.
Pigtailed Macaques (<i>Macaca nemestrina</i>) Flack et al. 2006	Captive	Social Stability	Knockout experiment. The three most dominant males in the group play a significant role in maintaining social stability. Their presence and intervention in conflicts are associated with a reduced rate of aggression and lower conflict intensity. Interventions were directed at both conflict parties.
Rhesus Macaques (<i>Macaca mulatta</i>) Beisner and McCowan 2013	Captive	*Social Stability Dominance Assurance Mating Benefits	Impartial (undirected) and partial (directed at aggressor or victim) contacts were used and appear to reduce the intensity of aggression. Male and females intervened in conflicts but males intervened in female conflicts most and interveners tended to be higher ranking.
Bornean Orangutans (<i>Pongo pygmaeus</i>) Tajima and Kurotori 2010	Captive	Social Stability	An adult female and juvenile male intervened in conflicts directed against a newly introduced female by getting in between the opponents.
Mountain Gorillas (<i>Gorilla gorilla berengei</i>) Yamagiwa 1987	Wild	Social Stability	An all-male band persisted for 3 years and aggressive policing of conflicts is suggested as a major factor promoting group stability. All initial aggression was initiated by older, dominant males against younger, subordinate males and policing behavior was performed by younger males in support of the victims.

Table 3.1 Summary of key studies of third-party initiated interactions with aggressors in primates, continued

Species	Setting	Hypotheses Tested	Conclusions
Mountain Gorillas (<i>Gorilla gorilla berengei</i>) Sicotte 1995	Wild	Social Stability	Infants and females in 2 bimale groups intervened in male conflicts by simply positioning themselves between the conflict participants. Interpositions increased the time between male-male conflicts.
Mountain Gorillas (<i>Gorilla gorilla berengei</i>) Watts 1997	Wild	*Social Stability *Mating Benefit	Males intervened in female conflicts, typically in support of the less able competitor. This may help maintain social stability by promoting egalitarian relationships among females and it may also help males retain females by protecting immigrant females.
Chimpanzees (<i>Pan troglodytes</i>) van Rohr et al. 2012	Captive	*Social Stability Dominance Assurance Mating Benefit Self-Protection	In one group, policing occurred at a relatively high rate after introduction of new members and male rank reversal. The alpha and beta males were the interveners. In a comparison on 3 groups, policing was most common during instability and high ranking males and females intervened. Interventions reduced the number of conflicts.

Table 3.2 The *Pan paniscus* Colony at the San Diego Zoo (San Diego, CA, United States) and Main Sub-Group Composition

Name	Initial	Sex	Age Class	DOB	Mother/Father
Lana	N	F	Adult	13 April 79	Linda/Kakowet
Lolita	O	F	Adult	20 April 89	Louise/Vernon, nursery
Ikela	I	F	Adult	27 Nov 91	Louise/Akili, nursery
Yenge	G	M	Adult	25 Dec 82	Salonga/Mato, Frankfurt
Junior	J	M	Adult	14 Jan 95	Lana/Maiko
Mchumba	B	F	Adolescent*	22 Dec 00	Lolita/Congo
Kesi	K	F	Juvenile*	15 Aug 04	Lana/Yenge
Makasi	M	M	Juvenile*	22 April 04	Loretta/Jumanji, San Diego Safari Park, nursery
Mali	Y	F	Infant*	4 Sep 07	Ikela/Yenge, nursery
Tutapende	T	M	Infant*	29 Oct 07	Lolita/Yenge, nursery, adopted by Ikela

Group	Dates	%Time
BINJKYT	8/10/2009 – 9/16/2009	8%
INGJKYMY	10/14/2009-11/8/2009	6%
NGJKYM	9/28/2009-12/16/2010	52%
BINOKT	9/14/2009-12/3/2010	34%

*The adolescent was included with the adults in analysis and the 2 juveniles and 2 infants were combined as immatures.

