Abstract

Megan E. Upshaw. RECONCILIATORY BEHAVIOR IN CAPTIVE FEMALE CHIMPANZEEES (*Pan troglodytes*). (Under the direction of Dr. Linda D. Wolfe) Department of Anthropology, May 2008.

Between May 29th and July 31st I studied the behaviors of the nine adult female chimpanzees at the North Carolina Zoological Park in Asheboro, North Carolina. Data were collected using focal animal observations in which females were observed for 20-minute intervals. A standard ethogram was employed. While resting was generally recorded most often, the females engaged in affiliative behaviors an average of 19.78% of the time, with a range of 8% to 32%. The two highest ranking mothers in the group, MG and RT, had the highest levels of affiliation (28% and 32%, respectively). During the study period I also recorded four conflicts between eight of the nine females: MG, RB, BA, TM, RT, AM, MK, and TR. In all four conflicts, one of the females was chased by at least one other female, and in two conflicts, a female was struck by BA, the daughter of the highest ranking female, MG. After three out of the four conflicts, I observed reconciliation between those involved. These post-conflict reconciliation behaviors included kissing, grooming, sitting close to one another, and reaching. The data show that there is an association between rank, age, and affiliation in the post-conflict reconciliation.
RECONCILIATORY BEHAVIOR IN CAPTIVE FEMALE CHIMPANZEEES

(Pan troglodytes)

A Thesis Presented to
The Faculty of the Department of Anthropology
East Carolina University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Arts in Anthropology

by
Megan E. Upshaw

May 2008
RECONCILIATORY BEHAVIOR IN CAPTIVE FEMALE CHIMPANZEES
(Pan troglodytes)

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Chapter I

Introduction

Much has been written on the subject of chimpanzee alliances and reconciliatory behaviors. However, the focus has been on the males of this species. My project, on the other hand, concentrated on the reconciliation behaviors in female chimpanzees. During this study I collected data on the nine female chimpanzees living at the North Carolina Zoological Park in Asheboro, North Carolina. Because the females in this zoo were separated from the males for much of the study, dominance and other social relationships have to be mitigated through their own actions. Furthermore, this kind of study is important for understanding how captivity affects behavior. Not only are the demographics of their group determined by their keepers, but the nature of their captivity makes reconciliation even more important. Because fleeing from aggression is not an option, the females have to resort to other methods of conflict resolution, namely reconciliation. How the females of this group cope with tension and aggression through reconciliation is, therefore, a facet of their life in captivity. The living condition of the nine females, segregated from the males, constitutes a natural experiment of female reconciliation.
Through this research, I found that the females do use reconciliation. However, they do not seem to engage in conflicts very often, which may explain why so little has been done to study female reconciliation. Several patterns emerged when looking at how reconciliation occurred, who initiated reconciliation, toward whom reconciliation was directed, and so forth. In general, there seems to be an association between dominance rank, aggression level, and age with conflict and post-conflict behaviors.

A more in depth description of these findings and the study follows in the subsequent chapters. Chapter II discusses the objectives of this study and its theoretical background. Chapters III, IV, and V review the relevant chimpanzee literature, including the history of chimpanzee studies in chapter III, social patterns among chimpanzees in chapter IV, and reconciliation in chapter V. My hypotheses for the study and expected results are described in chapter VI. In chapter VII, I describe the methods for this study. It includes my descriptions of the subjects, the study area, and the data collection and analysis techniques. Chapter VIII presents the results of data collection. The descriptions of the conflicts and post-conflict behaviors I observed comprise chapter IX. Finally, chapter X presents the discussion and conclusions of the study.
Chapter II

Objectives and Theoretical Background

There are two main aims for this thesis project. The first is to gain a better understanding of reconciliation in a non-human primate species closely related to our own species. Chimpanzees, as evidenced by their complex social structure and behaviors, possess social cognitive abilities, not unlike our own (Koyama et al., 2006). The second aim is to better understand how female chimpanzees use reconciliation in their social relationships. This topic has been overshadowed by reconciliation and coalition formation among male chimpanzees. The absence of males in the study group provides a unique opportunity to study these behaviors without the distraction of showier versions of reconciliation in males.

The theoretical background in which this study was conducted is based in socioecology. Socioecology argues that the environment that a species lives in is related to its social structure (Sussman, 1997; Wolfe, 1997). Environmental factors shape a variety of elements in the social structure of a species, including the ways in which individuals array themselves on the landscape, how or which species can coexists within the same habitat, and which sex is most likely to disperse from its natal group.
However, it may seem counterintuitive to apply socioecology to a group living in an artificially controlled environment. Lately, the validity of reconciliations observed among captive chimpanzees has been questioned, but numerous studies have found that these questions are generally unfounded. Preuschoft et al. (2002) confirmed the presence of reconciliation in captive chimpanzees using more stringent methods, the PC-MC method (see below for description). Furthermore, Colmenares (2006) concluded that the distinction between wild and captive studies was largely meaningless. First, he argues that the range of variation in behaviors exhibited in the wild and in captivity often overlap, thus not as straightforward as the wild/captive dichotomy would assume. Second, variation in site-specific behaviors may make captive-specific factors, like the lack of predators and food dispersal, less important. For example, social behavior may be affected more by the sex ratio among adults or group size (Colmenares, 2006). Third, methodological differences between studies may, at least partially, account for differences between wild and captive studies. Lastly, there is little empirical evidence to suggest a dichotomy between wild and captive studies in general (Colmenares, 2006). It is not, therefore, a stretch to apply socioecological theory to a study of captive chimpanzees.
Chapter III

