Effect of Food Availability on Social Behavior in a Captive Group of Bonobos (*Pan paniscus*)

A Senior Project

presented to

the Faculty of the Biological Sciences Department

California Polytechnic State University, San Luis Obispo

In Partial Fulfillment

of the Requirements for the Degree

Bachelor of Science

by

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February, 2012

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Abstract:

Bonobos (*Pan paniscus*) tend to have low frequencies of aggression due to a suite of affiliative behaviors that are thought to relieve group tensions. A few of these possible behaviors are grooming, sociosexual activities, and strategic positioning in regards to proximity with other individuals at food sites, where most aggression occurs. This observational study sought to determine whether captive bonobos exhibit certain social behaviors at different rates, and have differing proximity preferences in regards to other individuals, when food was and was not available. Results show that when food was available, the apes were less affiliative with fewer counts of grooming, but with higher rates of sexual activity. In addition, animals were found to be in proximity with at least one group member less often when food was available. There were very few recorded aggression events throughout the study, and no significant difference in rates of aggression when food is and is not available.

Introduction:

Primates are known to be very social creatures and they express this through an extensive repertoire of behaviors. Bonobos (*Pan paniscus*) are no exception. When researchers attempt to describe the demeanor of bonobos they often draw comparisons with their well known and heavily studied closest relative, the common chimpanzee (*Pan troglodytes*). Despite the similarities in their appearance, bonobos and chimpanzees have very different social systems and engage in some very different social behaviors.

The degree and dynamics of intraspecific aggression differs profoundly in these two species of *Pan*. Closely related male chimpanzees tend to have affiliative relationships with each other. They can form coalitions to dominate and defend their social groups. Females, on the other hand, tend to remain mostly solitary in "core areas" within their party's range (Goodall, 1986, 1992). Chimpanzees are often characterized by their violent behavior which extends to all sex combinations (Wrangham and Peterson, 1996; Parish, 1994; Goodall, J. 1986, 1992). In comparison, bonobos show relatively little aggression and exhibit some unique tension-reducing strategies and appeasement behaviors (Wrangham and Peterson, 1996; de Waal, 1987). Neither sex seems to be completely dominant over the other and females, rather than males, form tight, lasting bonds (Parish, 1994).

Bonobos, like other apes, have a dispersal pattern where females emigrate from their natal groups, therefore leaving their relatives, upon reaching maturity (Parish, 1994). Despite not being related, female bonobos traveling together in a party tend to form tight bonds with each other (Parish, 1994; Wrangham and Peterson, 1996; de Waal and Lanting, 1997). These affiliative relationships are thought to be formed as a way to ensure group cooperation and make it possible for females to secure control over food resources instead of males (Parish, 1994). During instances when a male acts aggressively toward a female or tries to take over a food source it is not uncommon for other females in the group to offer support by "ganging up" to drive the male away (Wrangham and Peterson, 1996; Parish, 1994). Due to this female support network, male-female violence is rare and most of the aggression that occurs within a group of bonobos is between males. Researchers have noted, however, that these aggressive events occur less often and are less severe than those that occur between all sex combinations in common chimpanzees (Wrangham and Peterson, 1996; Kano, 1992). Researchers have also noted that

food is involved in most aggressive bonobo exchanges, such that aggressive events with out food, or similar excitement as a catalyst, are rare (Sannen et. al., 2004; de Waal, 1987).

The way that animals position themselves at a food source seems to be of some importance in terms of reducing aggression. White and Lanjouw found that when possible, foraging bonobos typically avoid sitting within one arms length of other individuals (White and Lanjouw, 1992). When feeding at smaller food patches, however, it is harder for the animals to feed without coming into close proximity with each other. Dominant females often band together to gain preferential access to the food source and are often able to maintain their access by displacing males and lower ranking females (Parish, 1994). Unequal access to food and more confined feeding conditions are two possible reasons why more aggression typically occurs at small food sources compared to larger, spaced out ones (Kano and Mulavwa, 1984; White and Wrangham, 1988). In response to the tendency of food patch size to influence aggression, studies have shown that the size of bonobo parties in the wild relate to the size of available food patches (White and Wrangham, 1988). This means that when only small patches of food are available the animals passively reduce competition and increase feeding efficiency by splitting into smaller groups, so as not to crowd their food source (White and Wrangham, 1988). Due to the confines of captivity, bonobos in zoos cannot use fission-fusion to decrease tension in their groups and so they must find other ways to decrease tension.

The general lack of aggression among bonobos suggests that these apes use behavioral mechanisms to reduce tensions before they have a chance to boil over to full blown aggression. Sannen et al. (2004) investigated the possibility of a tension-reducing mechanism in the captive bonobo colony at the Wild Animal Park Planckendael (Belgium) and found that when the apes were crowded into a smaller, indoor enclosure during winter the rate of aggression amongst the

group did increased, but this change was slight in comparison to the increases in allogrooming and sociosexual behavior (Sannen et al., 2004). The role of these behaviors had been ascertained prior to the Sannen et al. (2004) study. Allogrooming can bring some immediate relief to group tension through the production of endorphins that cause a relaxing effect on participants (Henzi and Barrett, 1999). Grooming may also contribute to the long term stability of a group by facilitating the formation and maintenance of long-term social bonds and may even be used as a "currency" in exchange for grooming reciprocation, or for services such as agonistic support (Henzi and Barrett, 1999; Kanngiesser et al., 2011; Dunbar, 1991; Vervaecke and Van Elsacker 2000). Sociosexual behavior can also have a strong impact on group stability. Bonobos have an extensive, and in many ways, unique repertoire of sexual behaviors. Copulation, mounting, genital rubbing, and other sexual contacts occur between bonobos regardless of sex and age classes (adult-adult, juvenile-juvenile, adult-juvenile, homosexual, heterosexual), and these behaviors are especially frequent during feeding, or when a new food patch is discovered (Parish, 1994, White and Lanjouw, 1992; Kano, 1992). Sociosexual behavior is thought to reduce tension during these highly excitable circumstances when there is the most potential for aggression and can also serve as a reconciliatory measure should tensions boil over (Hohmann and Fruth, 2000; Parish, 1994; de Waal, 1987).

This study seeks to determine whether captive bonobos at the San Diego Zoo's Safari Park exhibit certain social behaviors more frequently, and have differing levels of tolerance and preference in regards to the proximity of other individuals in different contexts; when provisioned food is and is not available. This study predicts that there will be more aggressive (increased tension) and sociosexual behaviors (diffusion of tension) when food is available and more grooming activity (maintenance and encouragement of long term social stability) when

food is not available. It also predicts that animals will spend less time in close proximity to others when food is available and that the group members that an individual prefers to have in close proximity will change depending on the food circumstance.