TABLE 3.3 Inter-Animal Distances (IADs), Behaviors, and Conflict Intensity and Context

IAD Code	
0	in contact
1	within arm's reach
3	just beyond lunge distance
5	far
Scan Behaviors	
<i>AFFILIATIVE</i>	
carry	Carry another ventrally or dorsally
contact	Any other friendly contact
groom	With hand(s) and/or mouth
peer (+)	Stare at mouth of eater (+ get food)
play	Wrestle, tickle, chase etc. with other
sex	Any genital contact with other (except grooming)
<i>AGGRESSIVE</i>	
aggress	Threaten, charge, chase, serious bite, hit, etc.
displace	Displace another from its place
display	Push or drag branch & charge, agent only if undirected (<i>not</i> conflict); if directed, charge
Third-Party Interventions	
Affiliative	Groom, embrace, sex
Interference	Interposition, obstacle, take/grab display branches

Table 3.4 Aggressors and Conflict Dyads Receiving Third-Party Affiliation or Interference (Interventions) During Conflicts

Aggressor	No. Conflicts with Intervention	% of Total Interventions
G	31	79.5%
I	1	2.6%
J	5	12.8%
N	2	5.1%
Total	39	

Dyad	No. Conflicts with Intervention	% of Total Interventions
BI	1	2.6%
BN	1	2.6%
GJ	34	87.2%
GN	1	2.6%
JM	1	2.6%
JN	1	2.6%

Table 3.5 Third-Parties Intervening with Aggressors During Conflicts

Third-Party	No. Times Affiliation Offered	% Times Affiliation Offered	Third-Party	No. Times Interfered	% Times Interfered
B	1	1.6%	B	---	---
G	1	1.6%	G	---	---
K	14	23.0%	K	14	93.3%
M	17	27.9%	M	1	6.7%
N	4	6.6%	N	---	---
T	5	8.2%	T	---	---
Y	19	31.1%	Y	---	---
Total	61		Total	15	

Table 3.6 Third-Party Initiated Affiliation with Aggressors During Conflict by Aggressor and Third-Party Identity

Aggressor	Third-Party	No. of Times TP Initiated Affiliation	Percentage of Total Affiliation
G	K	12	19.7%
G	M	16	26.2%
G	N	3	4.9%
G	T	3	4.9%
G	Y	19	31.1%
I	B	1	1.6%
I	T	1	1.6%
J	K	2	3.3%
J	M	1	1.6%
J	N	1	1.6%
N	G	1	1.6%
N	T	1	1.6%

Table 3.7 Comparison of Rate of Aggression Third-Parties Received from Aggressors and the Rate of Affiliation Offered to Aggressors

Third-Party	Aggressor	No. Times Affiliation Offered	% of Total Affiliation	No. Times TP Received Aggression from Aggressor	Total Conflicts Initiated by Aggressor	% of Aggressor's Total Aggression Directed at TP	Aggression Received Above or Below Aggressor's Average
B	I	1	1.6%	18	45	40.0%	above
G	N	1	1.6%	2	78	2.6%	below
K	G	12	19.7%	3	70	4.3%	below
K	J	2	3.3%	2	46	4.3%	below
M	G	16	26.2%	5	70	7.1%	below
M	J	1	1.6%	11	46	23.9%	above
N	G	3	4.9%	5	70	7.1%	below
N	J	1	1.6%	1	46	2.2%	below
T	G	3	4.9%	0	70	0.0%	below
T	I	1	1.6%	0	45	0.0%	below
T	N	1	1.6%	5	78	6.4%	below
Y	G	19	31.1%	0	70	0.0%	below
Average Rate of Aggression Each Aggressor Directs at Each Victim							
G		20.0%					
I		16.7%					
J		14.3%					
N		14.3%					

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CONCLUSION

Group living in primates is an adaptation to ecological and/or predation pressures (van Schaik, 1983; Wrangham, 1980) but it also entails significant costs that emerge from conflicts of interest over access to ecological and social resources (Gowaty, 1996; Parker, 1979; Trivers, 1972; Walters and Seyfarth, 1987) that can manifest themselves in aggressive conflicts. Reconciliation, friendly interaction between former opponents shortly after a conflict, and consolation, friendly interaction directed at the victim of aggression by a third party, appear to be two important mechanisms primates have evolved to help cope with the costs of conflict (Aureli and de Waal 2000). These behaviors have been well-studied in many primates, particularly chimpanzees and cercopithecines, using the framework of the Valuable Relationships hypothesis (Watts 2006): post-conflict affiliation repairs damage to social bonds and, therefore, dyads with valuable relationships should be more likely to reconcile after conflicts. The current study examines the occurrence of reconciliation and consolation in bonobos, testing VR, as well a significant component of VR that, while intuitive, has yet to be widely demonstrated—that reconciliation repairs relationships (Relationship Repair hypothesis: Koyama 2001). Data presented here also examine third-party initiated interactions with aggressors during conflict, which have not been reported in bonobos and were not part of the original study. However, during the course of data collection observations of third-party affiliation during ongoing conflicts prompted me to collect data on those interactions and test their possible functions.