History of Chimpanzee Studies

Robert Yerkes was one of the first to study chimpanzees, studying them both in the wild and in a captive breeding colony he established at Yale University in the early 20th century (Yerkes, 1943). However, the most well-known study was, and still is, conducted by Jane Goodall on the chimpanzees at Gombe in Tanzania. In 1960, Louis Leakey sent her to Gombe to study wild chimpanzees, thus beginning one of the longest running studies on chimpanzees (Stanford, 2008). In addition to Gombe, there are a total of six field sites that have conducted research for twenty or more years- Gombe and Mahale in Tanzania; Budongo, Ngogo, and Kanyawara in Uganda; and Taï forest in Ivory Coast (Stanford, 2008). The studies conducted at these and many other research sites in Africa have increased our knowledge of chimpanzees several times over- observing tool-use (Goodall, 1988; Boesch and Boesch-Achermann, 2000; etc.), cooperative hunting (Boesch and Boesch-Achermann, 2000), and many other behaviors thought to be limited to humans. Even now, primatologists are debating the existence of chimpanzee material culture, long held as the distinctive human behavior (Stanford, 2008).
Yet, while we learn more and more about our closest living relatives, there is still much that we do not understand.
Chapter IV

Social Patterns among Chimpanzees

Although studies of chimpanzees had begun much earlier, their social organization wasn’t understood until the mid-1970s when it was discovered by Toshisada Nishida and his team (Stanford, 2008). Chimpanzee societies are described in terms of fission and fusion-large communities consisting of smaller, separate parties within a territory. These parties vary in age, sex, and number and their composition changes throughout the day as members leave and join the party, making chimpanzee society one of the most complex societies among mammals (Stanford, 2008). This fluid system is largely a response to fluctuations in food availability (Strier, 2003). In this way, chimpanzees come together when food is readily available, but separate to reduce competition when it is not. Communities may not be highly cohesive, but their territory is well-defined and guarded by patrolling males (Stanford, 2008).

While all chimpanzees are sociable, sex-specific differences have been observed. Males are more gregarious than females; they are often seen in the company of other males, engaging in social or cooperative behaviors like hunting, grooming, or patrolling their community borders (Stanford, 2008). This increased sociality may be
due to two factors. The first is that males remain in their natal communities after reaching sexual maturity. This would mean that males have kin with which to be social. Second, increased male cohesion is important when defending territory from neighboring males. Intragroup competition between males for dominance and access to females also leads them to form alliances and coalitions with other males.

Females, conversely, travel principally with only their youngest offspring, although this varies between communities (Stanford, 2008). In addition to the lack of kin other than their offspring, an explanation of decreased sociality among females is that it decreases competition for resources. While access to females limits the reproductive success of males, it is access to resources that limits female reproductive success. Therefore, females, especially those with offspring, maximize their reproductive success by avoiding others (Stanford, 2008). The exception to this is when a female is seeking mates.
Reconciliation

Reconciliation is defined as a “post-conflict friendly reunion of former opponents that restores their social relationship disturbed by the conflict” (Aureli and de Waal, 2000: 388). Reconciliations normally occur within a short time after the conflict, but sometimes it takes hours for a reconciliation to occur. de Waal (1998) observed that the former opponents were tense from the end of the conflict to the reconciliation, but that the tension would dissipate as soon as the reconciliation occurred. de Waal and his students found that reconciliation has a distinctive behavioral pattern—outstretched arm with an open hand, increased eye contact, more kissing, yelping, and soft screams (1989). These behaviors are more likely to be observed during the first post-conflict contacts, while others, like play, are rarely seen at all (de Waal, 2000). They also found that reconciliation is initiated by dominants and subordinates equally, although dominants are less likely to initiate after severe attacks (de Waal, 1989).

The concept of reconciliation presents several interesting ideas about the nature of those we study. First, this concept “implies (a) an increased probability for friendly interaction after aggressive conflicts, (b) that former opponents actively seek out one another for these
friendly reunions, and (c) that these contacts function to mend a disturbed relationship” (Preuschoft et al., 2002: 30). Second, reconciliation requires that individuals are able to identify other individuals and to shift quickly between emotions (de Waal, 1989). This is an indication of the high cognitive and social abilities of subjects. Finally, the idea that reconciliation is a mechanism for conflict resolution among valuable relationships helps to explain why these behaviors are performed between close or cooperative individuals (de Waal, 1998).

The dominant method by which researchers study reconciliation is the post-conflict observation- matched control observation, or PC-MC, method. This method is used to determine whether affiliation observed after a conflict is a result of that conflict or part of normal behavior (Veenema, 2000). One day after an observed conflict and post-conflict affiliation, an observation sample is conducted at the same time as a control. With these data, three kinds of investigations are used to test for the influence of conflict. The first uses the time in which it takes subjects to engage in affiliation in both PC and MC observations. If affiliation only takes place or takes place sooner in the PC, then the pair is attracted; if it only takes place in the MC or later in the PC, then the pair is dispersed (Veenema, 2000). A pair
can also be classified as neutral if affiliations occur at the same time in both the PC and MC or if no affiliations occur at all. The second type of investigation compares the rates of affiliation between the PC and MC (Veenema, 2000). The third defines the frequency of first affiliations as a function of time and compares them in the PC and MC (Veenema, 2000). The main advantage to these, and the PC-MC method as a whole, is that they provide a mechanism by which reconciliation can be quantified and its study standardized, allowing for comparison between species (Veenema, 2000).

Reconciliation, as a concept, is relatively new, having only emerged in 1979 (Colmenares, 2006). In the 1960s, scientists studied the possible evolutionary heritage of human aggression and assumed that aggression is inherently destructive (de Waal, 2000). Studies like Goodall’s (1988) study at Gombe showed that chimpanzees were not the peaceful vegetarians that we once thought; they engaged in both intergroup and intragroup violence, hunted and ate other primates, and sometimes engaged in cannibalism. However, this, and other studies from the time, often made reference to reassurance and appeasement behaviors (de Waal, 2000). These kinds of behaviors were overlooked by the sociobiological stance of the 1970s, which emphasized conflict. Yet the groundwork was laid, so that by the end
of the 1970s, conflict resolution studies could come about. We had come to know the functions of grooming as tension-relieving, knew that there was a connection between an aggressive event and the affiliation that followed, and could distinguish the difference between social interactions and social relationships (de Waal, 2000).