Methods:

Behavioral observations were conducted on the bonobo colony at the San Diego Zoo's Safari Park in Escondido, California. The troop consisted of six members, four mature adults and two juveniles (table 1). Loretta, Lenore, Erin and Kalli have lived together at the Safari Park as a stable group for several years, while Ikela and Tutapenda were moved into the group from a bonobo colony at the San Diego Zoo about three months before observations for this study began. It should be noted that Erin and Kalli are Loretta's biological offspring and Tutapenda is Ikela's adopted son. This study does not control for kinship, even though several of the individuals in the group are related (Table 1).

Observations were conducted from guest viewing areas and from an area at the edge of the mote that contains the animals that is not accessible to guests. There were typically three observation sessions a day, every Monday through Friday from June 27th, 2011 to August 5th, 2011, totaling in 30 days of observation. Two ethograms were used each day that were a part of a larger project. Two of the daily sessions focused on the animal's social behavior and consisted of ten minute focal follows with continual scan sampling for certain aggressive and affiliative social behaviors (table 2, ethogram 1). These sessions were conducted at the time that the animals were released from their indoor bedrooms in the morning, usually around 9:15am, and again at 2:30pm. Keepers scattered food before the bonobos were released in the morning but in the afternoon there was no provisioned food available. A midday session used a different ethogram

and consisted of 15 minute focal follows that captured the bonobo's overall activity budget and also involved continual sampling for several aggressive and affiliative social behaviors as well as some abnormal behaviors that are being analyzed in another study (table 3, ethogram 2). This session was conducted every day starting at 11:00am and covered a mid-day food toss. Therefore, food was provisioned in the morning when the animals were first granted access to their outdoor enclosure and at about 12:00pm, toward the end of the midday observation session, when the keepers fed them lunch. There was no provisioned food available at the start of the midday session or during the afternoon session.

All information was gathered using a clipboard and stopwatch with behavioral states recorded at one-minute intervals. Occurrences of specific behavioral events were also tallied continuously for each focal animal. The order in which each individual was observed rotated each day. There were a total of 81 focal sessions per individual. The total amount of observation time spent using ethogram 1, which included proximity data along with social and activity budget data, summed to 67 hours. The total amount of time using ethogram 2, which included social and activity budget data, but not proximity data summed to 43 hours and 30 minutes.

Summaries of behaviors were first calculated by dividing either the number of minutes each animal performed a behavioral state, performed a behavioral event, or was in close proximity with another individual, by the number of minutes that the focal animal was visible during the observation session. These proportions take into account that the animals were not always visible to the observer during focal periods. The average proportions of each behavioral state and each social-affiliative and social-aggressive event were compared for the entire group by performing t-tests to compare behaviors when provisioned food was and was not available. The same protocol was used to determine if there were any differences in proximity preference

for the entire group and for each individual when provisioned food was and was not available. Microsoft Excel was used to perform all statistical tests.

Along with comparing the social events in regards to the amount of time that the animals were visible, the affiliative and aggressive social event counts were also calculated as proportions where the counts for each event were divided by the total number of counts in either the aggressive or affiliative category. The affiliative counts were further analyzed by dividing the number of event counts by the amount of time that the group spent being social-affiliative during either food or non-food periods. This could not be done for the aggressive events because of the rarity of aggressive events and the minimal recorded time spent in an aggressive behavioral state. Both of these analyses, the category counts as a proportion in regards to each other and the counts with the amount of time spent being affiliative taken into account, were compared during times with and without food using t-tests.

Individual	Sex	Age (years)	Lineage	Relationships
Loretta	Female	37	Kakowet x Linda	Mother of Erin and Kalli, Louise's sister, Ikela and Lenore's aunt
Lenore	Female	27	Vernon x Louise	Shares mother with Ikela, shares father with Erin, Loretta's niece
Ikela	Female	20	Akili x Louise	Shares mother with Lenore, Tutapenda's adoptive mother, Loretta's niece
Erin	Male	20	Vernon x Loretta	Shares father with Lenore, shares mother with Kalli, Loretta's son
Kalli	Female	6	Jumanji x Loretta	Shares mother with Erin, Loretta's daughter
Tutapenda	Male	4	Yenge x Lolita	Ikela's adopted son

Table 1: The study group.

Behavioral States	
Locomote	Focal animal is moving from one location to another
Eat/drink	Focal animal is consuming water or provided food, does not include regurgitate.
Social (affiliative)	Focal animal is engaging in affiliative social behavior (embrace, patting, grooming, other, presenting, or breeding)
Social (aggressive)	Focal animal is engaged in agonistic social behavior (teeth-baring, kicking/hitting, biting, charging, or clashing)
Inactive	Focal animal is sitting or lying down and not engaging in any other behavior
Other	Focal animal is engaging in a behavior not previously listed above
Not visible	Focal animal is not visible or the behavior of the focal individual cannot accurately be determined.
Proximity	Score all animals within one arms length (touching distance) or less of the focal animal.
Behavioral events	
Social affiliative	
Embrace	Focal animal places one arm around the other's shoulder, back or waist, or putting both arms around the other while pulling another animal closer
Patting	Focal animal places one hand on another individuals body, usually the head or back, making a series of gentile patting or stroking motions
Grooming	Focal animal engages in a series of behavioral elements such as stroking the hair, picking the hair, removing things with hand(s) or lip(s) and scratching another individual
Present	Focal animal turns flat on his or her back with legs spread apart, the genital region facing another individual or the genitals are brought close to or pressed against another individual by presentation of the hindquarters while standing quadrupedally
Mating	Mating takes place using one of many different postures (eg ventro-ventral mount, ventro-dorsal mount, or opposite mount)
Genital rubbing	Genital to genital rubbing performed by females with each other.
Penile penetration	Male mounting and penetration not for mating (may occur male with male)
Play	Focal animal is engaging in social or solitary play. This can include play bite, pirouette, acrobatic play, play retrieve, play run, play slap or rough and tumble play.
Social aggressive	
Teeth baring	Focal animal retracts lips resulting in partial or complete exposure of the teeth and gums without vocalizing
Kick/hit	Focal animal uses arm or leg with good force making contact with another individual
Bite	Focal animal physically closes moth around part of another individual with force
Charge/chase	Focal animal makes a sudden, vigorous charge past another individual or after another individual, usually with pilo-erection.
Clash	Focal animal is engaged in series of behavioral events including colliding and

	clinging to another individual which can include violent swinging and screams.
Display	Tensed running or swinging, but NOT toward another individual. Can include pushing or carrying an object.
Vocal – scream	Loud piercing vocalization given in conjunction with physical pain or fear.
Displace	Force another individual to move (>2 body lengths) from their location; usually without physical contact

Table 2: Ethogram 1. Focused on social behavior, administered twice a day, first when the bonobos where released into their day-time enclosure and again at 2:30pm.