Testing the Valuable Relationships Hypothesis

VR predicts that individuals will be more likely to reconcile conflicts with valuable partners. Analysis of the patterns of conflict management in the San Diego Zoo bonobo colony is inconsistent with this prediction. Overall, the group had a low rate of reconciliation (23.6% of conflicts reconciled), a low CCT (corrected conciliatory tendency; 6.71%), and there was no relationship between reconciliation and relationship quality. Additionally, there was no clear relationship between other relevant variables (sex of conflict participants, conflict intensity or context) and the rate of reconciliation. Consolation occurred more frequently than reconciliation; 47.7% of conflicts were followed by consolation and the group mean TCT was 22.76%.

Patterns of post-conflict behavior presented here are more consistent with the Relationship Security (RS: Schaffner et al. 2005) hypothesis than VR. RS argues that if reconciliation functions to repair damaged social bonds, then secure relationships may not be damaged by conflict and therefore would not require reconciliation, while insecure relationships would be more likely to be damaged by conflict and therefore more likely to reconcile. Of 3 other studies of captive and free-ranging bonobos, one supported RS and two supported VR (Clay and de Waal 2013; Fortunato 2009; Palagi et al. 2004). Taken in the broader context of highly variable support for VR in captive and wild chimpanzees, these results suggest that conflict management behavior in *Pan* may not be best explained by VR and that other proximate factors should be taken into account, including personality and group history.

Testing the Relationship Repair Hypothesis

The relationship repair hypothesis predicts that unreconciled conflicts will lead to a decrease in affiliation and an increase in aggression in the short- and long-term (Koyama 2001). I found that reconciled conflicts were less likely to be followed by continued aggression on the same day than were unreconciled conflicts, which is consistent with RR. However, analysis of long-term patterns of interaction (10 days following conflicts) shows inconsistent support for RR and is more consistent with the predictions from RS. In the 10 days following unreconciled conflicts, there was no decrease in affiliation compared to baseline rates, which suggests the precipitating conflict did not damage the relationship. Similarly, in the 10 days following unreconciled conflicts, there was no change in the rate of aggression. Both of these results are inconsistent with RR.

RR predicts that after reconciled conflicts there will be no change in the rate of affiliation since the reconciliation presumably serves to repair the relationship, i.e. return it to the status quo. The results presented here are consistent with this prediction, rates of affiliation after reconciled conflicts did not differ from baseline rates. However, RR also predicts that aggression will decrease or at least stay the same in the long-term after reconciled conflicts and the results presented here show that aggression actually *increased* in almost all dyads after reconciled conflicts.

The results of this analysis, taken in context with the previous chapter's results and other studies of PCB in both *Pan* species, suggest that VR may not be the most effective explanation for patterns of post-conflict behavior in our two closest living relatives. Personality and group history may be important variables to consider, particularly in captive populations, which are smaller than wild populations and in

which feeding competition is dramatically reduced and group composition may not mirror natural patterns. It is notable that analogous captivity effects are much less marked in monkeys, suggesting that proximate factors play a larger role in determining the behavior of bonobos and chimpanzees. Additionally, data on a variety of social behaviors (e.g., dominance hierarchy, strength of intersexual bonds, rates of aggression, postconflict behavior) in *Pan* vary not only between captive and wild populations but also among captive and wild populations (Boesch and Boesch-Achermann 2000; Colmenares 2006; de Waal 1994; Stevens et al. 2008).

It is also very likely that the methods used to examine reconciliation and other PCB are limited in their ability to capture the complex dynamics at work in *Pan* relationships. The PC-MC method focuses on the first 10 minutes after a conflict. Limiting the time period to 10 minutes makes it reasonable to claim that interactions that take place in those 10 minutes are causally linked to the conflict but there is no reason to believe that *Pan* relationships unfold in 10-minute increments. Bonobos and chimpanzees are highly intelligent, complex animals who form life-long bonds but also live in a flexible, fission-fusion system in which alliances, friendships, and competitors change over time. It is entirely possible that interactions outside of the 10-minute PC observation period are related to the conflict but PC-MC does not have a mechanism for taking that into account. The challenge for primatologists is to develop a method for examining the relationship between interactions that are farther apart in time, including perhaps days apart. *Pan* live in fission-fusion societies in which individuals may go weeks without interacting with each other, presumably their

previous interactions will influence the form of future interactions even if they are far apart in time.