It is through this theoretical background that de Waal’s recognition and discovery of reconciliation in a nonhuman species emerged. This discovery in 1975 came about while he was studying a group of captive chimpanzees housed in an indoor enclosure. After a charging display that led to a male attacking a female, there was silence within the enclosure until the chimpanzees hooted while the attacker and his victim embraced (de Waal, 1989). It was then that de Waal realized that reconciliation was not limited to humans. Since his discovery, much has been done to study reconciliation in nonhuman animals. Studies of other species have been conducted, finding the same kinds of behaviors, as well as the replication of chimpanzee studies (de Waal, 2000). Methods for studying reconciliation in a standard and quantifiable way, like the PC-MC method described above, have emerged. Finally, evolutionary models for why these kinds of behaviors exist, like the Relational Model, have been posited and debated among scientists (de Waal, 2000). As more
studies are published, we learn more about the process of 
reconciliation and the social relationships that are maintained through 
reconciliation.

Although the importance of these studies cannot be 
overestimated, they have generally ignored half of the communities 
they study- females. Focus has been on coalition formation and 
reconciliations among male chimpanzees because these behaviors 
have profound effects on dominance rankings (de Waal, 1998). 

Wrangham and Peterson (1996), for example, regard female strategies 
as important but entirely secondary to those of males. They recognize 
that females are capable of aggression and alliance formation, but 
claim that “female chimpanzees act as if they just don’t care about 
their status as much as males do” (Wrangham and Peterson, 1996: 
191). Some of the only alliances attributed to females are those they 
form with males. Examples of female associations exist in the 
literature, like those in Bossou, Guinea; however, in order for stable 
relationships to emerge among females, they need to spend time 
together (Wrangham and Peterson, 1996). Because females in the 
wild spend much of their time alone, the opportunity to do so is 
severely limited. It is therefore among captive groups that the most 
stable female relationships come about. Captivity provides the
opportunity for constant contact that allows females to form and sustain alliances (Strier, 2003). The alliances that females are able to form are an important part of reconciliation studies, and may account for why so little has been done to study female reconciliation behaviors.

However, aggression and alliance formation behaviors are present in female chimpanzees. At Gombe, Goodall (1988) noted that the females had their own dominance hierarchy, with Flo as the alpha female. Flo gained her high rank due to the fact that she “was exceptionally aggressive toward her own sex, and she would tolerate no insubordination from young adolescent males” (Goodall, 1988: 124). However, the Gombe females did not form alliances. Goodall often saw the mothers Flo and Olly travel together, but their relationship was not like that of a male coalition. Neither would go to the other’s aid and Flo was frequently aggressive towards Olly. Goodall writes that the “only time I did see them united was when they ganged up on a young stranger female” (Goodall, 1988: 124-125). This kind of alliance was observed at other times and only among adult females. Goodall posits that this may be due to increased territoriality among females because their ranges are smaller than that of males or jealousy. Females at Taï forest are much
different than those at Gombe. Boesch and Boesch-Achermann (2000) found that Taï forest females frequently associated with one another, shared food, and supported each other. They were also more active grooming partners than seen at other sites and interfered in male interactions, something not seen in other chimpanzee populations. They argue that high levels of competition between females and the fact that they often interfere in male interactions make female friendships and alliances important at Taï (Boesch and Boesch-Achermann, 2000). To these two examples we can add de Waal’s study of captive chimpanzees. At the Arnhem colony, de Waal (1989) found that 47% of male-male conflicts resulted in reconciliation, while only 18% of female-female conflicts ended in reconciliation. This sex difference in reconciliation may be due in large part to the fact that males reconcile to formalize and stabilize the dominance hierarchy; females reconcile based on personal preference (de Waal, 1989).
Chapter VI

Hypotheses and Expected Results

Using the above knowledge, I posit two hypotheses. First, I hypothesize that among the North Carolina Zoo females there will be both aggression and reconciliation. Conflicts coupled with the inability to avoid or escape during or after these conflicts, make reconciliation important among these chimpanzees. In order to maintain an overall peaceful setting, former combatants would need to reconcile more often than corresponding combatants in the wild. Second, the individual that initiates reconciliation after a conflict will be determined on an individual level by effects of dominance rank and levels of aggression. This is consistent with the valuable-relationships hypothesis, for which Watts (2006) found support among the chimpanzees at Ngogo. This hypothesis states that variation observed in social relationships is due to the value of the specific relationship. Value is based on the benefits that an individual is likely to gain from the actions of the other in the relationship and can be unequal between partners (Watts, 2006). This value influences reconciliation. Because the variables of dominance rank and level of aggression affect relationships, and therefore the value of relationship, I would predict that these factors would also affect reconciliation tendencies.
Based on the above-mentioned hypotheses, I have made several predictions as to the results of my study. A previous study of these chimpanzees noted high levels of aggression, especially by the four highest ranking females (Griffin, 2006). However, because these females live in a confined area, I would expect to find large numbers of reconciliations among these chimpanzees. I further expect that reconciliations will be initiated more often by the lower ranking and less aggressive female involved in an aggressive encounter. Although de Waal (1989) noted that dominants and subordinates are equally likely to initiate reconciliation, I feel that the tyrannical nature of the highest ranking females will make them less likely to initiate. My null hypothesis will be that there is no correlation between age, rank, and level of aggression on initiation and participation in reconciliations.
Chapter VII

Methods

Subjects

Table 1: Subjects

<table>
<thead>
<tr>
<th>Name</th>
<th>Birth Date</th>
<th>Mother</th>
<th>Father</th>
<th>Rank</th>
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<td>Unknown</td>
<td>3</td>
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<tr>
<td>RB</td>
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<tr>
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In the following section, I describe each of the chimpanzees listed in Table 1 and give my overall impression of them.
Because her birth origin is unknown, keepers estimate TR’s age to be approximately 38, making her the oldest chimpanzee at the NC Zoo. She arrived at the NC Zoo in 1980. Probably due to her old age, she is distinguishable as largely bald - her face and back of her neck are completely bald while her hair is thin on the rest of her body. Her skin is very dark, although she has some pink mottling on her chin. She is also recognizable by her large but thin physique.

TR often spent most of the day napping or lounging in a shady spot in the enclosure, but this laid-back persona, to me, often felt like a cover for her tougher interior. She was quick to anger and was often at the forefront when investigating arrivals to the indoor enclosure or threatening the occasional raccoon wandered past their enclosure. The keepers remarked that although she was lower ranking than MG
and BA, she often did not recognize her lower status and tried to act as the alpha female.
RB- RB is the daughter of RT and KO and was born at the NC Zoo on December 16, 1996. She was taken by keepers when RT rejected her and was raised with JO. RB looks like a younger version of her mother, complete with a droopy lip and prominent brows. She has some pink mottling around her mouth and chin and a gray beard.