Behavioral States	
Locomote	Focal animal is moving from one location to another
Forage	Focal animal is consuming provided food, does not include regurgitate
Drink	Focal animal is consuming water
Social (affiliative)	Focal animal is engaging in affiliative social behavior (embrace, patting, grooming, other, presenting, or breeding)
Social (aggressive)	Focal animal is engaged in agonistic social behavior (teeth-baring, kicking/hitting, biting, charging, or clashing)
Play	Focal animal is engaging in social or solitary play. This can include play bite, pirouette, acrobatic play, play retrieve, play run, play slap or rough and tumble play.
R/R	Focal animal is engaging in the behavior of regurgitation and reingestion. This can include attempts to regurgitate including putting hand in mouth.
Other undesirable	Focal animal is engaging in any abnormal or stereotyped behavior (ear covering, hair pulling or other self-injurious behavior)
Inactive	Focal animal is sitting or lying down and not engaging in any other behavior
Other	Focal animal is engaging in a behavior not previously listed above
Not visible	Focal animal is not visible or the behavior of the focal individual cannot accurately be determined.
Behavioral events	
Abnormal	
Regurgitate	Either through the use of hand or other indirect process the focal animal brings up partially digested food. Regurgitant must be seen in order to score behavior.
Reingestion	After regurgitating focal animal consumes regurgitant
Hand in mouth	Focal animal places more than half of their hand in their mouth
Other regurgitant	Focal animal consumes regurgitant from other individual
Observe other	Focal animal has head directed towards and is watching another animal engage in r/r. this can include observing another individual attempting to regurgitate by putting hand in mouth
Ear covering	Focal animal has one or both ears covered with their hand(s).
Hair pull	Focal animal is using hand or mouth to remove hair from their body. Actual hair

	removal must be observed in order to be recorded.
Social affiliative	
Embrace	Focal animal places one arm around the other's shoulder, back or waist, or putting both arms around the other while pulling another animal closer
Patting	Focal animal places one hand on another individuals body, usually the head or back, making a series of gentile patting or stroking motions
Grooming	Focal animal engages in a series of behavioral elements such as stroking the hair, picking the hair, removing things with hand(s) or lip(s) and scratching another individual
Present	Focal animal turns flat on his or her back with legs spread apart, the genital region facing another individual or the genitals are brought close to or pressed against another individual by presentation of the hindquarters while standing quadrupedally
Mating	Mating takes place using one of many different postures (eg ventro-ventral mount, ventro-dorsal mount, or opposite mount)
Social aggressive	
Teeth baring	Focal animal retracts lips resulting in partial or complete exposure of the teeth and gums without vocalizing
Kick/hit	Focal animal uses arm or leg with good force making contact with another individual
Bite	Focal animal physically closes moth around part of another individual with force
Charge/chase	Focal animal makes a sudden, vigorous charge past another individual or after another individual, usually with pilo-erection.
Clash	Focal animal is engaged in series of behavioral events including colliding and clinging to another individual which can include violent swinging and screams.

Table 3: Ethogram2. Focused on abnormal behaviors that was administered once a day at 11:00am.

Results:

In order minimize the effects possible behavioral differences due to the time of day, the data for the morning observation session and the period during the midday food toss were combined into a "provisioned food" category. The data that was collected before the midday food toss and during the afternoon observation session were compiled into a "no provisioned food" category. Before combining the morning and during food toss data into a designated "provisioned food" time and the afternoon and before food toss data in to a "no provisioned food" time, t-tests were performed to make sure that the time periods that were being combined were not significantly different in regards to social behaviors. These tests confirmed that the

proportion of time that the entire group spent in each of the six recorded behavioral states categories did not differ significantly between the morning and during food toss time periods (table 4). When the afternoon observation session and before food toss times were compared, t-tests determined that the group spent a significantly higher proportion of time eating and drinking and doing other, undefined activities during the afternoon session and spent more time being inactive before the food toss (table 4). However, the proportion of time that the bonobos spent locomoting and engaging in social affiliative and social aggressive behaviors did not differ significantly between these times (table 4).

In order to further confirm that combining the morning and during food toss and afternoon and before food toss times would be appropriate, further analysis was done using t-tests to determine if the number of instances that each recorded social event occurred differed between the times we wanted to combine. The tests showed that there were no significant differences in the occurrences of the recorded social events for the times in question (table 5). Based on the lack of significant difference in regards to affiliative and aggressive social behaviors it was decided that it was appropriate to combine the morning observation session and the portion of the midday session when the food toss was occurring and designate it as the time when provisioned food was available. We also combined the afternoon observation session and the part of the midday session before the food toss started and labeled the combination as the time when no provisioned food was available.

T-tests determined that the bonobos spent significantly more time locomoting and eating/drinking when there was food available and more time engaging in social affiliative behaviors and being inactive when food was not available ($p = <0.000$ for all, figure 1). The amount of time that the group spent engaged in aggressive social behaviors and doing undefined,

other activities was not significantly different between these times ($p = 0.49$ and 0.12, respectively, figure1).

T-tests were also used to compare how many counts were recorded for certain affiliative social behaviors during the amount of time that focal animals were visible. We found that significantly more grooming bouts occurred during the time when no provisioned food was available ($p < 0.000$, figure 2). However, there was no significant difference between the amount of times that members of the group embraced, patted each other, presented, or engaged in sexual activity when there was and was not provisioned food available ($p = 0.97$, 0.42, 0.36 and 0.35, respectively, figure 2). There was also no significant difference between the amount of times that focal animals exhibited aggressive social behaviors such as bearing their teeth, kicking/hitting, and biting ($p = 0.29$, 0.96, and 0.64, respectively, figure 5). However, tests did show that the number of times that focal animals charged was significantly higher when food was available ($p = 0.0074$, figure 5).

The number of counts for each affiliative social event was also compared in regards to the amount of time that the group spent engaged in affiliative activities in order to offset the difference in time spent being social when food was and was not available. The results indicate that there were significantly more instances of presenting and sex when food was available ($p = 0.0021$ and 0.00033, respectively, figure 3) and more instances of grooming when food was not available ($p = 0.023$, figure 3). There was no significant difference in the number of counts of embracing or patting during times when food was and was not available when the overall amount of time spent being affiliative is taken into account ($p = 0.39$ and 0.86, respectively, figure 3). Due to the low number of aggressive events and low amount of time spent in aggressive behavioral states this type of comparison could not be made for aggressive behaviors.