Analysis of data collected using PC-MC also treats each conflict as an isolated event, rather than as one event in an on-going relationship. Hinde (1976) argues that interactions through time constitute relationships and that the sum of relationships in a social group constitutes the social structure. This model presents a strong theoretical framework for understanding the complexity of primate lives but the methods used to assess those relationships fail to get at all of the levels. PC-MC looks at conflict at the level of the interaction and only incorporates one other aspect of relationships, rates of affiliation, when comparing rates of reconciliation between dyads. Even examining the long-term consequences of conflict and reconciliation in testing RR treats “a conflict plus 10 days” as isolated from the rest of a relationship.

What is needed is a method that allows measuring and analyzing relationships diachronically, looking at patterns of interaction over long periods of time. It may be that social network (Wey et al. 2008) or systems analysis (Forster 2002) are more effective analytical methods for capturing the complexity of primate conflict and conflict management behaviors. These are common analytical tools in mathematics but are not widely used in the behavioral sciences. In order to get at the complexity of primate relationships, methodological innovation is necessary.

Third-Party Initiated Interactions with Aggressors

Consolation, third-party initiated affiliation with victims of aggression, has been well-studied in the primate conflict management literature. Less understood are third-party initiated interactions with aggressors during conflicts. The data presented

here serve as a test of the four main hypotheses about third-party initiated interactions with aggressors: social stability, dominance assurance, mating benefits, and self-protection. These hypotheses predict that adults will be most motivated to offer affiliation to aggressors or interfere non-aggressively in conflicts to promote social stability, gain dominance or mating benefits, or to promote self-protection by affiliating with frequent aggressors. None of these hypotheses were supported by the analysis presented here.

Nearly all of the affiliative interactions with aggressors in the San Diego bonobo colony were initiated by immature individuals and were directed at one adult male, G. This pattern of immatures initiating third-party affiliation more than adults is not unique to the present study; Clay and de Waal (2013) reported that immatures were more likely to console victims after conflict than adults were. Immatures presumably have little social power to police the conflicts of adults, are not as invested in the dominance hierarchy as adults, and are not interested in improving their mating access to other individuals. Immatures might be motivated to affiliate with their own frequent aggressors in an effort to curry favor and reduce the likelihood the aggressor will direct aggression at them but G, the recipient of the overwhelming majority of third-party interactions from the 3 immature individuals, very rarely directed aggression at any of them.

G was the only individual in the group to show consistent, clear evidence of stress during and after conflicts, whether he was the aggressor or the victim. It is possible that the immature individuals were motivated to affiliate with him in an effort to calm him. If this is the case, it demonstrates that the capacity for empathy emerges

early in bonobos and that young individuals can be motivated to act in response to the emotional states of others. This, of course, begs the question of why adults do not offer affiliation to aggressors since they presumably also have a capacity for empathy. It may be that the other social concerns of adults—dominance, mating, competition over social partners—must be taken into consideration when deciding whether or not to affiliate with aggressors.

General Conclusions

This dissertation serves as an additional test of VR and the first test of RR in bonobos, as well as the first description of third-party interactions with aggressors during conflicts in bonobos. None of the hypotheses tested here were supported. What this suggests is that, while VR has been a very productive framework for nearly 40 years, it may be time to reevaluate its role in understanding PCB in nonhuman primates, particularly *Pan*. Support for VR in the literature is strong, particularly in cercopithecines, but studies of *Pan* have demonstrated highly variable results that require examination. Reconciliation and consolation are clearly important components of conflict management in *Pan* but the dynamics of relationships may be more complex than the hypothesis captures. Similarly, additional conflict related behaviors such as third-party affiliation with aggressors need to be examined more systematically and in more species. With this dissertation, there are still only 4 studies of reconciliation and consolation in bonobos using standard methods and the VR framework and all 4 studies have been with captive populations. In order to get at the nature of conflict management in bonobos, more research is required, particularly with wild populations.

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