RB is the most social of the chimpanzees at the NC Zoo. She interacted with all of the other chimpanzees, grooming and being groomed for much of the day. She interacted with zoo visitors, and she was the only female of the group that regularly acknowledged my presence. She would often greet me by “blowing kisses” and would not stop until I made the same face to her.
MK - Born March 6, 1994 at the NC Zoo, MK is the daughter of TM and KO or RD. She is thin and small, with a body that is all black except for a gray beard. She is easily identified by her bottom, which is very pink and sticks out farther than any of the other female.

MK is a quiet chimpanzee that spent much of her time out of sight. She would often come out in the morning to eat, disappear into the dry moat that surrounds the outdoor enclosure, and not reappear until she got hungry again in the afternoon. When she was visible, she socialized with most of the other chimpanzees, not picking up the anti-social behavior of her mother, TM.
MG- MG’s birth date is estimated to be around 1973. Her birth origin is unknown. She arrived at the NC Zoo in 1980. MG is easily identifiable by the fat deposits on her back legs when she walks, and her severely hunched position when she sits. In addition to her hunched position, she also has scrunched, old-looking face with a gray beard, making her look like a crotchety old lady.

MG is the alpha female in the group. She rarely started fights among the females, but she almost always got involved once one was started. She was groomed by almost all the other females, but groomed only a few of them. Overall, she both looked and acted in a very gruff manner.
The daughter of MG and KO, BA was born at the NC Zoo on December 18, 1987. She is recognizable by the little hair she has on her face, shoulders, and arms, her prominent brow ridges, and large ears that stick out. She also has a large belly and a white beard.

Of all the chimpanzees at the NC Zoo, BA seemed to be the most aggressive. As the daughter or MG, the alpha female, she had a constant ally and used this to her advantage. She was involved in most of the fights and was the most likely to hit or bite another chimpanzee. This is best reflected in a fight in the indoor enclosure during which she bit off a portion of AM’s left pinky toe.
RT- Although we know that RT was born in the wild, the location of her birth is unknown. Keepers estimate that she was born around 1971, and she was brought to the NC Zoo in 1980. She is the largest of the chimpanzees and is distinguishable by the large bald spot on her back and shoulders. She is also fairly bald on her face and has a droopy lip, giving her a sort of goofy expression most of the time.

RT has a laid-back personality; it takes a lot to get her riled-up. She is the mother of RB, as well as other chimpanzees that have been removed from the zoo. She refused all of her babies and they had to be cared for by the keepers. Because she would not care for her
infants, she was placed on several different kinds of birth control
before finally having a tubal ligation in 2001.
Photo 7: BT

BT- Brought to the zoo in 1979, keepers estimate BT’s birth date to be around 1973. She was wild born, but the exact location is unknown. She is the mother of AM. She is recognizable by the white mottling on her face, especially around her nose. Her hands and feet also seemed whiter than the other chimpanzees’. She is one of the smallest of the chimpanzees, with a little gray behind her head and a gray beard.

BT is a quiet chimpanzee. She rarely got involved in squabbles and spent most her time hanging out on the fringes of the higher ranking groups. She spent most her time with TR. She did not spend much time with AM; in my opinion, she spent most of her time keeping
her own position in the group secure and didn’t have time to, or didn’t want to, associate with her low-ranking daughter.
AM - AM was born at the NC Zoo on December 24, 1983. She is the daughter of BT and KO. She has the whitest back of all the other females with some spots that appear whiter on her sides. She is also identifiable by the shape of her mouth; when closed, it forms a W-shape. She has some pink mottling around her mouth and a little pink spot under her left nostril.

AM is the second lowest ranking female in the group. She was often the victim of the other females’ aggression, especially by BA, and was not aided by her mother. According to the keepers, the only reprieve that she gets is when her estrus is fully swollen. However, once it starts to deflate, one of the higher ranking females will attack
her, to “put her in her place”. Despite this, AM is still fairly social and hangs out as close to the group as they will allow her.
TM - TM was born in the wild, somewhere in central Africa, sometime around 1971. She is easily recognizable due to the large area of depigmentation on the left side of her chin. She is fairly small, with some gray hair on the top of her back, and appears to be going bald on the top of her head. She often sat with her shoulders hunched and her arms crossed.

TM is the lowest ranking female, and has a reserved demeanor. She spent most of the mornings in the moat around the outdoor enclosure while the rest of the group was out, and then spent most of the afternoon in the hammock in the horizontal tree while the group lounged in the shade of the moat. This is not to say that she never
interacted with the other chimpanzees, but she rarely did so and
stayed on the fringes of groups. She often bore the brunt of the other
females’ aggression and was quick to try and appease them. MK is her
daughter, but I rarely observed the two interacting.
HN - HN is estimated to have been wild born around 1975, but his birth location is unknown. He was confiscated, along with KO, when his owners returned to the United States from Africa, and then brought to the NC Zoo in 1978. HN has a very gray beard and hair on his head and back. His right eye is cloudy.

HN is the easiest of the chimpanzees to like. He spends most of his time in front of the windows, which makes him a favorite of the zoo visitors. He quickly learned to recognize me, head-bobbing in the morning to greet me. He is the alpha male of the group. He receives special treatment from the keepers due to a terminal illness.
JO- JO was born at Emory University in Atlanta on December 7, 1996. He was brought to the NC Zoo to be raised with RB by keepers. He is easily recognizable as one of the youngest chimpanzees, due to his still mostly brown face. His skin is mottled near his eyes, hairline, and on his ears. He also does not have a beard. Despite being larger than HN and many of the other chimpanzees, he is fairly low ranking.