By calculating the proportion of times an animal performed a certain affiliative behavioral event compared to all of the other recorded affiliative events we were able to determine which social affiliative activities are performed the most often in regards to each other during times when provisioned food is and is not available. T-tests determined that there was no significant difference between the proportion of embracing or presenting during times when food was and was not available ($p = 0.52$ and 0.08, respectively, Figure 4). There was, however, a significantly higher proportion of patting and mating during times with food and a significantly higher proportion of grooming at times when there was not food ($p = 0.03$, <0.000 and <0.000, respectively, Figure 4). As for aggressive social events, t-tests determined that there were no significant differences between the proportion of teeth bearing, kicking/hitting, or biting when there was and was not provisioned food available ($p = 0.43$, 0.078, and 0.11, respectively, figure 6). There was a significant difference in the proportion of charges that occurred compared to all recorded aggressive events during these times ($p = 0.021$, figure 6)

More t-tests were used to analyze whether proximity tolerances and preferences differed with the availability of food. The total proportion of time the group spent in close proximity with at least one other individual was greater than the amount of time that individuals spent alone when food was not available ($p = <0.000$, figure 7). When food was available the opposite trend occurred and individuals spent a significantly greater proportion of time not in proximity to any other individuals ($p = <0.000$, figure 7).

Proximity was also examined on an individual basis. When there was no provisioned food available there was no significant difference between the amount of time that focal animals spent in close proximity to any one individual group member (table 6, figure 8). However, during these times focal animals spent more time not in close proximity to anyone than with any one

individual (table 6, figure 8). When there was food available, the group as a whole spent more time in proximity with Tutapenda than with Kalli, Loretta, Erin or Lenore (table 7, figure 8). Also, group members spent significantly more time with Ikela than with Kalli, Loretta, Erin or Lenore (table 7, figure 8). There was no significant difference between the amount of time that was spent with Tutapenda verses Ikela (table 7, figure 8). T-tests determined that there was no significant difference in the amount of time spent in proximity in combinations between Loretta, Erin, Kalli and Lenore when food was available (table 7, figure 8). Finally, when food was not available, less time was spent in proximity with any individual group member than was spent alone (table 7, figure 8).

Finally, t-tests determined that other group members spent significantly more time with Kalli, Loretta, Erin, and Lenore when there was no provisioned food available compared to when food was provided ($p < 0.000$ for all, figure 8). There was no significant difference between the amount of time that group members spent with Tutapenda or Ikela when food was and was not provided ($p = 0.98$, and 0.13, respectively, figure 8).

Behavioral State	Morning session vs. midday session during food toss	Afternoon session vs. midday session before food toss
locomote	0.87	0.54
eat/drink	0.45	**0.002**
Social, aggressive	0.95	0.49
Social, affiliative	0.11	0.42
inactive	0.56	**2.9×10^{-5}**
other	0.24	**0.05**

Table 4: P-values determined by T-tests that compare the amount of time that the study group spent in each recorded behavioral state per amount of time visible during the morning session and the time that the midday food toss took place, and during the afternoon session and the midday session before the food toss took place. Bold text indicates statistically significant values.

Behavioral Event	Morning session vs. midday session during food toss	Afternoon session vs. midday session before food toss
Embrace	0.23	0.63
Patting	0.74	0.51
Grooming	0.41	0.32
Present	0.27	0.75
Mating	0.79	0.97
Teeth baring	0.70	NA
Kick/hit	0.54	0.62
Bite	0.70	0.34
Charge/chase	0.64	0.24

Table 5: P-values determined by T-tests that compare the number of times that the study group performed each recorded social affiliative and aggressive behavior event per amount of time visible during the morning session and the time that the midday food toss took place, and during the afternoon session and the midday session before the food toss took place. Bold text indicates statistically significant values.

	Loretta	Erin	Tutapenda	Lenore	Ikela	no one
Kalli	0.20	0.83	0.51	0.34	0.52	**3.2×10^{-4}**
Loretta		0.32	0.05	0.76	0.50	**0.03**
Erin			0.41	0.49	0.70	**0.002**
Tutapenda				0.11	0.18	**1.2×10^{-5}**
Lenore					0.72	**0.01**
Ikela						**0.003**

Table 6: P-values determined by T-tests results comparing the proportion of time that group members spent in close proximity with other individuals when food was not available. Bold text indicates statistically significant values.

	Loretta	Erin	Tutapenda	Lenore	Ikela	no one
Kalli	0.34	0.54	**1.7×10^{-5}**	0.87	**3.4×10^{-5}**	**1.3×10^{-31}**
Loretta		0.71	**0.001**	0.45	**0.002**	**1.1×10^{-27}**
Erin			**2.3×10^{-4}**	0.69	**4.4×10^{-4}**	**8.2×10^{-29}**
Tutapenda				**5.4×10^{-5}**	0.83	**3.0×10^{-15}**
Lenore					**1.1×10^{-4}**	**2.3×10^{-30}**
Ikela						**6.3×10^{-15}**

Table 7: P-values determined by T-tests results comparing the proportion of time that group members spent in close proximity with other individuals when food was available. Bold text indicates statistically significant values.