JO is a fairly quiet chimpanzee. He came to the glass to interact with the zoo visitors occasionally. He preferred to spend his time hanging out with RB or MK. He particularly liked to hang out on and under the viney tree.
**LN, SK, and KN**

LN, SK, and KN are the newest members of the chimpanzee group at the NC Zoo. They were all just coming out of quarantine when I began my research at the zoo, and were being introduced throughout my study period. LN and SK are 6 year-old males and were brought to the NC Zoo from the Miami Metro Zoo in Florida. KN is an 8 year-old male and had previously been in the entertainment industry.
**Study Area**

During the summer of 2007, I collected data at the North Carolina Zoological Park (NC Zoo) in Asheboro, North Carolina, which is located in the Uwharrie Mountains approximately 75 miles west of Raleigh. Spread over 11 acres total, the NC Zoo endeavors to recreate the natural habitats of the animals it holds (Hackney and Jones, 2008). The chimpanzees are located in the African portion of the zoo, in the BB&T Kitera Forest exhibit (see Figure 1).

**Figure 1: Kitera Forest Exhibit Site Plan**

[Image: http://www.ursainternational.org/nczchimp.html]
This one-acre exhibit includes two viewing areas, a smaller one designed to look like a field research station and the main viewing and interpretation area (see Photos 12 and 13 below). From these two viewing areas, I made all of my observations. The only portion of the exhibit not visible from these two areas was the dry moat which surrounded the exhibit on three sides.

**Photo 12: Main Viewing Station**
Photo 13: Research Station
Data and Analysis

I conducted my study Mondays through Fridays, from May 14th to July 31st at the North Carolina Zoological Park, for a total of 37 days or 172 hours. I began with initial observations during the first two weeks of my study, May 14th through May 24th. During this initial period, I learned to identify the subjects, familiarized myself to their outdoor enclosure, and identified behaviors to use on my checksheet (see Appendix B). These two weeks account for 9 days or 42 hours of my total observation time.

Between May 29th and July 31st I collected the actual data for my study using focal animal sampling. Each of the nine females were observed continuously for a sample period of twenty minutes, several times during the day. To insure that the same female was not observed at the same time every day, I randomized the order in which the females were observed for each study day. This was done by giving each female a number and then using the random number generator function on a TI-83 calculator to generate the daily order. Additional data were collected using ad-lib sampling of conflict and post-conflict behaviors. When a conflict was observed, the focal sampling was temporarily stopped and the participants and their behaviors were recorded for the conflict. After the conflict, focal
animal sampling data were recorded for one of the participants, preferably one that had not been recorded already that day. During post-conflict observations, special attention was paid to affiliative gestures between participants, as evidence of reconciliations. Data were recorded using diary entries and checksheets (see Appendix B). The checksheet included affiliative, submissive, aggressive, vocalizations, and other behaviors. A standard ethogram was employed (see Appendix A). The behavior that the focal animal was performing at the beginning of the minute was recorded on the checksheet for each of the twenty minutes. Also, if the focal animal was interacting with another chimpanzee, the initials of that chimpanzee were also recorded.

I was originally informed that the chimpanzee group would be divided into one group with the nine females and another with males HN, JO, and the newer males. Instead, when I first arrived, there was a coed group- consisting of TR, RB, MK, HN, and JO- and an all female group- containing MG, BA, RT, BT, AM, and TM. The other males came out of quarantine just as I was beginning my observations. Because the focus of this study was on the female chimpanzees, data were not collected on the males. However, if a male was interacting with the focal female, I did record those observations. The chimpanzees
remained in these groups until June 11th, when the females were reintroduced to one another. They came back onto display June 14th. On June 27th, the keepers decided to pull RT out of the female group to be introduced to KN, since his introductions to HN and JO had not gone well. She remained out of the group until July 31st, when she was reintroduced and TM was pulled out to be introduced to KN. HN and JO were introduced to the two younger males- LN and SK- on July 25th with no problem.

The chimpanzees had an irregular schedule for being on and off display. From May 14th through June 11th, the keepers tried to keep to a schedule of two days on, two days off, but this was not always possible. Quite frequently, one of the chimpanzees would refuse to come inside and shift so that the other group could be let outside. Between June 11th and June 28th, only the females were on display. After June 28th, the groups would alternate on and off display.
Chapter VIII

Results

The following pie charts show the various behaviors collected by focal animal sampling methods. Pie charts for total behaviors and affiliative behaviors are shown for each female. Some females have additional charts for specific affiliative behaviors, depending on whether they were observed engaged in the behavior and if they engaged in the behavior with more than one other female.
This figure represents the total percentage of observed behaviors performed by the female AM during the study period. She was most often observed resting. She was observed to engage in affiliative behaviors 10% of the time.
This figure shows the total percentage of observed affiliative behaviors engaged in by AM. The majority of her affiliative behaviors involved sitting close to another individual, especially her mother BT (21% of all affiliative behaviors). AM also only received grooming and reached out to her mother.
This figure represents the total percentages of grooming performed by AM on another individual. AM engaged in allo-grooming equally towards BT, BA, and TR.
This figure indicates the total percentage of time AM sat or lay close to another individual. She was most often observed close to BT, 25%, followed by TR at 21% and MG at 18%.

These figures (Figures 2, 3, 4, and 5) show aspects of AM’s behavior. It is interesting to note that AM engaged in affiliation less than resting and feeding. She was also observed to be out of sight more often than affiliating. AM engaged in affiliative behaviors most often with BT. She was observed to engage in allo-grooming, receive
grooming, sit close to and reach to BT during the study period. It should be noted that AM is the daughter of BT.
This figure shows the total percentage of observed behaviors by the female BA. She was most often observed as resting, 35%, and was out of sight 25% of all observations. She was observed to be engaged in affiliative behaviors 20% of the time.
Figure 7: Total Percentage of Affiliative Behaviors- BA

This figure represents the total percentage of affiliative behaviors observed for BA. For 24% of the total affiliative behaviors, BA was observed to sit close to TM. She was only observed to engage in mutual grooming with RT.
This figure represents the total percentage of allo-grooming BA performed on another individual. She was observed to groom MG, her mother, and MK an equal percentage of samples.
This figure depicts the total percentage of grooming received by BA from another individual. She was observed to receive grooming from TM and BT, most frequently from TM, 60%.
This figure shows the total percentage of time that BA was observed to sit or lay close to another individual. She was most frequently observed close to TM, 33%, and MG, 29%.