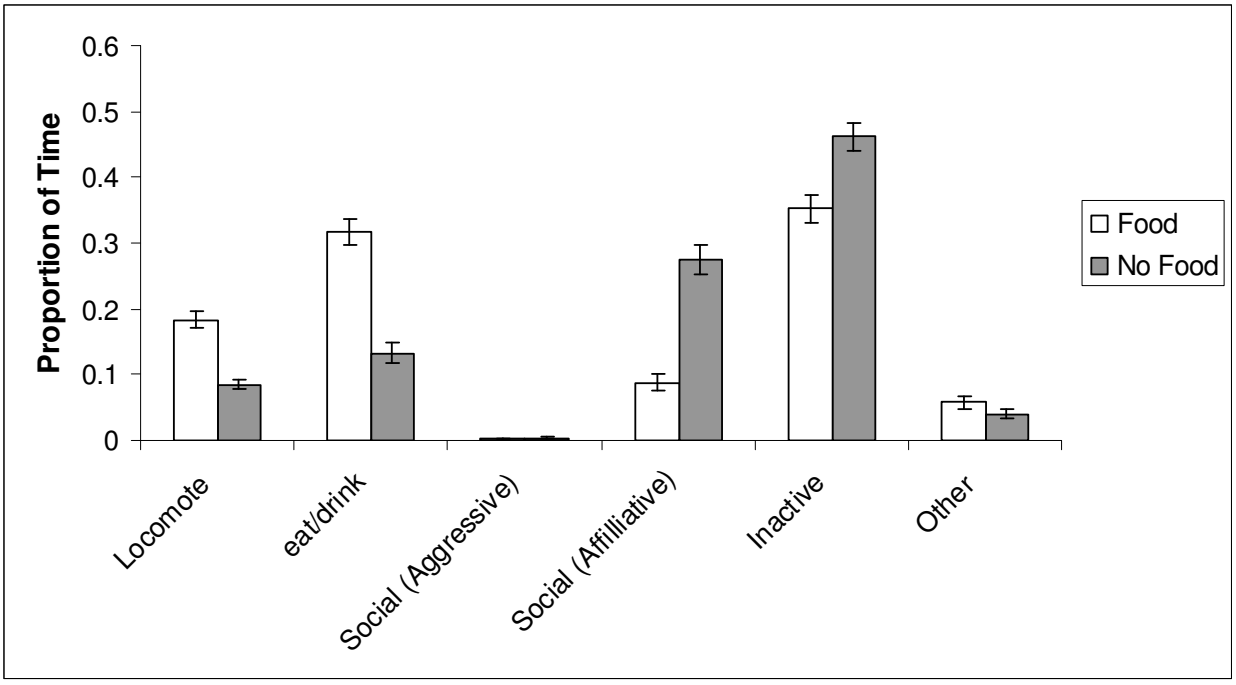

Figure 1: The average proportion of time that the group of bonobos spent engaged in behavioral states per the amount of time that they were visible during focal periods when provisioned food was and was not available.

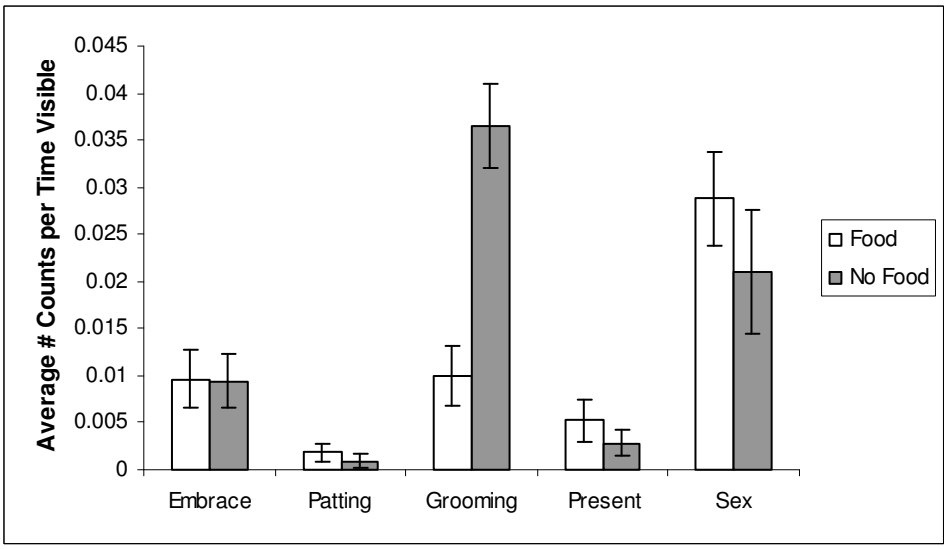

Figure 2: The average number of times affiliative social events occurred per amount of time visible during focal periods when provisioned food was and was not available.

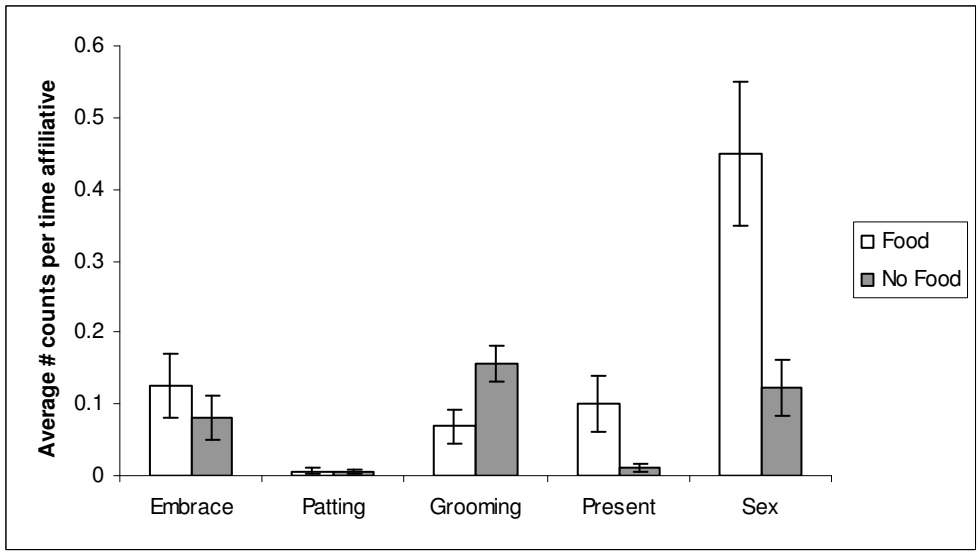

Figure 3: The average number of times affiliative social events occurred per the amount of time spent in affiliative social behavioral states when provisioned food was and was not available.

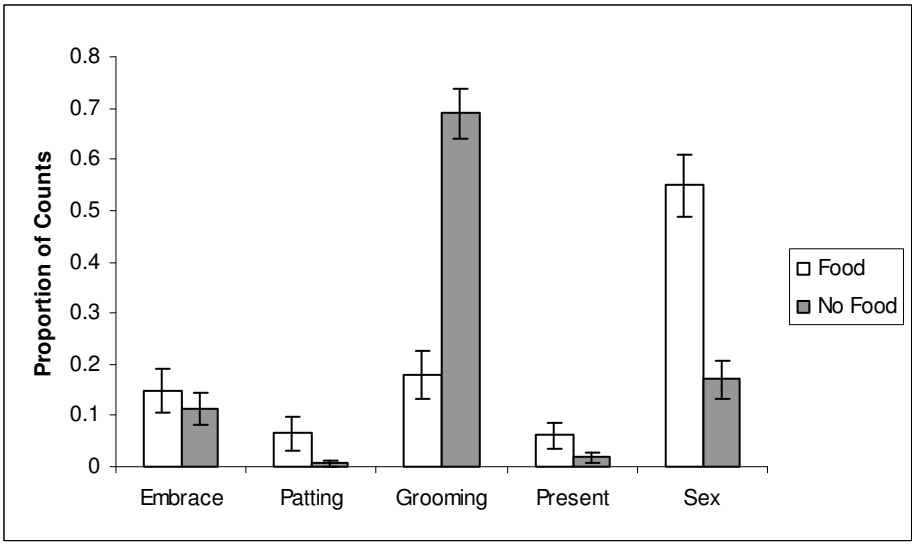

Figure 4: The proportion of counts for each social affiliative behavior recorded for focal animals during observation periods when provisioned food was and was not available.

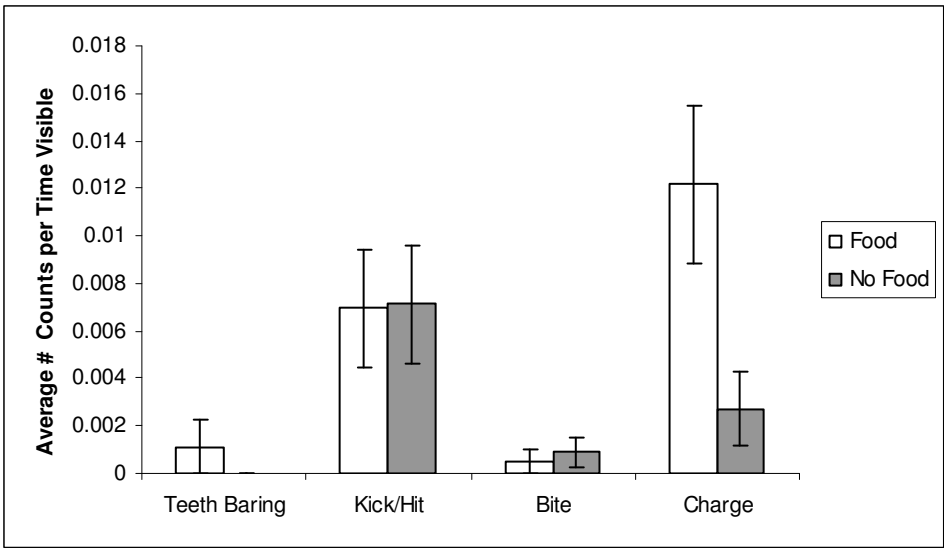

Figure 5: The average number of times aggressive social events occurred per amount of time visible during focal periods when provisioned food was and was not available.

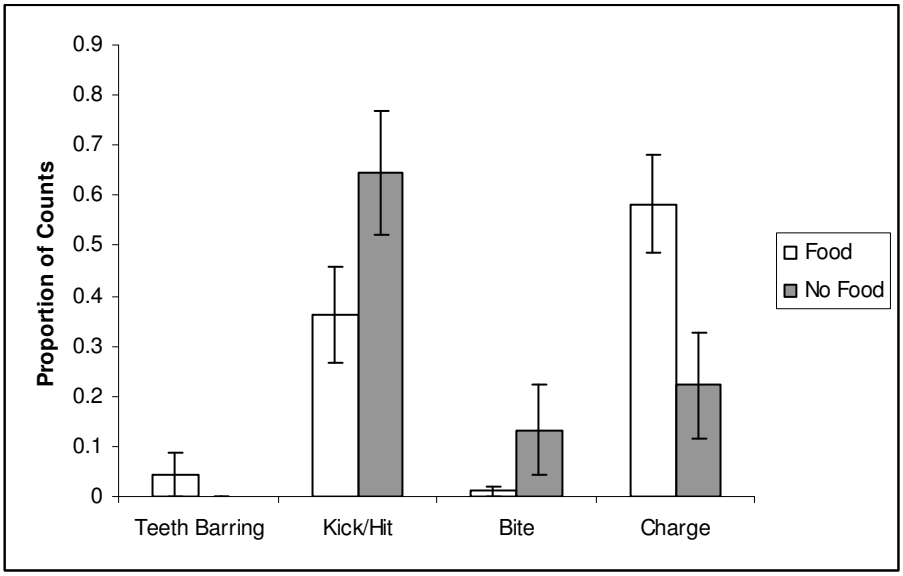

Figure 6: The proportion of counts for each aggressive social behavior recorded for focal animals during observation periods when provisioned food was and was not available.

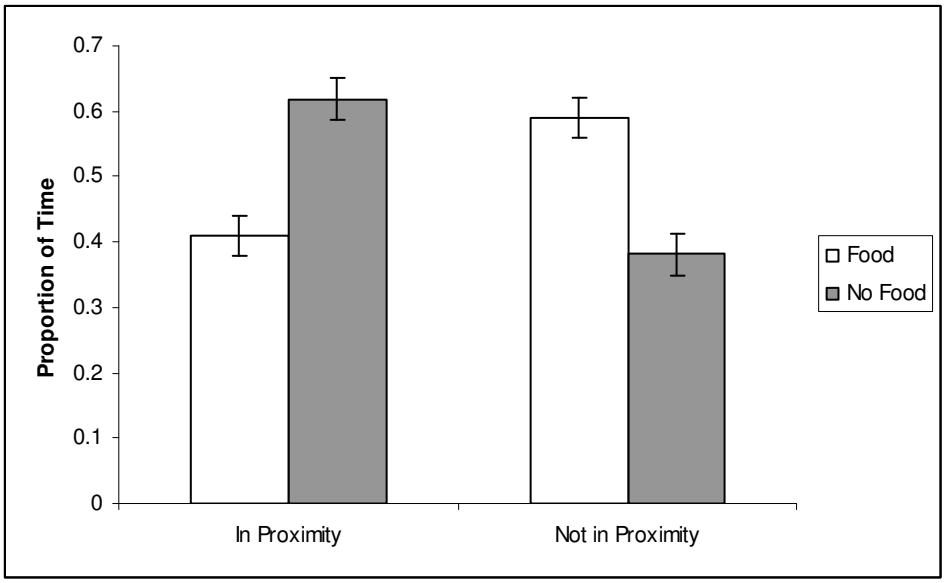

Figure 7: The average proportion of time that the group of bonobos spent in proximity with at least one other individual or not in close proximity to any other individuals in the morning when provisioned food was available and in the afternoon when provisioned food was not available.