These figures (Figures 6, 7, 8, 9, and 10) show an unexpected pattern of the behavior of BA. She often engaged in affiliative behaviors with the lowest ranking females, especially TM. For example, she was observed to sit close to TM 24% of all her affiliative behaviors. This is unexpected both because BA is a high ranking
female and because she often directed aggression towards lower ranking females (see conflict descriptions below).
This figure represents the total percentage of behaviors observed for BT. She was observed resting most frequently- 38% of the time. BT engaged in affiliative behaviors 23% of the time.
This figure shows the total percentage of affiliative behaviors performed by BT. She was most frequently observed sitting close to AM, her daughter. She was also frequently observed sitting close to TR and RT, two females close to her in age and rank. She was only
observed to engage in mutual grooming with AM and only received grooming from TM.
This chart depicts the percentage of grooming performed by BT on other individuals. BT was most frequently observed to groom TR, 37%, followed by MG, 29%.
This figure represents the total percentage of time BT spent sitting close to another individual. She was observed to sit close to AM (29%), RT (21%), and TR (20%).

These figures (Figures 11, 12, 13, and 14) show that BT engaged in affiliation with AM more often than with other females. This mirrors what I found with AM. BT also affiliated often with TR. BT groomed TR the most and sat close to TR quite frequently. Finally, BT was observed to sit close to all of the females in the group.
Figure 15: Total Percentage of Behaviors- MG

This figure represents the total percentage of behaviors observed for MG. She was the only female to be observed most frequently engaging in affiliative behaviors- 28%. She was also frequently observed to be out of sight- 27%- or resting- 24%.
This chart represents the total percentage of affiliative behaviors engaged in by MG. She was most often observed sitting close to RB. She also only groomed RB.
This figure depicts the total percentage of grooming received by MG. She was groomed 25% of the time each by RT and RB and 19% of the time each by AM and TR. The rest of the time MG received grooming from BT.
Figure 18: Total Percentage of Sitting or Laying Close - MG

This graph represents the percentage that MG was observed to sit or lay close to another individual. She was most frequently observed to sit close to RB. She also sat close to TR and BA.

These figures (Figures 15, 16, 17, and 18) show MG to engage in affiliation often and with most of the group. As mentioned above, MG was the only female observed to engage in affiliation more than any other behaviors. Further, she was observed to engage in affiliation with all the females of the group, except MK. It appears that MG had a preference for RB; she was only observed to groom RB, received
grooming 25% of all observations from RB, and sat close to RB most often.
This chart represents the total percentage of behaviors performed by MK. She was most frequently out of sight, accounting for 25% of all observed behaviors. She was observed to engage in affiliative behavior 19% of the time, the same percentage as feeding and resting.
This figure represents the total observed affiliative behaviors for MK. She was most frequently observed grooming herself. She only engaged in mutual grooming with the young male JO.
This chart shows the total percentage of grooming performed by MK on other individuals. She most frequently groomed MG.
This graph depicts the percentage of grooming received by MK by others. JO and TR were observed to groom MK equally.
This figure shows the total percentage that MK was observed to sit or lay close to another individual. She was most frequently observed to sit close to the alpha male, HN, and the alpha female, MG.

These figures (Figures 19, 20, 21, 22, and 23) show MK to be both social and antisocial. While she was observed to engage in affiliative behaviors 19% of all observations, she was observed to be out of sight 25% of all observations. Furthermore, of all the observations of affiliative behaviors, 53% were auto-grooming.
However, MK did engage in affiliation with most of the group, especially JO, AM, and MG.
This figure represents the total percentage of behaviors observed for RB. She was most frequently observed as resting. She engaged in affiliative behaviors 24% of the time.
Figure 25: Total Percentage of Affiliative Behaviors - RB
This chart represents the total affiliative behaviors observed for RB. She most frequently engaged in auto-grooming.
This figure represents the grooming performed by RB on other individuals. She groomed JO, TR, RT, and MG equally.
This figure represents the total percentage of mutual grooming that RB engaged in. She engaged in mutual grooming equally with TR and RT, 40% each, and the rest of the time with MG.
This graph shows the total percentage of grooming received by RB. She was groomed the majority of the time by JO.
This figure represents the total percentage that RB was observed to sit or lay close to another. She was observed to sit close to all of the other chimpanzees, but most frequently RB was observed to sit close to MG.

These figures (Figures 24, 25, 26, 27, 28, and 29) show RB as the social butterfly I observed her to be. She had a high percentage of affiliative behaviors and affiliated with both the male and female members of the group. RB was also the only female who engaged in both submissive and aggressive behaviors.
This chart represents the total percentages of observed behaviors for RT. She was most frequently observed to be resting. RT has the highest percentage of affiliative behaviors- 32%.
This figure shows the total percentage of affiliative behaviors engaged in by RT. She was most frequently observed to engage in mutual grooming with AM and sitting close to TR.
Figure 32: Total Percentage of Allo-grooming- RT

This graph shows the percentages of grooming performed by RT. She was observed to groom MG most frequently.
Figure 33: Total Percentage of Mutual Grooming- RT

This figure represents the total percentage of mutual grooming engaged in by RT. The majority of mutual grooming was between RT and AM.
This figure represents the percentage of grooming received by RT. She was observed to receive the most grooming from RB, her daughter.
This figure shows the percentage that RT was observed to sit or lay close to another. She was most frequently observed sitting close to TR, 25% of the time, as well as RB and BT, 23% each.

These figures (Figures 30, 31, 32, 33, 34, and 35) show RT as a very social chimpanzee. She engaged in affiliation more than any of the other females. It seems as though she preferred to engage in affiliation most frequently with the females of her own rank and those above her own rank. She also engaged in a lot of affiliation with her
daughter, RB. The only females RT didn’t affiliate with were MK and TM.
This chart represents the total observed behaviors for TM. She was most frequently observed to rest. She also had the lowest percentage of affiliation of any of the females - 8% of all behaviors.
Figure 37: Total Percentage of Affiliative Behaviors- TM

This figure shows the total observed affiliative behaviors for TM. 91% of the time TM was observed to engage in auto-grooming.
Figure 38: Total Percentage of Sitting or Laying Close- TM

This chart shows the percentages of time that TM was observed to sit or lay close to another. She sat close to TR 75% of the time and sat close to RB 25% of the time.