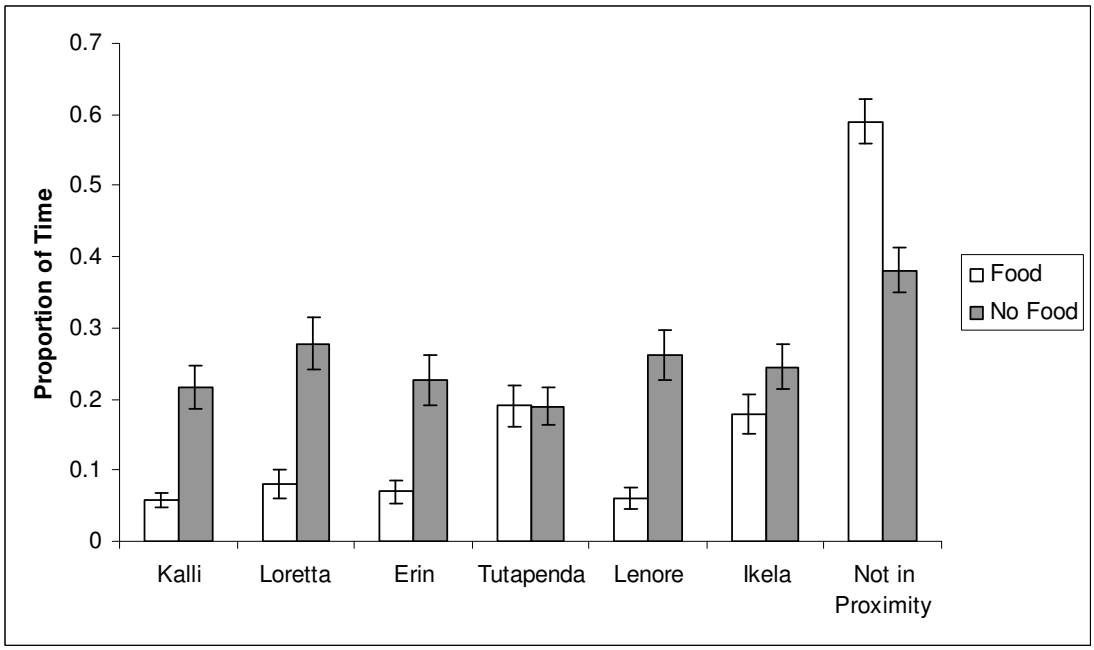

Figure 8: The average proportion of time that the group of bonobos spent in proximity to other individuals in the time that they were visible during focal periods in the morning when provisioned food was available and in the afternoon when provisioned food was not available.

Discussion:

The results presented in this paper indicate that the presence of food plays a significant role in bonobo social behavior. Behavioral observations of bonobos at the San Diego Zoo's Safari Park demonstrated that the amount of time that animals spent moving around their enclosure, consuming food and water, being inactive, and engaging in affiliative behaviors varied during times when provisioned food was and was not available. This is not surprising as having food available intrinsically implies that the animals will spend time eating and moving between large, scattered patches of food. After feeding time there are no large clumps of food to motivate the troop to move around the enclose, and the apes spend more time pursuing social behaviors, which often do not require much locomotion. The only time the animals eat when provisioned food is not available is when they find scant leftovers from their last meal or when they find non provisioned food in their enclosure such as palm nuts. The fact that the troop spends less time being social when food is available is likely due in part to the simple trade-off in behaviors that must occur when the animals start to spend more time on eating activities. These results could also be attributed to increased competition brought on by food as well as the different types of social behaviors that are preformed when food is and is not available.

Numerous researchers have noted that acts of aggression seem to be a rare occurrence among bonobos except when there is food available (Kano and Mulavwa, 1984; Sannen et. al., 2004; Kano, 1992). Finding food obviously induces considerable excitement and tension. One of the consequences of the possibility of increased aggression is that the bonobos tend to space themselves away from other individuals while feeding. In a study investigating the food preferences of wild bonobos that were provisioned at an artificial feeding site, Kano and Mulavwa noted that when food was concentrated in a small area it forced the apes to feed at a

closer proximity to one another than they typically would. This resulted in more aggression amongst the group than was normal in a natural setting (Kano and Mulavwa, 1984). It stands to reason that bonobos would want to limit aggression as much as possible so as to maximize feeding ability and decrease the social consequences and risk of injury that come with fighting (White and Wrangham, 1988). It seems that one passive way that the animals accomplish this is to avoid being in proximity to other individuals during feeding time. This trend was demonstrated in this study's results, which indicated that the bonobos spent significantly more time within an arms length of at least one other group member when food was not available, and spent more time not in proximity with group members when it was. The findings also showed that when there was no food, there was no significant difference in the amount of time spent near any one individual. Things changed, however, when food was provided. The group as a whole spent significantly less time within an arms length of Kalli, Loretta, Lenore and Erin when food was available.

The difference in the group's proximity preferences with Tutapenda and Ikela were not significant between times when food was and was not available. This may have been partially due to the fact that Tutapenda is Ikela's adopted son and, at four years old, is still fairly dependant on her. Each day when the apes were released from their indoor bedrooms, Tutapenda would ride out into the enclosure on Ikela's back. He typically stayed close to her side during feeding time and seemed to rely on her for protection from the rest of the group during the few times that the aggressive events occurred. Another factor contributing to the group maintaining about the same level of proximity to Tutapenda during times when food was and was not available was that the older, larger bonobos would sometimes steal food from him, especially during the afternoon feeding time. During this feeding period, the bonobo keeper would toss

food to specific individuals. It often took the keeper several attempts to get Tutapenda his lunch because if another troop member was close enough, they would take it from him.

While proximity preferences seemed to differ considerably between times when food was and was not available, aggressive actions showed less variation. There were very few aggressive interactions during the course of this study and the amount of time spent being aggressive did not differ between the two study conditions. The number of counts of teeth baring, kicking and hitting and biting did not differ depending of food availability. The only difference demonstrated by the results is that there were significantly more charges when food was available. A study by Sannen et. al. also briefly investigated the effects of food on aggressive behavior in the scope of a larger study that examined the effects of spatial crowding on the animals. This study found that full charges, which include a charge of over ten meters and possible aggressive contact, occurred more often when food was available, while occurrences of short charges, which cover a distance of two to ten meters and involve aggressive contact that is less sever than that of a full charge, did not seem to differ in regards to food (Sannen et. al, 2004). While my study does not differentiate between types of charges, it did seem to detect at least a slight escalation in aggression during times when food was provisioned. Parish also noted in her study that dominant females were able to displace other individuals from preferred food sources by chasing then away, either individually or in a group (Parish, 1994). The ability to access food is likely the main reason for increased instances of chasing, or charging when food is available.