These figures (Figures 36, 37, and 38) show TM to be an antisocial chimpanzee. She had the lowest percent of affiliation of all the females and the only females she was observed to interact with TR and RB. I seldom observed TM to interact with others, and this fits with my general impression of TM and her low rank in the group.
This figure represents the total percentage of behaviors observed for TR. She was observed to rest most frequently- 63%. TR engaged in affiliative behaviors 14% of the time.
Figure 40: Total Percentage of Affiliative Behaviors - TR

This figure represents the total observed affiliative behaviors for TR. She was most frequently observed to sit close to BA and MG. TR was observed to reach only to RB.
This chart represents the percentage of allo-grooming performed by TR. For 50% of observations, TR groomed RT.
Figure 42: Total Percentage of Mutual Grooming- TR

This chart shows the mutual grooming that TR engaged in during the study period. 50% of observations involved TR engaged in mutual grooming with RB.
This chart represents the grooming received by TR from others. She was most frequently observed to receive grooming from BT.
This chart represents the percentages that TR was observed to sit or lay close to another individual. She was most frequently observed to sit close to BA, 23%, and MG, 21%.

These figures (Figures 39, 40, 41, 42, 43, and 44) show that, despite her high rank, TR engaged in affiliation only 14% of all observations. However, she did engage in affiliation with many of the females. Her grooming partners tended to be those close to her dominance rank, i.e., RB, RT, and BT. TR was also observed to sit close to most of the members of the group, with the exceptions of HN, RT, and TM.
Chapter IX

Conflicts and Post-Conflict Behaviors

While at the NC Zoo, I observed four instances of conflict between the females. Below, I describe these conflicts and the post-conflict observations which followed. As mentioned above, after each conflict I chose one of the main participants for focal animal sampling, preferably one that had not already been observed that day. Eight of the nine females were observed in at least one of the conflicts: MG, RB, BA, TM, RT, AM, MK, and TR. In all four conflicts, one of the females was chased by at least one other female, and in two conflicts, a female was struck by BA, the daughter of the highest ranking female, MG. After three out of the four conflicts, I observed reconciliation between those involved. These post-conflict reconciliation behaviors included kissing, grooming, sitting close to one another, and reaching.

June 22nd

At 12:00 pm, I observed screaming and running by most of the group. BA ran at TM, and was followed by MG and RB. BA struck, with her hands, TM several times. RB’s behavior during this conflict was interesting. She chased TM with the others, but it appeared as though she struck BA a few times. BA, MG, and RB eventually stopped
chasing her, but TM continued to scream until 12:02. At 12:03, MG, with piloerection, or raised hair, displayed at the observation windows.

At 12:04 I began post-conflict observations on TM. The group seemed to settle down into grooming groups except for TM, who sat by herself on the horizontal climbing tree. Around 12:07, RB and MK moved close to TM in the tree and RB smelled or kissed TM’s foot, which seemed to be wounded. TM barked twice and moved off a little, but RB moved close again. She looked at TM’s face and kissed her face. At 12:11, RB stopped kissing TM but remained sitting close. MK moved closer. At 12:12, RB resumed kissing TM’s foot while TM held it up, but RB moved off at 12:13 and MK moved off at 12:14. TM spent the rest of the observation period resting in the hammock and licking her wound.

Around 2:00 that same afternoon, MG briefly swayed at TM (a presumed aggressive act), who was sitting at the fringe of the group. TM groomed MG until 2:03 when BA approached the dyad and brandished a stick at TM. TM grinned and walked to RT. BA joined the group but sat on the other side of RT. TM groomed RT for a minute and then just sat with MG and RT until 2:08.
June 27th

At 9:14 am, RT and AM were engaged in mutual grooming near MK. The three began screaming and RT chased AM until all three females were sitting in the horizontal climbing tree. MK’s role in this conflict is unclear. She ran in front of AM, but separated before RT finished chasing AM. It appeared as though she was mostly in the way, but she could have been involved. The entire conflict took place in less than a minute.

At 9:15, post-conflict observation was conducted on AM. AM reached her hand toward RT but was refused. AM then wrapped her arms around herself. From 9:17 to 9:18, MK sat close to AM and they engaged mutual grooming. They moved off for a minute, but returned to sit close to each other near RT. AM traveled to the water fountain and RT followed her. After a drink, AM walked out of sight over the top of the left hill. At 9:27, AM returned over the middle of the left hill, eating and resting. At 9:30, BT appeared over the same area and sat close to AM for approximately two minutes before moving off. AM stayed on the hill for the remainder of the observation period.

July 23rd

At 11:51 am, I observed AM coming up the back hill from out of sight. She hooted in greeting to MG and TR, who were sitting close to
each other. TR got up to watch AM, while MG began to sway. TR then
chased a screaming AM for a short distance. MG followed, but walked.
TR and MG stopped and sat on the left hill. AM continued to run
screaming over the right hill and out of sight.

At 11:54, I began post-conflict observations of AM. At this
point, AM walked up to MG on the left hill and kissed her face. BA
arrived soon after and walked up to AM, who walked off. BA followed
her, sniffing her bottom. AM walked toward TR, but skirted around her
and just sat near. BA sat close to AM, who began to groom herself.
Around 11:56, TR and BA ran off to the right hill. AM stayed put for a
few seconds before moving behind the left hill to forage. She went in
and out of sight as she foraged until 12:01 pm, when she traveled
from the left hill to the fallen tree and eventually the horizontal
climbing tree to sit and feed. At approximately 12:11, BA moved near
AM in the horizontal climbing tree where they both stayed until the
end of the observation period.

**July 24th**

At 10:58 am, RB ran past the windows of the main viewing area.
Two minutes later, TR ran past followed by BA. BA then hit TR in the
back. Both screamed at each other and TR chased BA onto the
horizontal climbing tree. MG followed the two, but walked along and was not really involved in the conflict.