Affiliative social behaviors had more variation and occurred more often when compared to aggressive social behaviors. The data for affiliative interactions were examined three different ways, yielding three different results which leave some complicated implications in terms of my hypotheses. When the number of counts of each of five behaviors under investigation are taken

into account in terms of the amount of total amount of time that the animals were visible, the results indicated that grooming was the only category where a significant difference occurred. While this study had predicted that there would be more instances of grooming during times when there was no food provided, it was surprising that the results indicated that there was no significant difference in the occurrence of sexual behaviors. They not only indicate that there is no difference in the amount of sex occurring throughout the day, but also there were more instances of grooming when there was no food available than there were counts of sexual behaviors during either time period. Based on observation, sexual activities tend to happen quickly and often, while grooming bouts tended to be lengthy with fewer new sessions occurring over time. Because these results are based on counts, not length of time, the outcome of these tests seemed odd. These results only take the number of counts and the amount of time that the animals are visible into account, and so they provide a candid indication of what types of behaviors the bonobos do most often throughout the day. Yet the fact that grooming is rated as a more common occurrence than sex, despite the apparent differences in the amount of time each activity takes to complete and the disparities in the ability to quickly start a new session suggests that it may not be the most accurate test for determining the relative importance of these animals' behaviors in regards to food availability.

What these findings do not take into account is the fact that the bonobos spent considerably more time engaged in affiliative behaviors when food was not available. This weights the data toward the time when there is more social behavior occurring, perhaps explaining the lack of significance in sexual behaviors and the substantial dominance in counts of grooming. When the data were compared while taking the amount of time spent being social into consideration some of the results turned out differently. These tests still show that grooming

occurs more often when food is not available, yet and they also detect significantly more counts of presenting and sexual activity when food is available. This is more consistent with our prediction and with other studies that emphasize the important role of sociosexual behaviors in reducing tension when food is available (Parish, 1994; Hohmann and Fruth, 2000; White and Lanjouw, 1992; Kano 1992).

The data were also analyzed as proportions to compare the number of counts in each category to each other. These findings showed that a higher proportion of grooming occurred when food was not available while a higher proportion of sexual behaviors occurred when it was. These two activities ranked the highest during both time periods, with grooming making up 69 percent of behavioral counts when food was not available and 18 percent when it was. Sex, on the other hand, made up 17 percent of the counts when food was not available and 55 percent when it was. This illuminates the tradeoff in activities that occurs between these two time periods and also demonstrates the apparent importance of sex and grooming in the bonobos' social repertoire.

This study did not take into account the relatedness of the focal animals, nor did it take into account fertility status. All of the bonobos at the San Diego Zoo's Safari Park, except for Tutapenda, who was adopted by Ikela when she and another female at the San Diego Zoo swapped offspring, are all fairy closely related (table 1). It is uncertain whether they are aware of their kinship status as all half siblings were raised apart except for Erin and Kalli. It is interesting to note, however, that for the duration of behavioral observations Erin never attempted any sort of sexual activity with his mother Loretta, or his half-sister Kalli. Other studies have also noted a lack of sexual contact between mothers and adult sons (Hohomann et. al., 1999). The lack of sexual behavior between these possible dyads undoubtedly affected my results, as the troop is

fairly small and there are only so many possible dyad combinations. It's possible that a group of largely unrelated bonobos would have yielded a different outcome, perhaps with more occurrences of sex.

It is also possible that there might have been more instances of sex had the animals' reproductive statuses been different. Loretta was possibly the only member of the group that could have been able to reproduce at the time of the study. Lenore had undergone a hysterectomy and Erin had been vasectomized. Ikela had been taken off of birth control upon being introduced to the Safari Park colony and did not undergo menses for the duration of the study. Kalli may have been nearing sexual maturity but Tutapenda was still very young. While female bonobos are known to engage in sex regardless of the phase of their menstrual cycle it tends to happen the most often during ovulation (Parish, 1994). It is possible that a fully reproductive group of bonobos would have had different trends in their social behaviors.

There are many factors that affect an animal's behavior. The fact that the bonobos under investigation are on display as well as the fact that they have regularly scheduled feeding times and are unable to explore or forage outside of their enclosure certainly effects the way they behave around food. Also the fact that these apes cannot participate in a fission-fusion society like their wild counterparts do is bound to affect the way they socialize with each other. It would be worth conducting a similar study on wild bonobos to compare with this one that was conducted using captive animals, if only to illuminate the undoubtedly many differences between the social lives of wild and captive apes.

References:

de Waal, F.B.M. 1987. Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). National Geographic Research 3: 318-335.

de Waal, F.B.M. and F. Lanting. 1997. Bonobo: the Forgotten Ape. University of California Press. Berkeley and Los Angeles, California

Dunbar, R.I. 1991. Functional significance of social grooming in primates. Folia Primatologica 57: 121-131.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. The Belknap Press of Harvard University Press. Cambridge, Massachusetts, and London, England.

Goodall, J. 1992. Unusual violence in the overthrow of an alpha male chimpanzee at Gombe. In: topics in primatology, vol 1, human origins (Ed by T. Nishida, WC McGrew, P Marler, M Pickford and FBM De Waal) pp 131-142. Tokyo: university of Tokyo press

Henzi S.P. and L. Barrett. 1999. The value of grooming to female primates. Primates 40: 47-59.

Hohmann G. and B. Fruth. 2000. Use and function of genital contacts among female bonobos. Animal Behaviour 60: 107-120.

Hohmann, G., U. Gerloff, D. Tautz, and B. Fruth. 1999. Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136: 1219-1235.

Kanngiesser, P., C. Sueur, K. Riedl, J. Grossman and J. Call. 2011. Grooming network cohesion and the role of individuals in a captive Chimpanzee group. American Journal of Primatology 73: 758-767.

Kano, T. 1992. The Last Ape: Pygmy Chimpanzee Behavior and Ecology. Stanford University Press. Stanford, California

Kano, T., and M. Mulavwa. 1984. Feeding ecology of the pygmy chimpanzee (*Pan paniscus*) at Wamba. In The Pygmy Chimpanzee: Evolutionary Biology and Behavior. R. L. Susman, ed. 233-274. New York: Plenum Press.

Parish, A.R. 1994. Sex and food control in the "uncommon chimpanzee": how bonobo females overcome a phylogenetic legacy of male dominance. Ethology and Sociobiology 15: 157-179.

Sannen, A., L. Van Elsacker, and M. Eens. 2004. Effect of spatial crowding on aggressive behavior in a bonobo colony. Zoo Biology 23: 383-395.

Vervaecke H. and L. Van Elsacker. 2000. Sexual competition in a group of captive bonobos (*Pan paniscus*). Primates 41(1): 109-115.

White F.J. and A. Lanjouw A. 1992. Feeding competition in Lomako bonobos: variation in social cohesion. In: topics in primatology, vol 1, human origins (Ed by T. Nishida, WC McGrew, P Marler, M Pickford and FBM De Waal) pp 67-79. Tokyo: university of Tokyo press

White, F.J. and W. Wrangham. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. Behaviour 105: 148-164.

Wrangham, R., and D. Peterson, 1996. Demonic Males: Apes and the Origins of Human Violence. Houghton Mifflin, Boston, MA, New York.