At 11:01 I began observation of TR, at which point she, MG, and BA walked over to the right hill. MG and BA paused to sit near TR but they moved on shortly. At 11:04, BT approached TR and sat close to her for two minutes. TR then moved behind the right hill but quickly returned to her spot at a banging noise coming from the indoor enclosure. She rested for a few minutes before moving to the back hill to look at the doors, and then moved to the left hill to sit near BA. At 11:13 she moved back to her spot on the right hill where she remained until the end of the observation period.
Conclusions

From my observations of these fights, I can conclude several things about the relationships of these female chimpanzees. First, aggression among the females is directed at lower ranking females. In all four conflicts, aggression was directed by a female or females toward a female who was lower ranking than themselves, and in three conflicts, aggression was directed toward the two lowest ranking females, AM and TM. Second, reconciliation, in all three cases it was observed, was initiated by the lower ranking female and, therefore, the recipient of the aggression. Third, reconciliation was first directed to the highest ranking female involved in the conflict. Following the two conflicts in which she was involved, MG, the alpha female, was the female to which reconciliation was directed. Furthermore, she was the only aggressor involved in these conflicts to which grooming and kissing were directed. The lower ranking females only sat close to the other females involved, if they did so at all. It is also interesting to note that no reconciliatory gestures were directed at BA. Finally, the two youngest females, RB and MK, were at the fringes of aggression in two of the conflicts, but were involved in post-conflict affiliation. In both cases, they engaged in grooming and sitting close to the recipient of the aggression.
It is also important to discuss the sole conflict in which reconciliation did not follow. The only conflict in which there was no reconciliation, between BA and TR, the females are very close in rank, second and third respectively. Additionally, I observed little affiliation between these two females. TR was observed to sit close to BA, but neither groomed the other at any point in my observations. It may be that neither wanted to acknowledge a lower rank by initiating reconciliation, or the lack of affiliation observed after the conflict was merely a return to their normal state of behavior towards each other.
Chapter X
Discussion and Conclusions

At the beginning of this project, I made several predictions about the results. First, I predicted that there would be large numbers of reconciliations between the females. I did not find this, largely because there were so few conflicts during the study period. Despite these low levels of aggression, 75% of conflicts I observed were followed by reconciliation. I also found that these conflicts were usually associated with some outside impetus. For example, the conflict on June 22nd was associated with the introduction of KN to HN and JO in the indoor enclosure. This suggests that female fights are very rare and that the high levels of aggression previously found was the result of some outside force. This may explain why so little attention has been paid to female reconciliation in the literature. However, no matter how rare these conflicts may be, the fact that reconciliation occurs emphasizes its importance.

My second prediction was that lower ranking and less aggressive females would be the ones to initiate reconciliations. I found support for this hypothesis in my study. Although there were low levels of aggression among all of the females, lower ranking females were the recipients of aggression, rather than the aggressors. Furthermore,
they were the only ones I observed who initiated reconciliation. The only case in which there was not reconciliation following a conflict, the females involved were high ranking and had both been aggressors in previous fights. Further studies need to be done to see if this is a normal pattern for females or idiosyncratic to the females at the NC Zoo. Because the females at the zoo have such a structured dominance hierarchy I would suspect that among other groups with a similar hierarchy, they would also share the same pattern for reconciliation.

The results of the time budgeting are also interesting. All of the females engaged in affiliation with the other females, but the amount of time they spent in affiliation varied. They ranged from 8% to 32% and averaged 19.78%. There was no real pattern that emerged to determine which females would have higher affiliation percentages. For the most part, higher ranking females had higher affiliation percentages, but TR, the third ranking female, engaged in affiliation only 14% of the time, the third lowest percentage. Mothers also generally had higher affiliation scores than non-mothers, but TM had the lowest score of all the females and RB had a higher score than two of the mothers, BT and TM. The lack of definite pattern in time budgets suggests that it is highly idiosyncratic.
Limitations of the Study and Implications for Future Research

This study was limited due to the small sample size—only nine females. It was further limited because of captivity. Although Colmenares (2006) and others found that captive studies are equally valid to field studies when studying behavior, the lack of food competition may account for the low levels of aggression I observed. These low levels of aggression also constitute a limitation for my study. It follows that without conflict, you cannot study post-conflict behaviors.

Despite these limitations, I feel that my study does have implications for further research. I observed that 75% of conflicts were followed by reconciliation, indicating that previous studies were mistaken to ignore reconciliation among females. The rarity of conflicts, however, indicates that long-term studies would have to be conducted in order to gather enough data to clearly understand the nature of female chimpanzee reconciliation.
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Appendix A: Ethogram

Affiliative

Allo-Groom- Grooming another chimpanzee

Mutual Groom- Grooming another while being groomed by the same individual

Receive Groom- Is groomed by another individual

Auto-Groom- Grooming self

Present for Groom- Presents body part to another individual to be groomed

Embrace- Puts arms around another individual

Kiss- Places lips on the lips or other body part of another individual

Co-Walk- Walks beside another individual with their hand on the other’s back

Sit/Lay Close- Sits or lays within arm’s reach of another individual

Reach- Extends arm and hand toward another

Reach and Run- Extends arm and hand toward another and runs hand over the back as the other individual walks past

Submissive

Pout- Facial expression in which the subject allows the bottom lip to droop
Grin- Facial expression in which the subject bares both top and bottom teeth

Present- Presents bottom to another

**Aggressive**

Head Bob- Bounces head up and down

Charge- Runs past or toward another, generally without touching, or the glass

Display- Attempts to exert dominance through threatening, charging, etc.

Sway- Moves from side to side while sitting or standing

Threaten- Attempts to intimidate another, normally through facial expression or brandishing weapon

Piloerection- Raises their hair

Hit- Strikes another, usually with their hands

Bite- Bites any part of another

**Other**

Beg- Reaches out to another individual for food

Feed- Eats

Forage- Searches for food while traveling, also includes feeding while traveling

Travel- Walks or runs
Rest- Lays, sits, or stands without doing anything else, especially beyond arm’s reach of another chimpanzee

**Vocalizations**

Bark

Hoo

Pant

Scream-Nervous

Whimper

Scream-Aggressive

**Out of Sight**
Appendix B: Checksheet

Subject:       Date:       Start Time:       Stop Time:       

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